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Monograph

Laboulbeniomycetes (Fungi, Ascomycota) of Denmark

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Abstract. In this study, the thallus-forming Laboulbeniomycetes (Herpomycetales and Laboulbeniales) from Denmark are presented as an illustrated monograph. Sixteen species and one genus are newly described based on morphology and ecology (host association). The new genus is named *Tanmaurkiella* Santam. gen. nov. and includes two species: *T. pselaphi* Santam. gen. et sp. nov. (type species) and *T. huggertii* Santam. gen. et sp. nov., both on *Pselaphus heisei* Herbst, 1792 (Col. Staphylinidae Pselaphinae). The other 14 new species are *Amorphomyces ventricosus* Santam. sp. nov. on *Myrmecocephalus concinnus* (Erichson, 1839) (Col. Staphylinidae Aleocharinae), *Cantharomyces papillatus* Santam. sp. nov. on *Bledius terebrans* (Schiødte, 1866) (Col. Staphylinidae Oxytelinae), *Cryptandromyces cryptophagi* Santam. sp. nov. on *Cryptophagus distinguendus* Sturm, 1845 (Col. Cryptophagidae), *Cryptandromyces danicus* Santam. sp. nov. on *Euconnus wetterhallii* (Gyllenhal, 1813) (Col. Staphylinidae Scydmaeninae), *Dimeromyces oculatus* Santam. sp. nov. on *Longitarsus luridu*s (Scopoli, 1763) (Col. Chrysomelidae), *Euphoriomyces enghoffii* Santam. sp. nov. on *Leiodes rugosa* Stephens, 1829 (Col. Leiodidae), *Euphoriomyces smicri* Santam. sp. nov. on *Smicrus filicornis* (Fairmaire & Laboulbène, 1855) (Col. Ptiliidae), *Laboulbenia inexpectata* Santam. sp. nov. on *Acupalpus exiguus* Dejean, 1829 (Col. Carabidae), *Laboulbenia pygidicola* Santam. sp. nov. on *Syntomus truncatellus* (Linnaeus, 1761) (Col. Carabidae), *Monoicomyces brachiatus* Santam. sp. nov. on *Atheta sodalis* (Erichson, 1837) and *Ocyusa picina* (Aubé, 1850) (Col. Staphylinidae Aleocharinae), *Monoicomyces crassicaulis* Santam. sp. nov. on *Oxypoda elongatula* Aubé, 1850 (Col. Staphylinidae Aleocharinae), *Monoicomyces reboleirae* Santam. sp. nov. on *Gnypeta carbonaria* (Mannerheim, 1830) (Col. Staphylinidae Aleocharinae), *Monoicomyces validus* Santam. sp. nov. on *Atheta vestita* (Gravenhorst, 1806), *Aleochara grisea* Kraatz, 1856, and *Geostiba circellaris* (Gravenhorst, 1806) (Col. Staphylinidae Aleocharinae), and *Stigmatomyces thoracochaetae* Santam. sp. nov. on *Thoracochaeta brachystoma* (Stenhammer, 1855) (Diptera Sphaeroceridae). The total number of laboulbeniaceous species from Denmark rises from 29 to 195, which means that 166 are here reported as new country records. Among these, *Kainomyces isomali* Thaxt. deserves special mention as it is a new European record. The same applies to nine species which are reported here for the first time after their original description. For this study, an intensive sampling programme has been realized, with 429 Danish localities screened including around 1900 collections with fungi. Two new synonymies are established: *Laboulbenia acupalpi* Speg. (Spegazzini 1915a) syn. nov. for *Laboulbenia stenolophi* Speg. (Spegazzini 1914), and *Monoicomyces oxytelis* Huldén (Huldén 1983) syn. nov. for *Monoicomyces invisibilis* Thaxt. (Thaxter 1900). The new combination *Peyritschiella oxyteli* (Cépède & F.Picard)

Santam. comb. nov. is proposed for *Rheophila oxyteli* Cépède & F.Picard including neotypification, and delimitation of *Peyritschiella protea* Thaxt. is incorporated. Lectotypes for *Laboulbenia polyphaga* Thaxt. and *Symplectromyces vulgaris* (Thaxt.) Thaxt. are designated. Nineteen species are illustrated here with photographs for the first time. Three species: *Eumonoicomyces papuanus* Thaxt., *Peyritschiella protea*, and *Stigmatomyces euconni* F.Picard, which were reported from Denmark in the literature should be removed from the Danish Funga. We have examined the following types of Thaxter from FH (Farlow Herbarium, Harvard University Herbaria): *Asaphomyces cholevae* Thaxt., *Dimorphomyces myrmedoniae* Thaxt., *Eumonoicomyces papuanus*, *Laboulbenia polyphaga*, *Peyritschiella protea*, *Rhadinomyces pallidus* Thaxt., and *Symplectromyces vulgaris*. *Ceratomyces pyrenaeus* Santam. is newly recorded from USA, and this is also a new record from the American continent. Description of the genus *Cryptandromyces* Thaxt. has been emended to incorporate the new species here described. Morphology of the antheridium in *Eumonoicomyces papuanus* is studied, and the status of the genus *Eumonoicomyces* Thaxt. vis-à-vis *Monoicomyces* Thaxt. is discussed. Identification keys are provided for genera and species. In support of the additional aim of this work to serve as a reference for the study of Laboulbeniomycetes fungi in Europe, we include maps and the Appendix 1 for comparison of the known species in the ten most diverse, better studied, European countries.

Keywords. Ectobiontic fungi, Europe, new taxa, species list, taxonomy.

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Introduction

Laboulbeniomycetes are fungi displaying unique characteristics. They are obligate ectobionts, living as parasites or commensals on arthropods, mainly insects. Their three-dimensional bodies, described as thalli, are minute, rarely exceeding 600 µm. Their development usually follows strict patterns.

The class Laboulbeniomycetes Engl. in the phylum Ascomycota (Berk.) Caval.-Sm. subphylum Pezizomycotina O.E.Erikss. & Winka currently includes three orders: Laboulbeniales Lindau, Herpomycetales Haelew. & Pfister and Pyxidiophorales P.F.Cannon, along with other two lineages named *Chantransiopsis* and *Laboulbeniopsis* clades (Blackwell *et al.* 2020). Laboulbeniales and Herpomycetales were originally established at the rank of suborders [Laboulbeniineae Thaxt. and Herpomycetineae (Thaxt.) I.I.Tav.] by Tavares (1981), but later elevated to orders by Haelewaters *et al.* (2019c) using molecular evidence. Together, these two orders form a rather large and homogenous group of ascomycetous fungi consisting of arthropod-associated biotrophs, including more than 2000 species in 145 genera comprising the new genus described here, *Tanmaurkiella* Santam. gen. nov., and bearing in mind the synonymy of *Monandromyces* R.K.Benj. with *Prolixandromyces* R.K.Benj. (Hyde *et al.* 2019). Throughout the 21st century, ten genera have been described as new. These are: *Benjaminomyces* I.I.Tav. (Tavares 2000), *Rossiomyces* R.K.Benj. (Benjamin 2001), *Capillistichus* Santam. and *Scepastocarpus* Santam. (Santamaria 2004), *Cesariella* W.Rossi & Santam. (Rossi & Santamaria 2008), *Rodaucea* W.Rossi & Santam. (Rossi & Santamaria 2012), *Opilionomyces* Santam. (Santamaria *et al.* 2017), *Thaxterimyces* Santam., Reboleira & Enghoff (Reboleira *et al.* 2018), *Pseudozeugandromyces* De Kesel & Haelew. (Haelewaters *et al.* 2020), and *Tanmaurkiella* Santam. gen. nov. (present work). A recent paper (Haelewaters *et al.* 2020) reinstated *Fanniomyces* T.Majewski and *Appendiculina* Berl., two genera that were considered synonyms of *Stigmatomyces*, and the number of genera would thus rise to 147. The estimated number of species for these fungi ranges between 15 000 and 75 000 according to Weir & Hammond (1997). Kirk (2019) calculated 2395 species and 167 genera, numbers based on raw data mostly from Index Fungorum (2019). Indeed, it is very daring to offer an exact number of described species, given the number of continuous taxonomical changes that any group suffers.

Informally named as the "thallus-forming Laboulbeniomycetes" (Blackwell *et al.* 2020), in this contribution we will from now on refer to these fungi as "Laboulbeniales" in a broad or classical sense. Traditionally, they have been defined as parasites, but only few species bear evident haustoria (Tragust *et al.* 2016). The absence of haustoria questions the universal parasitic nature of this large group of fungi. Most Laboulbeniales are host specific, at genus level or above, but some even at species level as, for example, *Aphanandromyces audisioi* W.Rossi on *Brachypterus urticae* (Fabricius, 1792) (Rossi 1982a), and *Laboulbenia cantabrica* Santam. on *Iberotrechus bolivari* (Jeannel, 1913) (Santamaria 1985). Herpomycetales comprise the single genus *Herpomyces* Thaxt. with 27 described species (Gutierrez *et al.* 2020), all associated with cockroaches (Blattodea Wattenwyl, 1882). Hosts of Laboulbeniales s. str. belong to three arthropod subphyla: the majority are insects (subphylum Hexapoda Latreille, 1825), mostly Coleoptera Linnaeus, 1758 and Diptera Linnaeus, 1758 (Majewski 2008), less frequently in subphylum Chelicerata Heymons, 1901: mites (Acarina Leach, 1817) and harvestmen (Opiliones Sundevall, 1833), or in subphylum Myriapoda Latreille, 1802: millipedes (Diplopoda Blainville in Gervais, 1844).

Studies of the Laboulbeniales focused on a single country are relatively common, mostly in the form of a series of papers, for France (Balazuc 1973a, 1974f), Spain and Portugal (Balazuc *et al.* 1982; Santamaria *et al.* 2020a), South Korea (Lee & Choi 1992a, 1992b), Belgium (De Kesel 1998; De Kesel & Haelewaters 2019), or Czech Republic and Slovakia (Rossi & Máca 2006; Rossi *et al.* 2010, 2019b). Several are in the form of separate papers, like those for Sierra Leone (Rossi & Leonardi 2018), Thailand (Rossi & Bernardi 2018), or Austria (Rossi & Christian 2020). Comprehensive monographs with full descriptions for the included taxa exist for Argentina (Spegazzini 1917), Italy (Colla 1934), Finland (Huldén 1983), Poland (Majewski 1994b), Spain (Santamaria 1989, 1998, 2003), and China (Shen & Ye 2006). Less frequent are check-lists, like the ones recently published for Belgium and the Netherlands (De Kesel *et al.* 2020; Haelewaters & De Kesel 2020).

This study deals with the Funga of the Danish Laboulbeniales (for the use of the term Funga instead of others like Mycobiota or Flora, see Kuhar *et al.* 2018). Rostrup (1916, 1935) was the earliest author to publish records of Laboulbeniales (three species) from Denmark. Later, occasional papers added a few new records (Ryberg 1947; Steenberg & Harding 2010; Enghoff & Santamaria 2015; Santamaria *et al.* 2016), though it was Høier (2009) who made the most substantial contribution publishing the results of his master thesis. All previous Danish records are summarized in Table 1. With the present study, the total number of laboulbeniaceous species known from Denmark rises from 29 to 195, i.e., 166 species are newly reported, including a new genus and 16 new species. Of the 29 species recorded from Denmark in literature, we have omitted *Coreomyces* sp. because no species was indicated, as well as *Eumonoicomyces papuanus* Thaxt., *Peyritschiella protea* Thaxt., and *Stigmatomyces euconni* F.Picard, because they are doubtful as stated in Table 1. This major progress has been possible due the study of around 1900 collections with fungi, from specimens captured in the field or preserved dry in museums, totalizing around 300 000 insect specimens that were checked. Around 4800 infected insects of various groups out of more than 250 000 specimens scanned were from field collections. Furthermore, an estimated number of around 50 000 specimens of dry mounted potential hosts, from the ZMUC collection and a few private collections, have been searched for fungi, resulting in the findings of around 200 infected specimens from various insect groups. All in all the total number of infected host species reported in this work adds up to 384 (Appendix 2). The quantity and quality of these samples allow us to get a quite accurate idea of what the Danish Funga of Laboulbeniales can offer. Of course, as always logical in such cases, this cannot be considered a definitive work, and the total number of species of these fungi may still increase to some extent in Denmark. This expectation will be discussed at the end of this work.

Notwithstanding the importance of the new records and the description of new taxa, we also want to emphasize the chance we had to study large series of fungi belonging to old and/or sometimes poorly described, unclear, debated species. When possible, we recommend some solutions for several taxonomic

Table 1 (continued on next page). Laboulbeniales reported from Denmark in literature. * = found again in this study; ** = species to remove from the Danish list; [1] = unverifiable, but on this host we have found other species.

Fungus	Reference	Host	Comments
Arthrorhynchus nycteribiae	Ryberg (1947)	Nycteribiidae spp.	
**Coreomyces* sp.	Sundberg *et al.* (2018b)	*Sigara* spp.	Species of *Coreomyces* not specified.
**Corethromyces stilici*	Høier (2009)	*Rugilus rufipes*	
**Diphymyces niger*	Huggert (1973)	*Ptomaphagus variicornis* (Rosenhauer, 1847)	As *Laboulbenia ptomaphagi*
**Ecteinomyces trichopterophilus*	Høier (2009)	*Acrotrichis intermedia*	
***Eumonoicomyces papuanus*	Rostrup (1916)	*Anotylus rugosus* (as *Oxytelus* Gravenhorst, 1802)	Doubtful. The drawing is unclear. See Tavares (1985: 216).
**Hesperomyces virescens*	Steenberg & Harding (2010)	*Adalia bipunctata*	
	Haelewaters *et al.* (2018a)	*Adalia bipunctata*	
**Laboulbenia argutoris*	Rostrup (1916)	*Pterostichus strenuus*	As *L. pterostichi*
	Høier (2009)	*Pterostichus strenuus*	
**Laboulbenia benjaminii*	Høier (2009)	*Badister bullatus*, *B. lacertosus*	
**Laboulbenia eubradycelli*	Siemaszko & Siemaszko (1932)	*Trichocellus cognatus*	As *L. polyphaga* (loc. as Danja, sic)
	Høier (2009)	*Leistus terminatus* (Panzer, 1793)	Fortuituous infection? According to the published photograph, identification seems correct.
**Laboulbenia flagellata*	Rostrup (1916)	*Paranchus albipes*, *Agonum fuliginosum* – as *Anchomenus* Bonelli, 1810 –	As *Laboulbenia* indet.
	Rostrup (1935)	*Paranchus albipes* – as *Anchomenus albipes* (Fabricius, 1796) –	
	Høier (2009)	*Harpalus affinis, Agonum muelleri, Anchomenus dorsalis*, *Loricera pilicornis*, *Pterostichus oblongopunctatus*, *P. vernalis*, *Nebria brevicollis*	Records on *Pterostichus* and *Nebria* are doubtful
**Laboulbenia inflata*	Høier (2009)	*Acupalpus flavicollis*	
**Laboulbenia leisti*	Høier (2009)	*Leistus ferrugineus*	
**Laboulbenia murmanica*	Høier (2009)	*Bembidion assimile*	
**Laboulbenia notiophili*	Høier (2009)	*Notiophilus rufipes*	
**Laboulbenia pedicellata*	Høier (2009)	*Bembidion aeneum*, *B. lampros*	
**Laboulbenia pseudomasei*	Rostrup (1916)	*Pterostichus nigrita*	As *Laboulbenia pterostichi* which is not present in Europe. Probably *L. pseudomasei.*
	Høier (2009)	*Pterostichus* spp., *Nebria brevicollis*	Record on *Nebria* is doubtful.
**Laboulbenia rougetii*	Rostrup (1935)	*Brachinus crepitans*	
**Laboulbenia thaxteri*	Høier (2009)	*Asaphidion curtum*	
**Laboulbenia vulgaris*	Høier (2009)	*Bembidion stephensii*	

Table 1 (continued). Laboulbeniales reported from Denmark in literature. * = found again in this study; ** = species to remove from the Danish list; [1] = unverifiable, but on this host we have found other species.

Fungus	Reference	Host	Comments
**Misgomyces dyschirii*	Huldén (1985)	*Dyschirius salinus*	
**Monoicomyces fragilis*	Høier (2009)	*Ocalea picata*	
***Peyritschiella protea*	Rostrup (1935)	*Anotylus rugosus* – as *Oxyteles rugosus*, sic –	Now is *P. oxyteli*.
	Høier (2009)	*Anotylus rugosus, Phloeopora testacea*	Now is *P. oxyteli*. Record on *Phloeopora* is doubtful, but according to photograph published in Høier (2007) seems correct.
**Rhachomyces canariensis*	Høier (2009)	*Trechus quadristriatus*	
**Rhachomyces furcatus*	Rostrup (1935)	*Othius punctulatus*	
	Høier (2009)	*Othius punctulatus*, *O. subuliformis*	
**Rhachomyces philonthinus*	Høier (2009)	*Philonthus varians*, *P. fumarius*	
**Rhynchophoromyces anacaenae*	Høier (2009)	*Anacaena limbata*	
Rickia laboulbenioides	Santamaria *et al.* (2016)	*Cylindroiulus* spp.	
	Haelewaters *et al.* (2018b)	*C. punctatus*	
Rickia uncigeri	Santamaria *et al.* (2016)	*Unciger foetidus*	
	Haelewaters *et al.* (2019a)		
**Stigmatomyces burdigalensis*	Ahlburg (2011)	*Crumomyia notabilis* (Collin, 1902)	
***Stigmatomyces euconni*	Balazuc (1974f)	*Euconnus wetterhalli*[1]	Cannot be confirmed. Reported in Huggert's correspondence.
**Stigmatomyces hydrelliae*	Majewski (2008)	*Hydrellia griseola*, *H. maura* Meigen, 1838	
Troglomyces triandrus	Enghoff & Santamaria (2015)	*Archiboreoiulus pallidus*	

problems that have been dragging on for many years. Some species have been reinstated from their status of synonyms. It is worth mentioning that some species known only from types were found again in this study.

All species found in this study are illustrated with photographs, some of them for the first time. Four appendices are annexed including: a list of Laboulbeniales for the ten most diverse European countries (Appendix 1), a list of hosts with respective Laboulbeniales in Denmark (Appendix 2), a series of photographs with collecting explanations for several selected habitats (Appendix 3), and some macro photographs of hosts with fungi (Appendix 4).

Material and methods

Denmark's geography, climate and vegetation

Denmark is the southernmost of the Nordic countries. Located between the North Sea to the West and the Baltic Sea to the southeast, is separated from Norway by the Skagerrak and from Sweden by the Kattegat and the Øresund. In the South it is bordered for 68 km by Germany. It consists of the peninsula of Jutland in the West, and hundreds of islands in the Baltic Sea, of which the largest are Zealand, on which Copenhagen is located, and Funen. The surface of Denmark is estimated to be 43 094 km^2 (not considering Greenland and the Faeroe islands with which it exceeds 2 million km^2). Denmark is characterized by

a temperate climate, with mild and windy winters and cool summers. The terrain is rather flat with a few moderately rolling plains; the highest point is 171 m a.s.l. (Møllehøj). Denmark is part of Europe's temperate deciduous forest belt. The natural vegetation in most of the country is a mixed forest, with beech (*Fagus sylvatica*) being the most common tree. However, almost all parts of the country are under cultivation today. Approximately 11% of Denmark has a forest cover, most of which has been planted. Coniferous trees prevail in parts of the former heath areas in western Jutland, and the dune areas have been forested with spruces (*Picea* spp.) and pines (*Pinus* spp.) (Lahelma & Olofsson 2020).

Localities

The studied material originates from 429 localities throughout all of Denmark (excluding Greenland and the Faeroe Islands). Generally, it was attempted to include as many habitats as possible. We include two maps of Denmark with UTM 10 × 10 squares where the number of species of fungi (Fig. 93) and number of localities providing fungi (Fig. 94) for each square are displayed. Investigated locations where no fungi were found have not been considered here and thus not marked. Photographs of several selected collecting sites (Fig. 96) with details of sampling are included in Appendix 3 at the end of the work.

Localities contain reference to the eleven faunistic districts (Enghoff & Nielsen 1977), coordinates, the UTM 10 × 10 square, dates, collector (leg.), and identifier (det.). Abbreviations and names for the districts are [(Abbreviation), Danish name / International name]: (B), Bornholm / Bornholm; (EJ) Østjylland / East Jutland; (F) Fyn / Funen; (LFM) Lolland, Falster, Møn / Lolland, Falster, Møn; (NEJ) Nordøstjylland / North East Jutland; (NEZ) Nordøstsjælland / North East Zealand; (NWJ) Nordvestjylland / North West Jutland; (NWZ) Nordvestsjælland / North West Zealand; (SJ) Sydjylland / South Jutland; (SZ) Sydsjælland / South Zealand; (WJ) Vestjylland / West Jutland (Fig. 92).

Sampling and microscopy

Most field collections were carried out by Jan Pedersen (JP) from 2013 to 2020, but also by other collectors as indicated in the "collections examined" sections. Hosts were obtained by means of the standard collecting methods utilized by entomologists (i.e., hand picking, sieving, beating, sweeping nets – aquatic and terrestrial –, mouth aspirator, light traps, pitfall traps, Berlese funnels, etc) (see Appendix 3 for some additional details). Specimens from recent field collections (286 localities), were preserved in 70% ethanol for transport to the laboratory, where they were carefully examined with a dissecting microscope, under 40–80× magnification, to isolate the infected insects in properly labelled vials. In Appendix 4 we add some macro photographs of insects bearing fungi. Thalli of fungi were removed from the hosts with a sharp entomological pin (#3) and transferred onto a permanent slide mount prepared following the methods described by Rossi & Santamaria (2015) with the help of a Zeiss Stereo Discovery V8 dissecting microscope. Also, a not negligible number of infected insects were found among dry specimens in Museum or private entomologists' collections (from 143 different localities), many of them belonging to very old collections that, despite their antiquity, were in a more than acceptable condition and still suitable for study. This fact emphasizes once again the importance of having well preserved and well curated museum collections (Santamaria *et al.* 2016). Only as a curiosity, 44 collections stem from the 19th Century, with the oldest four from the year 1849. It should be noted that the current state of conservation of most of these localities is unknown and, therefore, it could happen that some of the fungi collected there are already extinct in Denmark. Infected hosts and permanent slide mounts mentioned in the catalogue are deposited at the Natural History Museum of Denmark (with codes ZMUC C–F–XXXXXX). The preservation methods of the samples (70% ethanol or dry) are not suitable for carrying out molecular studies which have proven particularly difficult for Laboulbeniales (e.g., Haelewaters *et al.* 2015a, Sundberg *et al.* 2018a).

A Leica DMR compound microscope equipped with differential interference contrast optics (DIC) and a Jenoptik ProgRes 10+ digital camera has been used together with its software for observations,

measurements and taking photos. Images were fine-tuned and mounted in plates with Photoshop CS5 software.

During this study, the loan of slides from Roland Thaxter's original collection was very valuable when trying to clarify the status of some of the species included in or related to the list. These slides are kept in the Farlow Herbarium (FH) in the Harvard University Herbaria. Full data of these slides will be included in the respective "Other material examined" sections.

Morphological traits and terminology of thallus-forming Laboulbeniomycetes

The terminology of these fungi is very specific. As a rule we follow that utilized by Thaxter in his five monographs (Thaxter 1896, 1908, 1924, 1926, 1931) and later refined by Tavares (1985) who added some abbreviations used throughout in this work. Additional glossaries may be found in Santamaria (1998) and De Kesel *et al.* (2020).

These fungi never form mycelia or hyphae in the traditional definition of the terms. The vegetative body of these fungi is characterized by a compact hyphal system described as a thallus consisting of 100s or 1000s of cells, measuring on average between 100 and 600 µm. Thalli develop from single-septate, bicellular ascospores. Each of the two cells of the ascospore usually grows in a definite sequence. The lower longer cell sticks on the host integument by means of a usually darkened foot (**fo**) and develops into the receptacle, perithecia, and the secondary appendages. The upper shorter cell forms the primary appendage (**pa**). The original septum of the ascospore is often recognizable in mature thalli and is known as the primary septum (**a**). The original spore apex may remain unchanged in mature thalli of some species as a spinous process (**sx**). Appendages are the most hyphal-like structures in the thalli. They are filaments formed by superposed cells, and they may be unbranched or more or less profusely branched. Secondary appendages are developed from the lower cell of the ascospore.

The receptacle forms the core of the thallus and supports all other parts. We distinguish the lower, or primary receptacle (**pr**), which usually consists of a basal cell (**I**), a suprabasal cell (**II**), and a terminal cell (**III**), or their derivatives. The receptacle may vary enormously from a few to hundreds of cells. Sometimes we distinguish as secondary receptacle branches formed from cell II.

Sexual reproduction in these fungi works by means of a spermatization, although this is unknown in several species, and it could be suspected that these may be apomictic. Male gametes, of the spermatia type (**sp**), arise from antheridia (**an**) (sometimes also named phialides if one-celled and flask-shaped), that may be of the simple or of the compound type. Antheridia are usually found on appendages. Compound antheridia consist of a set of sterile and fertile cells, with the fertile phialides or simple antheridia ejecting their spermatia into a common chamber before they are released through an exit pore. Spermatia stick to a trichogyne (**tr**), a variable septate branch arising from the young perithecium. When the male nucleus penetrates through the trichogyne and reaches the carpogonial cell (**cp**), through an intermediate branch known as trichophoric cell (**tc**), the resulting fertilization starts producing an ascoma, named perithecium (**per**) (for a full explanation relating the sexual reproduction of Laboulbeniales, see Tavares 1985). After development of the perithecium, the base of the trichogyne often remains as a stump or scar on the upper part of the perithecial wall (**ts**). Antheridia and perithecia are found on the same thallus in monoecious species, or on separate thalli in dioecious species.

The perithecium development is a very complicated process (see Tavares 1985), that ends with the mature structure which consists of an outer wall ("peridium") and a central cavity ("centrum") containing asci and ascospores (**as**). Asci are evanescent, and no hamathecial elements are present. The perithecial outer wall is two layered and consists of four vertical rows of a variable number of cells (**w** cells). This number depends on the taxon and is an important characteristic for delimiting supraspecific ranks. The

inner wall also shows four vertical rows, of which only the upper cells (**p** cells) may be distinguishable. The perithecium is similar to those of "pyrenomycetous" fungi, with a venter, a neck and an ostiole. The perithecia are supported by a stalk cell (**VI**) and several other cells such as the secondary stalk cell (**VII**) and accompanying basal cells (**n**, **n'**, and **m**).

Catalogue organization

The taxonomic treatment under the results section includes all genera and species found during this study, arranged in suprageneric taxa and alphabetically for genus and species ranks. To understand the morphological relations between genera we add an identification key and a list with suprageneric taxa layout (Table 2); the key is adapted for known Danish taxa, building on previous keys given by Benjamin (1971), Tavares (1985) and Majewski (1994b) but simplified and partially modified. The classification system of Tavares (1985) is used with minor emendations by recent works (Haelewaters *et al.* 2019c). This system is based on morphological features (perithecial ontogeny, perithecial wall structure and characteristics of antheridia) and has been only partially supported by molecular evidence (Goldmann & Weir 2018). We are reluctant to use the term phylogenetic to define this generic arrangement in higher ranks because we are still far from a complete overview of these relationships (Haelewaters 2018). The order in which the taxa are presented in the catalog is merely expository and lacks any phylogenetic meaning, at least as regards tribes and subtribes in subfamily Laboulbenioideae.

A taxonomic summary is given for genera, including the type species, a full protologue reference, the MycoBank number, synonymy, and sections like "Brief description" for diagnosis, and "Remarks" with the number of species and any additional data when necessary. If more than one species is present in the genus, an identification key is given.

Species are given with mostly traditional synonymy, type original designation if available, MycoBank number, and sections entitled "Diagnostic features", "Distribution and hosts", "Collections examined from Denmark" and "Remarks". In the "Diagnostic features" paragraph we avoid full descriptions, and only remarkable characteristics to distinguish the species are incorporated. Literature references to suggested detailed descriptions other than original protologues (including the synonyms) are provided. In "Distribution and hosts" we include geographical distribution and host information. For this paragraph, two works (Santamaria *et al.* 1991; Majewski 2008) are used throughout as synoptic references, complemented with subsequent records or adjustments if any. Infraspecific taxa are usually not included in the catalogue, with only very few exceptions. Of course, new species have their own and distinctive format. In the "Collections examined" paragraph, the citation of specimens follows the guidelines of Chester *et al.* (2019) with minor modifications: records are grouped by hosts, then alphabetically arranged according to abbreviations of Danish geographical districts (including full Danish name), locality, and chronology. The end result: geographic coordinates, UTM square 10 × 10 km, collecting date, collector's name + collection number in italics, host determinator (det.), and herbarium reference to voucher specimen and slide. Example: **Nordøstsjælland (NEZ) •** Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 15 Jun. 2013; *JP 230*; JP det.; ZMUC C-F-122711. [**Danish geographical district name (Abbreviation) •** locality; geographic coordinates; UTM square 10 × 10 km; collecting date; *collector's name + collection number*; host determinator det.; herbarium reference.]

For type information in species treatments, the original typographical spelling is strictly presented without corrections, except for those considered essential at our discretion, with amendments or precisions if any, added between square brackets. If known, the acronym for the institutional herbaria where types are held is also included. Information like "type not designated" or "locotypic indication" (Ind. loc.) are given if required. According to information accumulated over the years, often by personal communications, we know that some types may be considered lost because of destruction or demonstrated unavailability. Examples of this are the Picard collection, which was acquired by Lepesme, but when he passed away, the

Table 2. Classification system of known Danish genera used in the text. * = genus to be removed from the Danish catalogue, not included in the key. Explanations under *Monoicomyces invisibilis*.

Order	Family	Subfamily	Tribe	Subtribe	Genus
Herpomycetales	*Herpomycetaceae*		**Herpomyceteae**		Herpomyces
Laboulbeniales	*Ceratomycetaceae*	Ceratomycetoideae	**Ceratomyceteae**	Helodiomycetinae	*Helodiomyces*
				Ceratomycetinae	*Autoicomyces* *Ceratomyces* *Eusynaptomyces* *Rhynchophoromyces*
			Drepanomyceteae		*Thripomyces*
	Euceratomycetaceae				*Euzodiomyces*
	Laboulbeniaceae	***Zodiomycetoideae***	**Zodiomyceteae**		*Zodiomyces*
		Laboulbenioideae	**Coreomyceteae**		*Coreomyces*
			Compsomyceteae	Compsomycetinae	*Compsomyces*
				Kainomycetinae	*Kainomyces*
			Hydrophilomyceteae		*Hydrophilomyces*
			Euphoriomyceteae	Euphoriomycetinae	*Euphoriomyces* *Phaulomyces* *Siemaszkoa*
			Teratomyceteae	Teratomycetinae	*Idiomyces* *Symplectromyces* *Teratomyces*
				Rhachomycetinae	*Microsomyces* *Rhachomyces*
				Asaphomycetinae	*Asaphomyces*
			Laboulbenieae	Chitonomycetinae	*Chitonomyces* *Hydraeomyces*
				Chaetarthriomycetinae	*Chaetarthriomyces*
				Misgomycetinae	*Misgomyces*
				Laboulbeniinae	*Botryandromyces* *Ecteinomyces* *Laboulbenia*
				Stigmatomycetinae	*Acompsomyces* *Aphanandromyces* *Arthrorhynchus* *Bordea* *Corethromyces* *Cryptandromyces* *Diphymyces* *Dipodomyces* *Distolomyces* *Hesperomyces* *Rhadinomyces* *Rossiomyces* *Sphaleromyces* *Stichomyces* *Stigmatomyces* *Tanmaurkiella* *Tavaresiella* *Troglomyces*
				Amorphomycetinae	*Amorphomyces* *Dioicomyces*
		Peyritschielloideae	**Peyritschielleae**	Peyritschiellinae	*Peyritschiella* *Rickia*
			Dimorphomyceteae		*Dimeromyces* *Dimorphomyces* *Trenomyces*
			Haplomyceteae	Haplomycetinae	*Camptomyces* *Cantharomyces* *Haplomyces*
		Monoicomycetoideae			**Eumonoicomyces* *Monoicomyces*

slides containing the fungi were misplaced (Rossi, pers. comm. received from Balazuc); the Siemaszko husband and wife collection, which was sadly destroyed during World War II (Majewski 1994b); and lastly, the slides from the Maire collection are at an unknown location after the Algerian independence, according to local sources consulted.

Abbreviations for authors of Fungal names follow the recommendations by Brummitt & Powell (1992). Citation of author and year for host species and host genus is given at least the first time they appear in the text but always in the "collections examined…" sections. Exceptions will be found in the references to hosts names in fungal types where the original spelling has been respected. The determination, verification and nomenclature of hosts follows: Petersen & Meier (2001) for Diptera, Löbl & Smetana (2003, 2004, 2006, 2007, 2008, 2010) for Coleoptera, Gustafson *et al.* (2018) for Phthiraptera, Hoffmann (2011) for Heteroptera, Beccaloni (2014) for Blattodea, Hopkins *et al.* (2020) for Dermaptera, and Andersson *et al.* (2005) for Diplopoda.

Abbreviations for morphological terms used in descriptions and illustrations

I	=	basal cell of receptacle
II	=	suprabasal cell of receptacle
III	=	terminal cell of receptacle
VI	=	perithecial stalk cell
VI'	=	additional perithecial stalk cell in *Helodiomyces* and *Asaphomyces*
VII	=	secondary stalk cell of perithecium
a	=	primary septum
ac	=	appendiculate cells; intermediate flattened cells of receptacle in *Coreomyces*
acc	=	accessory cell; cell on the outer and lower side of the perithecium, exterior to outer wall, in the Hydrophilomyceteae
an	=	antheridium or phialide
as	=	ascospores
ax	=	axis, axial; may be primary or secondary; when the receptacle consists of several superposed cells which form a ± straight row
bc a	=	basal cell of appendage
bc ia	=	basal cell of inner appendage in *Laboulbenia*
bc sap	=	basal cell of secondary appendage in *Laboulbenia*
bf	=	buffer projections; outgrowths just above foot in some genera (e.g., *Hydrophilomyces*, *Zodiomyces*) which apparently serve to keep the thallus in an upright position on the host. Often called buffer cells because the projection consists of only one cell
cc	=	corticating cells; cells derived from cell II in *Microsomyces*, which laterally grow into a crust-like series of cells onto the host cuticle
cp	=	carpogonial cell, fertile cell supporting trichophoric cell and trichogyne, resulting in asci after fertilization
fo	=	foot, the darkened basal part of cell I
ha	=	haustorium
ic	=	insertion cell; the lowermost cell of primary appendage in *Laboulbenia*; usually flat and blackened
li	=	ligula-like protuberances or ligules of perithecium
m	=	one of the three perithecial basal cells
n	=	one of the three perithecial basal cells
n′	=	one of the three perithecial basal cells
p	=	inner wall cells
pa	=	primary appendage
per	=	perithecium

po	=	antheridial exit pore
pr	=	primary or lower receptacle, formed by cell I, II and III or its derivatives
ro	=	rostrum; beak-like, prolonged apex of perithecium, in *Kainomyces*
sa	=	secondary appendage
sc-an	=	antheridial supporting cell, also called corner cell
sh	=	shield; grouped secondary receptacle cells in *Herpomyces*
sp	=	spermatium
sx	=	spore apex, spinous process or remains of the original spore apex
tc	=	trichophoric cell, cell separating carpogonial cell and trichogyne
tr	=	trichogyne
ts	=	trichogyne stump; the persistent base or scar of the trichogyne
w_n	=	perithecial outer wall cell of tier "n"

Herbaria and collections codes used in the text

BCB	=	Herbarium at the Universitat Autònoma de Barcelona, Barcelona, Spain
BR	=	Meise Botanic Garden, Meise, Belgium
C-F-	=	Copenhagen-Fungi, acronym for the fungi slides kept in ZMUC
FH	=	Farlow Herbarium, Harvard University Herbaria, Cambridge, Massachusetts, USA
KRAM	=	Herbarium at W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland
LPS	=	La Plata Spegazzini's Herbarium, Universidad Nacional de La Plata, Buenos Aires, La Plata, Argentina
MZH	=	Zoological Museum in Helsinki, Helsinki, Finland.
NHMD	=	Natural History Museum of Denmark, Copenhagen, Denmark
PC	=	Herbarium at the Muséum national d'histoire naturelle, Paris, France
RO	=	Herbarium at the Università degli Studi di Roma La Sapienza, Roma, Italy
UME	=	Herbarium at Umeå University, Umeå, Sweden
ZMUC	=	Collection at the Zoological Museum, University of Copenhagen, Copenhagen, Denmark

Other abbreviations used in the text

Col.	=	Coleoptera
coll.	=	Host collector
det.	=	Host identifier
ex	=	When used as a component of an author citation, it denotes the fact that an initial description did not satisfy the rules for valid publication, but that the same name was subsequently validly published by a second author or authors (or by the same author in a subsequent publication)
Ind. loc.	=	Indicatio locotypica, Locotypic indication. When the type is not explicitly indicated with a single specimen and locality, but with several samples and localities
in litt.	=	in litteris, in correspondence
JP	=	Jan Pedersen
MB	=	MycoBank
SS	=	Sergi Santamaria
sensu	=	according to
sic	=	thus was it written
s. str.	=	sensu stricto, in the strict sense
viz.	=	namely; in other words (used to introduce a gloss or explanation)

Results

Key to the Danish genera of thallus-forming Laboulbeniomycetes

1. On cockroaches (Blattodea). Dioecious. In female thalli, cell II gives rise to a secondary axis which forms perithecia and connects directly with host integument by means of a series of narrow cells perforating the integument directly by small haustoria; some of these cells may differentiate into shield-like structures ..... **Herpomycetales** Haelew. & Pfister. ***Herpomyces*** Thaxt.
– On other arthropods (species on Blattodea in this section are unknown in Europe). Dioecious or monoecious. Thalli not as above. Typically attached to the host integument by means of a single cell or foot (usually black) developed by transformation of the ascospore basal cell. If not a blackened foot, a conspicuous haustorium is present (except for *Laboulbenia hyalopoda* De Kesel) ..... 2 (**Laboulbeniales** Lindau)

2. Outer wall of perithecium consisting of more than eight equal or subequal superposed cells for each vertical row. (See also the genus *Compsomyces.*) 3
– Outer wall of perithecium consisting of 4–5(–8) unequal superposed cells for each vertical row ..... 9 (**Laboulbeniaceae** Peyr.)

3. Axis of receptacle consisting of a series of superposed cells. Most species on aquatic Coleoptera ..... 4 (**Ceratomycetaceae** S.Colla)
– Receptacle massive, multiseriate. On terrestrial Coleoptera Staphylinidae of the genera *Lathrobium* Gravenhorst, 1802 and *Lobrathium* Mulsant & Rey, 1878 (less frequently on other genera of Coleoptera as *Patrobus*, a carabid)..... **Euceratomycetaceae** I.I.Tav. ***Euzodiomyces*** Thaxt.

4. Receptacle consisting of a series of superposed cells, those in the lower part distinctly broadened. On Coleoptera Hydraenidae ..... **Drepanomyceteae** I.I.Tav. ***Thripomyces*** Speg.
– Cells of the lower receptacle similar to each other..... 5 (**Ceratomyceteae** Thaxt.)

5. Perithecial apex bearing four slender and rather long ligules surrounding the ostiole. On Coleoptera Dryopidae ..... **Helodiomycetinae** I.I.Tav. ***Helodiomyces*** F.Picard
– Perithecial apex simple or with subapical horns. On Coleoptera Hydrophilidae .....
..... 6 (**Ceratomycetinae** Thaxt.)

6. Perithecium with a very long slender neck and an inflated venter ..... ***Rhynchophoromyces*** Thaxt.
– Perithecium with indistinct neck and venter..... 7

7. Outer wall cells similar in height in all vertical rows ..... ***Autoicomyces*** Thaxt.
– Two vertical rows of flattened cells alternating with narrow elongated cells in the other two rows...
..... 8

8. Normal forms with a multicellular (more than five cells) lower receptacle. Bifurcate horns on perithecium. Thalli from claws without horns..... ***Eusynaptomyces*** Thaxt.
– Lower receptacle consisting of 2–4(–5) superposed cells. Simple horns on perithecium.....
..... ***Ceratomyces*** Thaxt.

9. Receptacle massive, multiseriate. Perithecia ± hidden, immersed in a cavity of the thallus upper region ..... **Zodiomycetoideae** (Thaxt.) I.I.Tav. ***Zodiomyces*** Thaxt.
– Receptacle different. Perithecia obvious, well visible 10

10. Antheridia unicellular, simple, consisting of a phialide; or not evident or unknown (supposedly some taxa may be apomictic) ..... 19 (**Laboulbenioideae** Peyr.)
– Antheridia multicellular, compound, consisting of several fertile cells or phialides located inside a common cavity. Spermatia are ejected through a pore of that cavity 11

11. Secondary receptacles giving rise to antheridia and perithecia. Antheridia consisting of 3–4 tiers of paired cells, where the median tier or 2nd + 3rd tiers give rise to 2–8 phialides. Spermatia are ejected through a duct between the upper tier cells... **Monoicomycetoideae** (Thaxt.) I.I.Tav. ***Monoicomyces*** Thaxt.
– Otherwise ..... 12 (**Peyritschielloideae** (Thaxt.) I.I.Tav.)

12. Dioecious. Cells VII and basal cells of perithecium not visible at maturity .... 13 (**Dimorphomyceteae** Thaxt.)
– Monoecious. Cells VII and basal cells of perithecium well-distinguished at maturity 15

13. Neither secondary appendages nor blackened foot. Haustorium well-developed. Mostly on Mallophaga (bird lice) ..... ***Trenomyces*** Chatton & F.Picard
– Secondary appendages and normal blackened foot present 14

14. Female thalli with a laterally elongated cell I, underlying a series of cells bearing both appendages and perithecia ..... ***Dimorphomyces*** Thaxt.
– Female thalli without a laterally elongate cell I supporting cells which give rise to lateral perithecia and appendages ..... ***Dimeromyces*** Thaxt.

15. Receptacle flattened and multiseriate. Antheridia flask-shaped ..... 16 (**Peyritschielleae** Thaxt.)
– Receptacle otherwise, with superposed and contiguous cells I, II and III..... ..... 17 (**Haplomyceteae** Thaxt.)

16. Receptacle consisting of a basal cell with three superposed tiers of horizontally arranged cells ..... ***Peyritschiella*** Thaxt.
– Receptacle consisting of a basal cell and 2–3 vertical series of superposed cells..... ***Rickia*** Cavara

17. Compound antheridium in the basal cell of primary appendage which continues above by simple or ramified sterile branches ..... ***Cantharomyces*** Thaxt.
– Compound antheridium terminal on primary appendage 18

18. Compound antheridium terminated with an efferent neck..... ***Camptomyces*** Thaxt.
– Compound antheridium spinose, pore for release of spermatia in a sublateral position .... ***Haplomyces*** Thaxt.

19. Perithecium terminal on a uniseriate receptacle consisting of cells I, II, III and a few flattened cells. Primary appendage disappearing when perithecium develops. On Heteroptera Corixidae .... **Coreomyceteae** Thaxt. ***Coreomyces*** Thaxt.
– Perithecium lateral, arising from cell II or its derivatives. Primary appendage present. On other hosts 20

20. Primary appendage is a continuation of the same axis of the primary receptacle. Antheridia unknown. Perithecial outer wall consisting of four vertical rows each with four cells of unequal height. On Col. Staphylinidae Pselaphinae of the genus *Pselaphus* Herbst, 1792..... ..... ***Tanmaurkiella*** Santam. gen. nov.
– Primary appendage seen as a lateral branch of the thallus 21

21. Perithecial vertical wall cell rows consisting of more than five cells, ± equal in height..... ..... 22 (**Compsomyceteae** Thaxt. p.p.)
– Perithecial vertical wall cell rows consisting of three, four or five cells, unequal in height 23

22. Receptacle multiseriate, with the cell II subdivided by horizontal and vertical septa. Perithecia supported on uniseriate multicellular stalks, with an apical rostrum and a subterminal outgrowth.... ..... **Kainomycetinae** I.I.Tav. ***Kainomyces*** Thaxt.
– Receptacle uniseriate, two-celled. Perithecium pedicel consisting of the stalk cell (cell VI) and an additional underlying cell which may be regarded as part of the secondary receptacle. Neither rostrum nor outgrowths on perithecium. On *Astenus* Dejean, 1833 (Col. Staphylinidae)..... ..... **Compsomycetinae** Thaxt. ***Compsomyces*** Thaxt. p.p. (***C. verticillatus*** (Thaxt.) Thaxt.)

23. Perithecium borne on secondary axis. On *Lesteva* Latreille, 1797 (Col. Staphylinidae) .... **Compsomycetinae**. ***Compsomyces*** p.p. (***C. lestevae*** Thaxt.)
– Perithecia borne on primary axis 24

24. One elongate accessory cell on the outer side of the perithecial venter wall (study of immature thalli may be necessary). Only on aquatic beetles .... **Hydrophilomyceteae** I.I.Tav. ***Hydrophilomyces*** Thaxt.
– Not such elongate accessory cell on the perithecium 25

25. Cell wall of cell VII and at least one of the perithecial basal cells (m, n, n') well distinguished at maturity..... 28
– Cell wall of cell VII and perithecial basal cells (m, n, n') vanishing, not visible at maturity .... 26 (**Euphoriomyceteae** I.I.Tav.)

26. Primary receptacle, below cell VI, two-celled (i.e., cells I and II)..... ***Phaulomyces*** Thaxt.
– Primary receptacle, below cell VI, consisting of more than two cells, by subdivision of cell II ... 27

27. Neither branches nor antheridia below the perithecium. Receptacle uniseriate..... ..... ***Siemaszkoa*** I.I.Tav. & T.Majewski
– Secondary appendages and antheridia below perithecia. Receptacle looking multiseriate..... ..... ***Euphoriomyces*** Thaxt.

28. Receptacle multicelled, ± multiseriate or corticated, with cells II and III horizontally and vertically divided, developing a cellular complex bearing lateral or terminal abundant crowded branchlets..... 29 (**Teratomyceteae** Thaxt.)
– Receptacle multicelled, uniseriate, or only with few vertical septa in the distal end .... 34 (**Laboulbenieae** Thaxt.)

29. Receptacle broadened distally into a cellular complex bearing numerous lateral and/or terminal crowded appendages which in turn bear intercalary seriated antheridia .... 30 (**Teratomycetinae** Thaxt.)
– Receptacle seemingly uniaxial or corticated, the latter with a conspicuous haustorium. Antheridia terminal..... 32

30. Receptacle almost symmetrical, four-layered, with cell II subdivided by horizontal septa into two superposed cells (IIa and IIb), and an uppermost fourth tier where cell III is divided repeatedly by vertical and oblique septa 31
– Receptacle clearly asymmetric, unilateral, with cell II subdivided into three cells (IIa, IIa' and IIb), IIb and IIa' separated by a vertical septum. On *Deleaster* Erichson, 1939 (Col. Staphylinidae) ..... ***Idiomyces*** Thaxt.

31. Appendages with pointed branchlets ..... ***Teratomyces*** Thaxt.
– Appendages without pointed branchlets ..... ***Symplectromyces*** Thaxt.

32. Blackened foot absent. Haustorium conspicuous. On Col. Silvanidae..... ***Microsomyces*** Thaxt.
– Blackened foot present. Lacking a noticeable haustorium 33

33. Thallus consisting of a primary bicellular receptacle (cells I and II) and a secondary receptacle formed by division of cell II, which represents the main axis, where lateral cells give rise to appendages. All perithecial basal cells (m, n, and n') well-distinguished .... **Rhachomycetinae** (Thaxt.) I.I.Tav. ***Rhachomyces*** Thaxt.
– Thallus only with one primary axis. Of the perithecial basal cells, only cell m is visible. On Col. Leiodidae ..... **Asaphomycetinae** I.I. Tav. ***Asaphomyces*** Thaxt.

34. Thalli dioecious. Male thalli consisting of 3–4 superposed cells, the uppermost cell functioning as a phialide. Female thalli with a uni- or bicellular primary appendage, sometimes embedded among thallial base cells and externally invisible ..... 35 (**Amorphomycetinae** (Thaxt.) I.I.Tav.)
– Thalli monoecious, or if dioecious, female and male thalli different from above..... 36

35. Female thalli consisting of a three-celled receptacle, cell III supporting a unicellular primary appendage. Male thalli four-celled, the uppermost cell functioning as a phialide .... ***Dioicomyces*** Thaxt.
– Female thalli consisting of a two-celled receptacle, with cells II–III not separated; primary appendage usually indistinguishable. Male thalli three-celled, the uppermost cell functioning as a phialide ..... ***Amorphomyces*** Thaxt.

36. Antheridia below the primary septum or the primary appendage consisting of a campanulate basal cell and a filiform distal cell. Only on aquatic beetles..... 37 (**Chitonomycetinae** I.I.Tav.).
– Antheridia on a well-developed primary appendage, borne above the primary septum 38

37. Perithecial outer wall consisting of four vertical rows, each with 3–4 cells of unequal height .... ***Chitonomyces*** Peyr.
– Perithecial outer wall consisting of four vertical rows of cells organized as two adjacent rows with 4–5 cells (formed from n) and the other two rows with 7–8 cells..... ***Hydraeomyces*** Thaxt.

38. Lower receptacle two-celled (below the perithecial stalk cell), consisting of superposed cells I and II. An inner sterile cell is formed from the appendage axis cell just above the perithecium (usually the third cell if only one perithecium is developed), as a corner cell. On *Chaetarthria* Stephens, 1833 (Col. Hydrophilidae)..... **Chaetarthriomycetinae** I.I.Tav. ***Chaetarthriomyces*** Thaxt.
– Lower receptacle (below the perithecial stalk cell) consisting of three or more cells, in a uniseriate row (by subdivision of cell II). If two-celled, characteristics are different from above. 39

39. Lower receptacle (below the perithecial stalk cell) three- to multicelled..... 40
– Lower receptacle (below the perithecial stalk cell) two-celled (i.e., cells I and II)..... 43

40. Antheridial cells embedded in an irregular mass of cells above the primary septum, bearing short efferent necks 41
– Antheridial cells are free phialides (i.e., flask shaped cells), usually on appendage branches..... 42

41. Cell III subdivided irregularly into several small cells. Perithecium with four outer wall cells of unequal height in each vertical row ..... **Misgomycetinae** (Thaxt.) I.I.Tav. ***Misgomyces*** Thaxt.
– Cell III subdivided into three cells, by a horizontal septum and the upper cell divided again by a vertical septum. Perithecium with three outer wall cells in two adjacent vertical rows and four in other two rows. On Col. Heteroceridae .... **Laboulbeniinae** Thaxt. p.p. ***Botryandromyces*** I.I.Tav. & T.Majewski

42. Antheridia are elongate phialides arranged in clusters supported by short branchlets arising from corner cells in lower receptacle. On Col. Heteroceridae ..... **Laboulbeniinae** p.p. ***Botryandromyces***
– Antheridia sessile or on short stalk cells in lower part of the primary appendage. On Col. Ptiliidae ..... **Laboulbeniinae** p.p. ***Ecteinomyces*** Thaxt.

43. Receptacle usually five-celled, with a two-celled lower receptacle (below perithecial stalk cell) and a three-celled upper receptacle formed by subdivision of the terminal cell (cell III) into three cells (namely III, IV and V). Perithecium with four outer wall cells in each vertical row, the cells distinctly unequal in height. Lowermost cell of primary appendage is the insertion cell, typically flat and usually blackened ..... **Laboulbeniinae** p.p. ***Laboulbenia*** Mont. & C.P.Robin
– Receptacle three-celled..... 44 (**Stigmatomycetinae** (Thaxt.) I.I.Tav.)

44. Perithecium with five outer wall cells in each vertical row, the cells equal or slightly unequal in height, but the two cells of the venter somewhat longer. Primary appendage usually unbranched, bearing lateral sessile or subsessile antheridia, or the cells functioning wholly as phialides. Mostly on Col. Staphylinidae Pselaphinae, also in Col. Cryptophagidae (so far only in Denmark!) ..... ***Cryptandromyces*** Thaxt.
– Perithecium with outer wall cells distinctly unequal in height (cells of the venter twice or more longer than any of the apical cells, especially the uppermost ones in the series) 45

45. Cell III supporting an unbranched, free appendage, consisting of two superposed cells and a terminal, spinose, flask-shaped phialide. On Col. Staphylinidae Pselaphinae..... ***Bordea*** Maire
– Appendage with different characters as above 46

46. Primary appendage consisting of three superposed cells, with the median and upper cells giving rise to antheridia, the upper cell bearing a dorsal spinous process. On *Cryptophagus* Herbst, 1863 (Col. Cryptophagidae) (see also *Cryptandromyces cryptophagi* Santam. sp. nov.) .... ***Rossiomyces*** R.K.Benj.
– Otherwise..... 47

47. Cell III narrow and adnate to the side of the perithecium, reaching one half or beyond its height. On Diplopoda Julida (millipedes)..... ***Troglomyces*** S.Colla
– With other characters. On insects 48

48. Primary appendage bent in sharp angle towards the perithecium, consisting of two superposed cells and a terminal, spinose phialide. Perithecium bearing two apical outgrowths. On Dermaptera Forficulidae (earwigs)..... ***Distolomyces*** Thaxt.
– On other insects and with other characters 49

49. Primary appendage consisting of a short branch which on the inner side of its basal cell produces an appendage giving rise many short lateral branches. On Heteroptera Hebridae (true bugs) ..... ***Tavaresiella*** T.Majewski
– On other insects and with other characters 50

50. On Diptera 51
– On Coleoptera 52

51. Cell I inflated, without a blackened foot but with a conspicuous haustorium. Cell II flattened. Cell III free. On Nycteribiidae (parasitic flies living on bats) ..... ***Arthrorhynchus*** Kolen.
– Cells I and II elongate, cell III laterally adnate to cell VI ..... ***Stigmatomyces*** H.Karst.

52. Primary appendage limited in growth, compact, terminating with antheridia 53
– Primary appendage not limited in growth, ± ramified and terminating with a sterile branch 56

53. Primary appendage caducous by breaking off the collapsing third cell which supports two cells and four antheridia. On *Brachypterus* Kugelann, 1794 (Col. Kateretidae).. ***Aphanandromyces*** W.Rossi
– Primary appendage perennial 54

54. Cell III in contact with cell I 55
– Cell III not in contact with cell I. On Col. Staphylinidae Paederinae ..... ***Sphaleromyces*** Thaxt.

55. Perithecium with five outer wall cells in each vertical row. Trichogyne V-shaped, with arms covered by globoid papillae ..... ***Acompsomyces*** Thaxt.
– Perithecium with four outer wall cells in each vertical row, bearing apical lobes. Trichogyne different. Mostly on Col. Coccinellidae ..... ***Hesperomyces*** Thaxt.

56. Branchlets bearing antheridia arising from corner cells of appendage axial cells 57
– Branchlets bearing antheridia not arising from corner cells 58

57. Cell III always bearing antheridial branchlets, rarely on appendage cells above. On ***Lathrobium*** (Col. Staphylinidae) ..... *Rhadinomyces* Thaxt.
– Cell III sterile, rarely bearing antheridial branchlets, which are abundant on appendage cells above. On *Sepedophilus* Gistel, 1856 (Col. Staphylinidae) ..... ***Stichomyces*** Thaxt.

58. Cell II adnate or parallel to cell VI. Mostly on Col. Leiodidae (less commonly on Col. Staphylinidae) ..... ***Diphymyces*** I.I.Tav.
– Cell II supporting the free cell VI. Mostly on Col. Staphylinidae ..... ***Corethromyces*** Thaxt.

Taxonomic treatment

Order Herpomycetales Haelew. & Pfister
Family Herpomycetaceae (Thaxt.) I.I.Tav.
Tribe Herpomyceteae Thaxt.

Genus ***Herpomyces*** Thaxt.
MB#2303

Proceedings of the American Academy of Arts and Sciences 38: 11 (Thaxter 1902). – Type species: *H. chaetophilus* Thaxt.

Brief description

Dioecious. Female thallus with an expanded, often branched, secondary axis consisting of a series of narrow cells which penetrate the host integument by small haustoria and sometimes differentiate into shield-like structures. Perithecium with an outer wall consisting of four vertical rows of numerous cells which are subequal in height. Eight spores for each ascus. Male thallus with a branched primary axis, bearing terminal long antheridia; secondary axis similar to that of the female thallus.

Remarks

The genus consists of 27 species, of which three in Europe, all in Denmark. The most recently described species is *H. spegazzinii* A.C.Gut. & D.Haelew. (Gutierrez *et al.* 2020). It is the single genus in the recently created order Herpomycetales. Species of *Herpomyces* show a particular pattern of development and organization which originally defined the suborder Herpomycetinae as separate from the Laboulbeniineae within the Laboulbeniales. According to Tavares (1985) this genus is ancestral and possibly coevolved little along with its hosts, the primitive cockroaches.

Herpomyces macropus Speg. described by Spegazzini (1917) on *Blabera* Serville, 1838 from Argentina has been considered by Thaxter (1931) a possible synonym of *H. paranensis* Thaxt. (Thaxter 1902), also on *Blabera* from several countries of America; in this case the number of species for the genus should be 26 instead of 27.

Key to the Danish species (partially following Santamaria 2003)

1. Perithecial apex bearing a subapical tooth-like outgrowth. Thallus with shield ..... 2.
– Perithecial apex without outgrowth. Thallus without shield. On *Blattella germanica* (Linnaeus, 1767) (Blattodea, Blattidae) ..... ***H. ectobiae*** Thaxt.

2. Shield entirely hyaline. On *Periplaneta americana* (Linnaeus, 1758) (Blattodea, Blattidae)..... ..... ***H. periplanetae*** Thaxt.
– Shield darkened at the base. On *Blatta orientalis* Linnaeus, 1758 (Blattodea, Blattidae) .... ***H. stylopygae*** Speg.

Herpomyces ectobiae Thaxt.
MB#200204
Fig. 1A

Proceedings of the American Academy of Arts and Sciences 38: 20 (Thaxter 1902). – **Type**: [Not designated] [Ind. loc.] "On *Ectobia Germanica* Scudd., Cambridge, Mr. Bullard. On *Ectobia* sp., Zanzibar; Mus. Comp. Zoöl., No. 1357; St. Kitts, West Indies; Mus. Comp. Zoöl., No. 1361"; FH.

Diagnostic features

Female thalli prostrate. Shield absent. Perithecium with an inflated venter, gradually tapering towards a well-distinguished long and narrow, strongly arcuate neck, and a truncate, bent apex. [Detailed descriptions: Thaxter 1908; Tavares 1980; Majewski & Sugiyama 1985; Majewski 1994b; De Kesel 2001; Santamaria 2003]

Distribution and hosts

Widely distributed with its synanthropic host, *Blattella germanica* (as *Ectobia germanica* or *Phyllodromica germanica* in old literature) (Blattodea, Blattidae). Reported from several countries in **Europe** (France, Poland, Spain, Belgium), **Africa** (Zanzibar), **Asia** (Burma, India, Japan, Philippines) and **America** (Argentina, Chile, USA, Saint Kitts and Nevis) (Santamaria *et al.* 1991; Majewski 2008). Recently

reported from Bulgaria (Rossi *et al.* 2019a), Hungary (Pfliegler *et al.* 2018), and USA (Haelewaters *et al.* 2019b).

Collections examined from Denmark

On *Blattella germanica* (Linnaeus, 1767) (Blattodea Blattidae)

DENMARK – **Nordøstsjælland (NEZ)** • København; 55°41.332′ N, 12°33.762′ E; UB47; 23 Sep. 1943; *N. Wolff Dry0026*; K. Th. Holst det.; ZMUC C-F-124040. – **Nordvestjylland (NWJ)** • Thisted; 56°57.279′ N, 8°41.599′ E; MJ81; *E. Petersen Dry0027*; K. Th. Holst det.; ZMUC C-F-124041.

Remarks

First record from Denmark. Although the Danish material is not in perfect condition, it is perfectly identifiable (Fig. 1A).

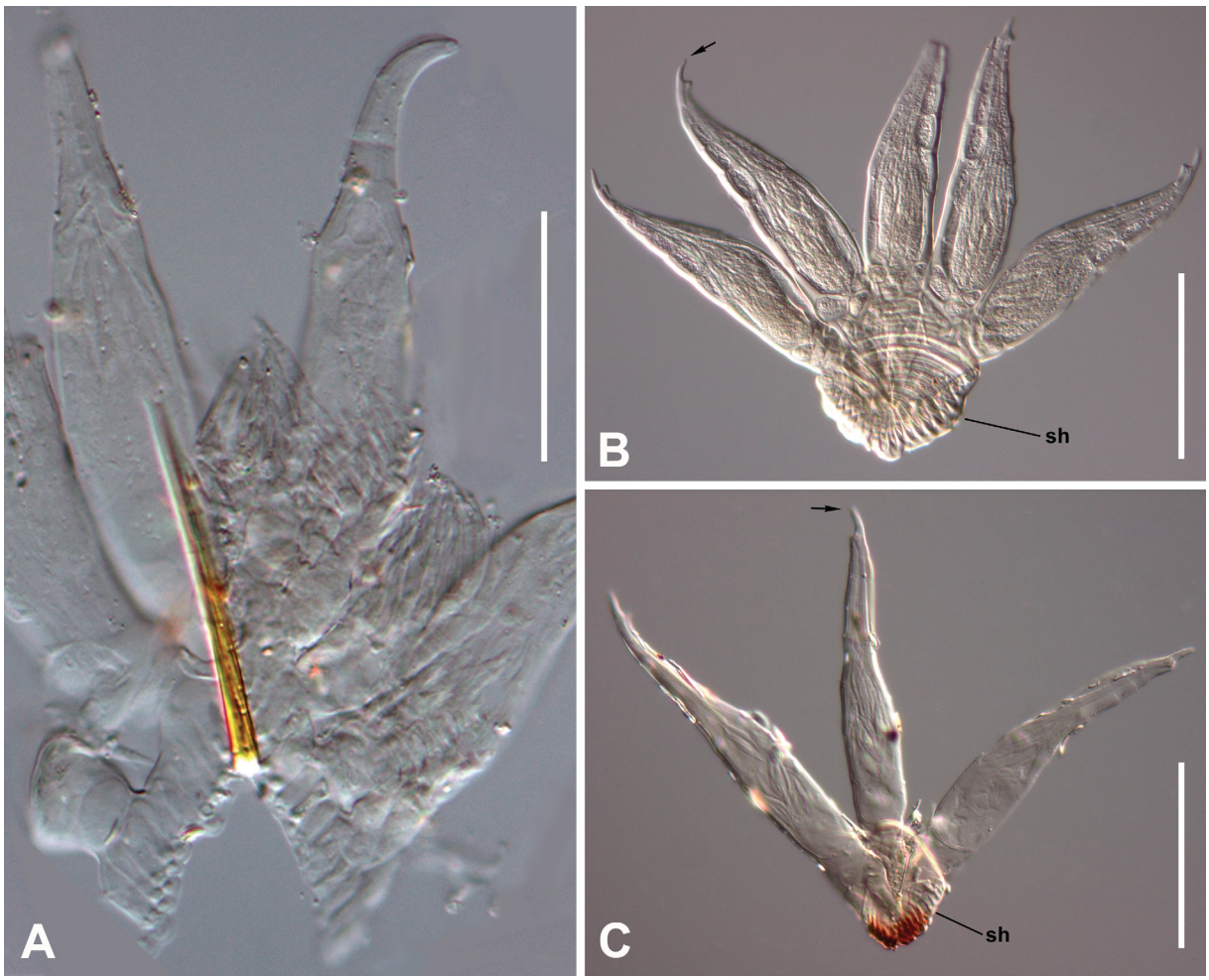

Fig. 1. *Herpomyces* spp. **A**. *H. ectobiae* Thaxt.; mature thallus. – **B**. *H. periplanetae* Thaxt.; mature thallus showing the distal acute tooth-like outgrowth on the perithecium (arrow), and shield (sh). – **C**. *H. stylopygae* Speg.; mature thallus showing the distal acute tooth-like outgrowth on the perithecium (arrow), and shield (sh). Scale bars: A = 50 µm; B–C = 100 µm. Photographs from slides ZMUC C-F-124041 (A), ZMUC C-F-123751 (B), and ZMUC C-F-124039 (C).

Herpomyces periplanetae Thaxt.
MB#231769
Fig. 1B

Proceedings of the American Academy of Arts and Sciences 38: 13 (Thaxter 1902). – **Type**: [Not designated] [Ind. loc.] "On *Periplaneta Americana* Sauss. (type form), Cambridge (Mr. Bullard): Bermuda; Mus. Comp. Zoöl."; FH.

Diagnostic features

Shield bilobate, ± symmetric, hyaline (Fig. 1B, sh). Perithecial neck bent, terminated in a pointed, subacute lateral tip, and a distal acute tooth-like outgrowth (Fig. 1B, arrow). [Detailed descriptions: Thaxter 1908; Majewski 1994b; De Kesel 2001; Santamaria 2003]

Distribution and hosts

As common as the other two European species; it grows on the antennae of several species of *Periplaneta* Burmeister, 1838 (Blattodea, Blattidae), usually *P. americana*. Reported from all continents except Oceania. **Europe** (France, Italy, Spain, Belgium), **Africa** (Somalia, Morocco, Bénin, D.R. Congo, Togo), **Asia** (China, Japan, Bali Island, Malaysia, India, Taiwan, Korea) and **America** (USA, Panama, Mexico, Bermuda Islands, Brazil, French Guiana) (Santamaria *et al.* 1991; Haelewaters *et al.* 2021). All records from *Blatta* Linnaeus, 1758 or its synonym *Stylopyga* Brunner von Wattenwyl, 1865 should be referred to *Herpomyces stylopygae* Speg. (see below).

Collections examined from Denmark

On *Periplaneta americana* (Linnaeus, 1758) (Blattodea Blattidae)
DENMARK – **Østjylland (EJ)** • Århus; 56°9.166′ N, 10°12.502′ E; NH72; 1 Oct. 1915; *E. Petersen Dry0021*; ZMUC C-F-124035. – **Nordøstsjælland (NEZ)** • København; 55°41.038′ N, 12°35.914′ E; UB47; 14 Nov. 1901; *leg. and coll. unknown*, *1224*; ZMUC C-F-123751.

On *Periplaneta australasiae* (Fabricius, 1775) (Blattodea Blattidae)
DENMARK – **Østjylland (EJ)** • Silkeborg; 56°10.059′ N, 9°32.930′ E; NH32; 18 Aug. 1930; *E. Petersen Dry0022*; ZMUC C-F-124036.

Remarks

First record from Denmark. Like the other two species of *Herpomyces*, the Danish material comes from dry collections and the specimens are not in optimal condition, although absolutely recognizable (Fig. 1B).

Herpomyces stylopygae Speg.
MB#232081
Fig. 1C

Anales del Museo Nacional de Historia Natural de Buenos Aires 29: 551 (Spegazzini 1917). – **Type**: [Not designated] [Ind. loc.] "Común sobre las antenas de la cucaracha casera, *Periplaneta* (*stylopyga*) *orientalis* en Montevideo, May. 1914, en Buenos Aires y La Plata, por los años 1914–16"; LPS.

Diagnostic features

Shield bilobate and strongly asymmetric, the basal area ± darkened (Fig. 1C, sh). Perithecial neck bent, terminating in a pointed, subacute lateral tip, and a distal acute tooth-like outgrowth (Fig. 1C, arrow). [Detailed descriptions: Tavares 1966; De Kesel 2001; Santamaria 2003]

Distribution and hosts

Often confused with *H. periplanetae* in old literature. This species grows on *Blatta orientalis* (Blattodea, Blattidae) and has been reported (sometimes as *H. periplanetae*) from **Europe** (Spain, Belgium, Poland, Hungary, France), **Africa** (Algeria), **America** (USA, Bermuda Islands?, Brazil?, Panama, Mexico, Uruguay, Argentina), **Asia** (China, India, Korea) (Santamaria *et al.* 1991; Majewski 2008; Haelewaters *et al.* 2015a). Recently reported from Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Blatta orientalis* Linnaeus, 1758 (Blattodea Blattidae)

DENMARK – **Østjylland (EJ)** • Hadsund; 56°42.900′ N, 10°7.020′ E; NH68; 9 Aug. 1936; *S. G. Larson Dry0023*; K. Th. Holst det.; ZMUC C-F-124037. – **Fyn (F)** • Dalumgård ved Odense; 55°21.804′ N, 10°22.448′ E; NG83; *S. G. Larson Dry0024*; K. Th. Holst det.; ZMUC C-F-124038. – **Nordøstsjælland (NEZ)** • København, Gothersgade 5; 55°40.889′ N, 12°35.084′ E; UB47; 1 Sep. 1973; *I. Casperson Dry0025*; ZMUC C-F-124039.

Remarks

First record from Denmark. Richards & Smith (1955a, 1955b) and Tavares (1966) studied this species intensively.

Order Laboulbeniales Lindau
Family Ceratomycetaceae S.Colla
Subfamily Ceratomycetoideae s. str.
Tribe Ceratomyceteae Thaxt.
Subtribe Helodiomycetinae I.I.Tav.

Genus ***Helodiomyces*** F.Picard
MB#2266

Bulletin de la Société Mycologique de France 29: 557 (Picard 1913). – Type species: *H. elegans* F.Picard (by monotypy).

Brief description

Monoecious. Receptacle multicelled and uniseriate. Primary appendage subtended by cell VII (Fig. 2A, VII). Perihecium solitary with a base consisting of two parallel cells (VI and VI') (Fig. 2A, VI, VI'). Outer wall of perithecium consisting of four vertical rows of many cells. An extra, short row of cells on the posterior side of the perithecium. Perithecial ostiole surrounded by four slender and rather long ligules (Fig. 2C, li).

Remarks

Monotypic. Seems not to be closely related with any other genus of Laboulbeniales.

Helodiomyces elegans F.Picard
MB#239522
Fig. 2A–C

Bulletin de la Société Mycologique de France 29: 558 (Picard 1913). – **Type**: [Not designated] [Ind. loc.] [Type lost!] "Sur le dessous et les côtés du corps de *Parnus prolifericornis* F., ruisseau du

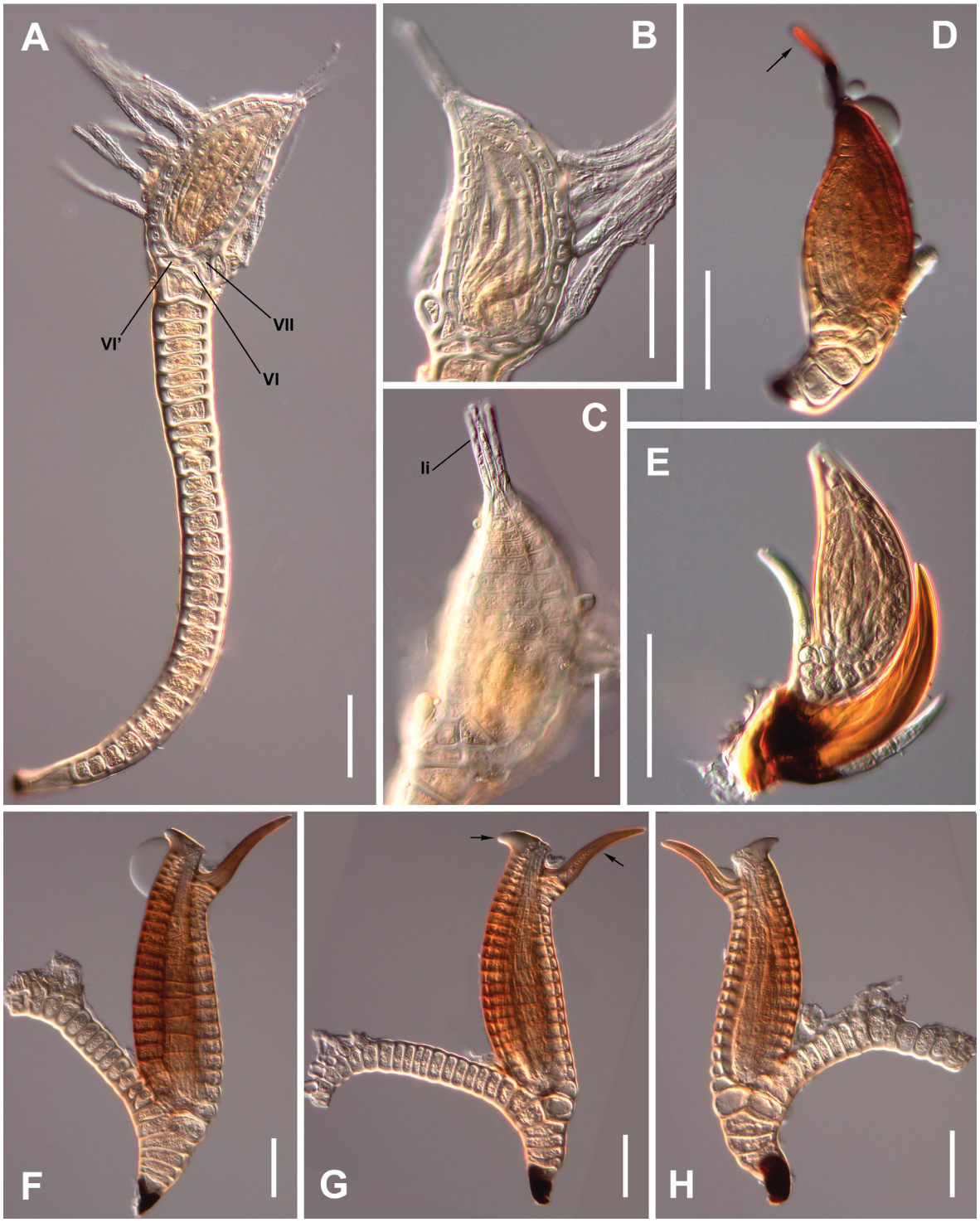

Fig. 2. A–**C**. *Helodiomyces elegans* F.Picard. **A**. Mature thallus with labelling of cells VI, VI' and VII. **B**–**C**. Details of perithecium, including ligules (li) in C. – **D**. *Autoicomyces aquatilis* (F.Picard) I.I.Tav.; mature thallus showing the perithecial outgrowth (arrow). – **E**. *Autoicomyces humilis* (Thaxt.) Thaxt.; mature thallus at the base of a host claw, and a sporeling on the right. – **F**–**H**. *Ceratomyces pyrenaeus* Santam.; mature thalli showing labelled perithecial excrescences (arrows in G). Scale bars: 50 µm. Photographs from slides ZMUC C-F-122583 (A–C), ZMUC C-F-122567 (D), ZMUC C-F-122566 (E), ZMUC C-F-123551 (F), and ZMUC C-F-123550 (G–H).

Verdanson, derrière l'École d'Agriculture, Montpellier (Hérault); et sur *Parnus hygrobates* Kies., mare de Gramont, environs de Montpellier (commune de Castelnau)". [France]

Diagnostic features

See the genus description. [Detailed descriptions: Majewski 1994b; Santamaria 2003; De Kesel & Haelewaters 2014b]

Distribution and hosts

Common on *Dryops* Olivier, 1791 (= *Parnus* Fabricius, 1792) (Col. Dryopidae) from **Europe** (France, Poland, United Kingdom, Germany, Italy, Finland, Hungary, Spain, Andorra) and **Africa** (Algeria) (Majewski 2008). Recently reported from Czech Republic (Rossi *et al.* 2010), Sweden (Huggert 2010), the Netherlands (Haelewaters *et al.* 2012), and Belgium (De Kesel & Haelewaters 2014b).

Collections examined from Denmark

On *Dryops anglicanus* Edwards, 1909 (Col. Dryopidae)
DENMARK – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 26 Apr. 2020; *JP 1606*; JP det.; ZMUC C-F-124360.

On *Dryops auriculatus* (Geoffroy, 1785) (Col. Dryopidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.301′ N, 12°16.244′ E; UB20; 27 Apr. 2013; *JP 180*; JP det.; ZMUC C-F-122659. – **Nordøstjylland (NEJ)** • Gammel Enge i Tofte Skov; 56°49.175′ N, 10°13.763′ E; NH79; 24 May 2005; *JP 108*; JP det.; ZMUC C-F-122585. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *JP 107*; JP det.; ZMUC C-F-122583.

On *Dryops griseus* (Erichson, 1847) (Col. Dryopidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.301′ N, 12°16.244′ E; UB20; 27 Apr. 2013; *JP 179*; JP det.; ZMUC C-F-122658.

On *Dryops luridus* (Erichson, 1847) (Col. Dryopidae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 14 Feb. 2019; *JP 1352*; JP det.; ZMUC C-F-123891.

On *Dryops similaris* Bollow, 1936 (Col. Dryopidae)
DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 15 Apr. 2018; *JP 1035*; JP det.; ZMUC C-F-123547 • Asserbo Plantage; 56°1.984′ N, 12°0.817′ E; UC11; 28 Apr. 2019; *JP 1454*; JP det.; ZMUC C-F-124005.

Remarks

First record from Denmark. Only the length and number of receptacular cells is variable depending on where the thalli grow on host body.

Subtribe Ceratomycetinae s. str.

Genus ***Autoicomyces*** Thaxt.
MB#466

Memoirs of the American Academy of Arts and Sciences 13: 434 (Thaxter 1908). – Type species: *A. acuminatus* Thaxt.

Brief description

Monoecious. Receptacle consisting of 2–4 superposed cells below cells VI and VI'. Secondary stalk cell (VII) intercalary in the main axis of thallus. Perithecial outer wall consisting of four vertical rows, each with many cells of similar length.

Remarks

The genus consists of 27 species, of which five in Europe, two in Denmark. The most recently described species is *A. chinensis* (Shen & Ye 2006). The subtribe Ceratomycetinae includes seven genera of which, at the very least, *Autoicomyces*, *Ceratomyces*, *Eusynaptomyces* and *Rhynchophoromyces* are hardly separable by morphological characteristics (Santamaria 2003).

Key to the Danish species

1. Perithecium bearing a horn-like outgrowth ..... ***A. aquatilis*** (F.Picard) I.I.Tav.
– Perithecium without a horn-like outgrowth ..... ***A. humilis*** (Thaxt.) Thaxt.

Autoicomyces aquatilis (F.Picard) I.I.Tav.
MB#105077
Fig. 2D

Mycologia Memoirs 9: 148 (Tavares 1985). – **Basionym**: *Ceratomyces aquatilis* F.Picard, *Bulletin de la Société Mycologique de France* 29: 560 (Picard 1913) [MB#225059]. – **Type**: [Type lost!] "Sur les segments ventraux de l'abdomen d'*Hydrochus carinatus* Germ., Trappes (Seine-et-Oise), dans les canaux attenants à l'étang de St-Quentin". [France]

Autoicomyces melanocerus Speg. (Spegazzini 1915b: 41) [MB#173533]. – *Ceratomyces melanocerus* (Speg.) Thaxt. (Thaxter 1931: 350) [MB#270804]

Diagnostic features

Thallus variably darkened. Receptacle three-celled. The uppermost wall cell of the anterior row develops a subapical horn-like, unicellular, variably curved, almost blackish brown outgrowth (Fig. 2D, arrow). [Detailed descriptions: Scheloske 1969; Majewski 1994b; Santamaria 2003]

Distribution and hosts

On *Hydrochus* Leach, 1817 (Col. Hydrochidae) from **Europe**: France, Germany, Hungary, Italy (as *A. melanocerus*), Poland, Spain (Majewski 2008) and Sweden (Huggert 2010); also in Cuba and USA (Thaxter 1931).

Collections examined from Denmark

On *Hydrochus crenatus* (Fabricius, 1792) (Col. Hydrochidae)

DENMARK – **Nordøstsjælland (NEZ)** • Heatherhill; 56°5.240′ N, 12°8.611′ E; UC21; 22 May 2016; *JP 91*; JP det.; ZMUC C-F-122567.

Remarks

First record from Denmark. Its presence in Denmark was expected given the presence of the species in neighbouring countries, such as Sweden and Germany.

Autoicomyces humilis (Thaxt.) Thaxt.
[not registered in MycoBank]
Fig. 2E

Memoirs of the American Academy of Arts and Sciences 16: 359 (Thaxter 1931). – **Basionym**: *Ceratomyces humilis* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 29: 94 (Thaxter 1894) [MB#227550]. – **Type**: "On legs and at the edges of the elytra of *Berosus striatus* Say. Kittery Point, Maine"; FH. [USA]

Autoicomyces anaceros Speg. (Spegazzini 1915b: 38) [MB#159363]

Diagnostic features

Thallus uniformly hyaline to pale yellow. Receptacle two-celled. Perithecium with a rather well-distinguished neck and a truncate apex. [Detailed descriptions: Sugiyama & Hayama 1981]

Distribution and hosts

Grows between the claws of its hosts. Described from *Berosus* Leach, 1817 (Col. Hydrophilidae) from USA, it has been reported on the same host genus from Sumatra and Philippines (Thaxter 1931), Taiwan (Sugiyama & Hayama 1981) and China (Shen & Ye 2006). Also on *Regimbartia* Zaitzev, 1908 (Col. Hydrophilidae) from Sumatra, China (Thaxter 1931), and on *Hydrochus* (Col. Hydrochidae) from Cuba and USA (Thaxter 1931). *Autoicomyces anaceros*, accepted as a synonym, was described on *Laccobius* Erichson, 1837 from Italy, but this may be a growth form of *A. crassus* Speg. (Santamaria 2003: fig. 11e–h). Santamaria (2003) reported it from Spain as a growth form of *A. aquatilis*.

Collections examined from Denmark

On *Hydrochus crenatus* (Fabricius, 1792) (Col. Hydrochidae)
DENMARK – **Nordøstsjælland (NEZ)** • Heatherhill; 56°5.240′ N, 12°8.611′ E; UC21; 22 May 2016; *JP 91*; JP det.; ZMUC C-F-122566.

Remarks

First record from Denmark. The status of this taxon as a separate species has been the subject of debate. According to some authors it should be considered a growth form found between the claws of male hosts, therefore related to sex-host specificity and mating behaviour. However, in our sample the same individual host bears the normal 'horned' form known as *A. aquatilis* on the elytra and the reduced form known as *A. humilis* between the claws. Moreover, Thaxter (1894) described this species growing on legs and elytral margins, which is contradictory with the 'concept' of growth form.

Genus ***Ceratomyces*** Thaxt.
MB#891

Proceedings of the American Academy of Arts and Sciences 27: 34 (Thaxter 1892). – Type species: *C. mirabilis* Thaxt.

Brief description

Monoecious. Primary or lower receptacle (below cells VI and VI') consisting of 2–4(–5) superposed cells. Secondary stalk cell (VII) intercalary in the main axis of the thallus. Perithecial outer wall consisting of four vertical rows, each with many cells of similar length; two vertical rows of flattened cells alternating with two vertical rows of narrow elongated cells. Simple horns on perithecium.

Remarks

The genus consists of 21 species. The most recently described species is *C. pyrenaeus* (Santamaria 1999), which is the only one known in Europe.

Ceratomyces pyrenaeus Santam.
MB#460468
Fig. 2F–H

Nova Hedwigia 68 (3–4): 352 (Santamaria 1999). – **Type**: SPAIN • "Lleida (Lérida): Vielha e Mijaran; Pleta de Mulleres, Boca Sud del Túnel de Vielha, below the margins of pronotum and elytra of *Hydrobius fuscipes* (Linné) (Coleoptera, Hydrophilidae, Hydrophilinae), 17.V.1986, leg. C. Hernando, SS1805c (Holotype)"; BCB.

Diagnostic features

Perithecial apex bearing two horn-like excrescences on opposite sides (Fig. 2G, arrows): one on the ventral side which is conspicuous, rigid, sigmoidal, and the other on the dorsal side which is broadened at the base and rounded at the apex. Both horns are formed by distal outer wall cells.

Distribution and hosts

Until now, the species was only known from the type. Other than the Danish material newly reported here, it is worth to mention its hitherto unreported presence in USA, according to a slide sent by Dr Richard Benjamin to SS many years ago which was labelled: "on anterior inflexed margins of elytra of *Hydrobius fuscipes* (L.), Wyoming, Albany Co, Pole Mountain, Wildlife Refuge, 5 May 1949, G.K.Todd coll. RKB1755" (slide is kept in BCB with the number SSE·355).

Collections examined from Denmark

On *Hydrobius rottenbergii* Gerhardt, 1872 (Col. Hydrophilidae)
DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 15 Apr. 2018; *JP 1036*; JP det.; ZMUC C-F-123550, C-F-123551.

Remarks

First record from Denmark. The distribution of this species is very patchy, probably due to lack of research. The host was previously considered as a subspecies of *Hydrobius fuscipes* (Linnaeus, 1758).

Genus ***Eusynaptomyces*** Thaxt.
MB#1947

Memoirs of the American Academy of Arts and Sciences 16: 340 (Thaxter 1931). – Type species: *E. borealis* Thaxt.

Brief description

Monoecious. As *Ceratomyces*, but differing from it by the preapical simple or bifurcate horns on the perithecium and by the multicellular lower receptacle consisting of more than five cells.

Remarks

The genus consists of six species on Hydrophilidae (Coleoptera), of which four in Europe, two in Denmark. The most recently described species is *E. cornutus* (Santamaria 2006).

Key to the Danish species (partially following Majewski 1994b)

1. Receptacle three- to five-celled. Between the claws of anterior tarsi in *Enochrus* Thomson, 1859 (Col. Hydrophilidae) ..... ***E. enochri*** Scheloske
– Receptacle consisting of more than 10 cells. On other host locations. On *Hydrobius* Leach, 1815 (Col. Hydrophilidae) ..... ***E. hydrobii*** (T.Majewski) I.I.Tav.

Eusynaptomyces enochri Scheloske
MB#330757
Fig. 3A

Parasitologische Schriftenreihe 19: 110 (Scheloske 1969). – **Type**: "Auf den Vorderbeinklauen der Männchen und der Unterseite des Halsschildvorderrandes der Weibchen von *Enochrus affinis*, *E. coarctatus*. Eine Form. die etwas von der auf den Klauen lebenden abweicht, fand ich an den entsprechenden Körperstellen bei *E. testaceus* (Col. Hydrophilidae). Die Wirte stammen aus einem Weiher bei Dechsendorf/Erlangen. Holotypus Abb. 20". [Germany]

Diagnostic features

[Reduced form] Receptacle consisting of up to five cells. Appendage basal cell (above cell VII) extending into one lateral outgrowth (Fig. 3A, arrow). [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

On *Enochrus* (Col. Hydrophilidae) from Germany (type), Poland (Majewski 1990b), Portugal (Santamaria 1999), and Belarus (Majewski 2008).

Collections examined from Denmark

On *Enochrus coarctatus* (Gredler, 1863) (Col. Hydrophilidae)
DENMARK – **Nordøstsjælland (NEZ)** • Heatherhill; 56°5.240′ N, 12°8.611′ E; UC21; 22 May 2016; *JP 94*; JP det.; ZMUC C-F-122569.

Remarks

First record from Denmark. According to Majewski (1994b), thalli of this species are differentiated into two forms which are seemingly related with the host surface points undergoing contact through mating behaviour (Scheloske 1969); the form B between the claws of tarsi of both anterior legs in male insects, and the form A or normal form under the right anterior margin of female pronotum. We have only found the claw form that is regarded to be more frequent (Majewski 2008). Such reduced forms (see also *Autoicomyces humilis*) pose true taxonomical problems. Moreover, the monotypic genus *Phurmomyces* has been questioned as a probably similar growth form of *Ceratomyces* (Tavares 1985).

Eusynaptomyces hydrobii (T.Majewski) I.I.Tav.
MB#105312
Fig. 3B–D

Mycologia Memoirs 9: 220 (Tavares 1985). – **Basionym**: *Rhynchophoromyces hydrobii* T.Majewski, *Acta Mycologica* 7(2): 274 (Majewski 1972a) [MB#322804]. – **Type**: "On metasternum of *Hydrobius fuscipes* L. (Col., Hydrophilidae): Lomianki Dolne, Nowy Dwor Maz. county, small water body south of village, 24.4.1970, leg. T. Majewski"; KRAM. (fig. 7a – holotype,…) (TM 245, Majewski, 2008: 69). [Poland]

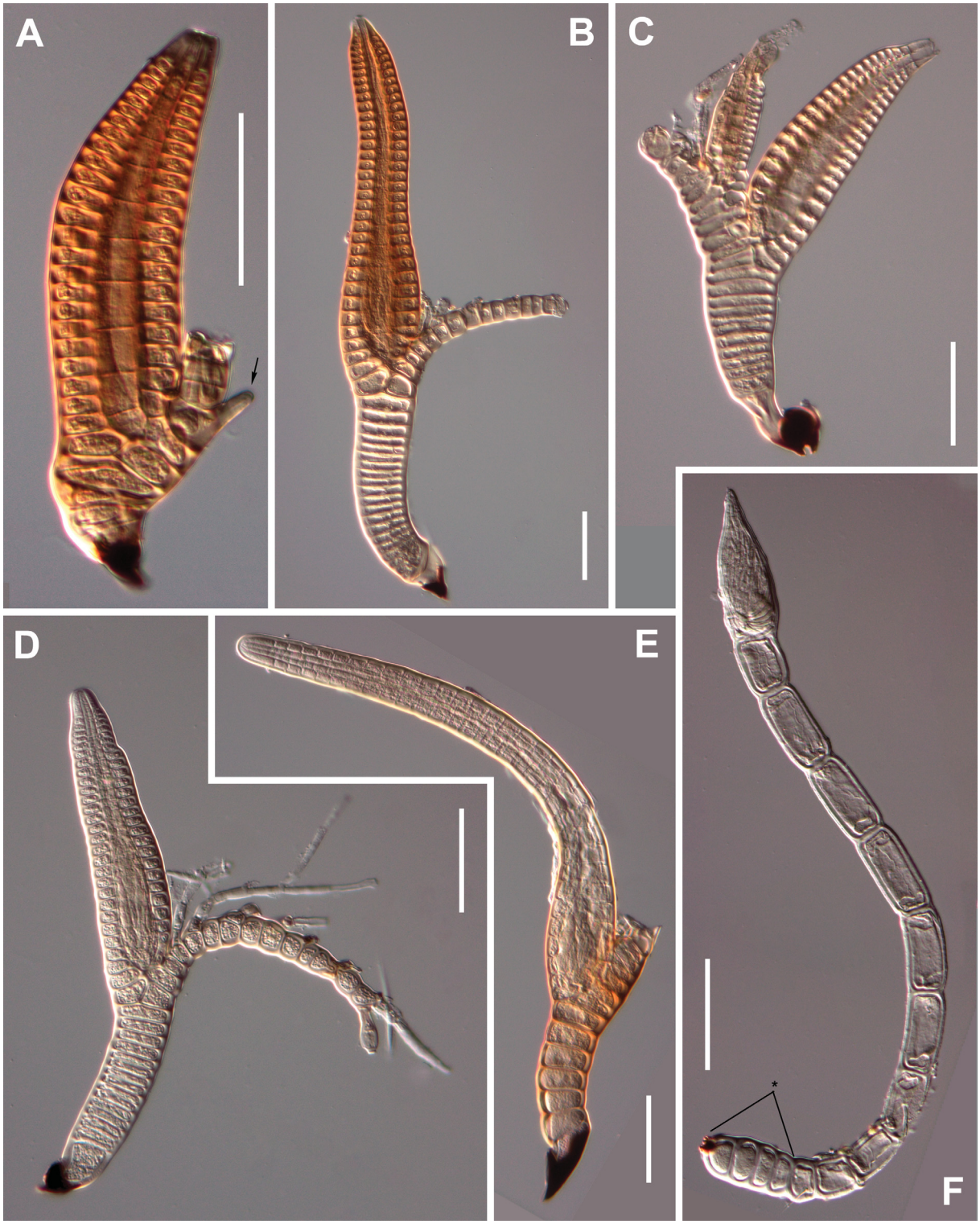

Fig. 3. A. *Eusynaptomyces enochri* Scheloske; reduced form showing the lateral outgrowth (arrow). – **B**–**D**. *Eusynaptomyces hydrobii* (T.Majewski) I.I.Tav.; mature thalli. – **E**. *Rhynchophoromyces anacaenae* Scheloske; mature thallus with broken appendage. – **F**. *Thripomyces italicus* Speg.; mature thallus showing the characteristic broadened cells at the base of the receptacle (*). Scale bars: 50 µm. Photographs from slides ZMUC C-F-122569 (A), ZMUC C-F-123552 (B–D), ZMUC C-F-123749 (E), and ZMUC C-F-122983 (F).

Diagnostic features

Receptacle very variable in length and number of cells, consisting of 11–80 superposed cells. Perithecium nearly straight to ± arcuate, with an almost undistinguished venter, tapering distally to an undifferentiated, rounded apex. [Detailed descriptions: Sarna & Milewska 1978; Majewski 1994b]

Distribution and hosts

Only known from Poland on *Hydrobius* and *Hydrophilus* Geoffroy, 1762 (Col. Hydrophilidae).

Collections examined from Denmark

On *Hydrobius rottenbergii* Gerhardt, 1874 (Col. Hydrophilidae)

DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 15 Apr. 2018; *JP 1036*; JP det.; ZMUC C-F-123552.

Remarks

First record from Denmark. Second world record, the first outside the type country. The separation of this species from reduced forms of *Eusynaptomyces benjaminii* Scheloske is difficult because such thalli lack the horn on the perithecial apex, which is not the case for the Danish thalli. The host was previously considered as a subspecies of *Hydrobius fuscipes*. A photo of this species is given here for the first time.

Genus ***Rhynchophoromyces*** Thaxt.

MB#4714

Memoirs of the American Academy of Arts and Sciences 16: 60 (Thaxter 1931). – Type species: *R. rostratus* Thaxt.

Brief description

Monoecious. As *Autoicomyces*, but differing from it by the very elongate and slender perithecial neck.

Remarks

The genus consists of eight species occurring on Hydrophilidae beetles. Two in Europe, one in Denmark. The last described species was *R. helophori* by Santamaria (1999).

Rhynchophoromyces anacaenae Scheloske

MB#338590

Fig. 3E

Parasitologische Schriftenreihe 19: 143 (Scheloske 1969). – **Type**: "Auf der gesamten Körperunterseite, der Basis der Extremitäten und den Epipleuren von *Anacaena limbata* (Col., Hydrophilidae), wobei ♂♂ und ♀♀ gleicher maβen befallen wurden. Die parasitierten Käfer erbeutete ich in Laubstreu aus Bruchwäldern bei Schwand/Nürnberg und Erlangen sowie in Weihern bei Dechsendorf/Erlangen. Deutschland. Holotypus Abb. 41". [Germany]

Diagnostic features

Lower receptacle consisting of 6–14 cells. Perithecium with a long, strongly bent neck, containing about 30 outer wall cells. [Detailed descriptions: Santamaria 1989; Majewski 1994b; De Kesel & Werbrouck 2008]

Distribution and hosts

Occurs on species of the genus *Anacaena* Thomson, 1859 (Col. Hydrophilidae); also reported on *Dryops* (Col. Dryopidae) by Balazuc (1974f), probably as an example of host switch. Only known in **Europe** from Spain, France, Germany, Italy, Poland (Majewski 2008), Belgium (De Kesel & Werbrouck 2008), Denmark (Høier 2009), Sweden (Huggert 2010), and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Anacaena limbata* (Fabricius, 1792) (Col. Hydrophilidae)

DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 14 Feb. 2019; *JP 1351*; JP det.; ZMUC C-F-123890. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1135*; JP det.; ZMUC C-F-123659. – **Nordøstsjælland (NEZ)** • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1222*; JP det.; ZMUC C-F-123749. – **Sydjylland (SJ)** • Tange ved Ribe; 55°19.340′ N, 8°48.647′ E; MG83; 8 Mar. 2020; *JP 1611*; JP det.; ZMUC C-F-124363.

Remarks

Sarna & Milewska (1978) described *R. anacaenae* subsp. *nasutellus* which is regarded as a synonym of the nominal subspecies.

Tribe Drepanomyceteae I.I.Tav.

Genus ***Thripomyces*** Speg.
MB#5456

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 71 (Spegazzini 1915b). – Type species: *T. italicus* Speg.

Brief description

Monoecious or dioecious? Receptacle uniseriate, consisting of numerous superposed cells bearing a terminal perithecium; 4–6 basal cells of the receptacle broad and flattened.

Remarks

With only two European species, one in Denmark. This genus included only the type species *T. italicus* until Majewski (1990c) described a second species from Poland, *T. tessinensis*, which is distinguished from the type by the presence of a lateral darkened foot, a shorter thallus (up to 200 µm, Majewski 1994b), and a stout, apically blunt, almost neckless perithecium.

This is a weird genus with an unclear systematic position. Tavares (1985) placed it in the Drepanomyceteae after studying the type collection of *T. italicus*. The presence of antheridia is not yet well understood and has led to the suggestion that the genus is perhaps dioecious, a feature which is supported by the presence of reduced, maybe male thalli joined by the base with normal mature perithecia-bearing thalli (Santamaria 1993a).

Thripomyces italicus Speg.
MB#235252
Fig. 3F

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 72 (Spegazzini 1915b). – **Type**: "Frecuente sobre el pecho entre las bases de las patas de una especie indeterminada de *Hydraena*, común en las zanjas cerca de Conegliano. Julio y Nov. 1913"; LPS. [Italy]

Diagnostic features

Receptacle base consisting of 4–6 short, flat and broad cells (Fig. 3F, *). Thallus length up to 640 µm. Perithecium with a slender and acute apex. [Detailed description: Thaxter 1931]

Distribution and hosts

Only known from the type in Italy and from Spain (Santamaria 1993a), infecting *Hydraena* Kugelann, 1794 (Col. Hydraenidae).

Collections examined from Denmark

On *Hydraena riparia* Kugelann, 1794 (Col. Hydraenidae)

DENMARK – **Sydsjælland (SZ) •** Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 499*; JP det.; ZMUC C-F-122983.

Remarks

First record from Denmark. Probably this species is more common than suggested by the scarce number of available records. Perhaps overlooked because of the unusual shape of the thalli which look like tissue strands, an aspect very infrequent in Laboulbeniales.

Family Euceratomycetaceae I.I.Tav.

Genus ***Euzodiomyces*** Thaxt.
MB#1953

Proceedings of the American Academy of Arts and Sciences 35: 449 (Thaxter 1900). – Type species: *E. lathrobii* Thaxt. (by monotypy)

Brief description

Monoecious. Characterized by the massive and multiseriate receptacle which bears unilateral series of fertile and sterile appendages and a variable number of perithecia. Outer wall of perithecium consisting of four vertical rows with 7–10 cells each, some of them bulging outward.

Remarks

Monotypic. Benjamin & Shanor (1951) completed a study on the morphology and development of the unique species in this genus. Tavares (1985) added information on the perithecial outer wall ontogeny.

Euzodiomyces lathrobii Thaxt.
MB#210799
Fig. 4A–D

Proceedings of the American Academy of Arts and Sciences 35: 449 (Thaxter 1900). – **Type**: [Not designated] [Ind. loc.] "On *Lathrobium punctatum* Zett., British Museum No. 442, Notting Hill, England; on *L. multipunctatum* Grev., British Museum No. 429, Europe; on *L. filiforme* Grav. British Museum No. 443, Notting Hill, England"; FH. [According to Majewski, 1994: 51, the type is on *Lathrobium zetterstedti* Rye]

Euzodiomyces capillarius Cépède & F.Picard (Cépède & Picard 1907: 782) [MB#203735]

Diagnostic features

See genus description. [Detailed descriptions: Thaxter 1908; Benjamin & Shanor 1951; Sugiyama 1973; Majewski 1994b; Santamaria 2003]

Distribution and hosts

Usually found on species of *Lathrobium* and *Lobrathium* (Col. Staphylinidae Paederinae), less commonly on other staphylinids like *Hom(a)eotarsus* Hochhuth, 1851 (Benjamin & Shanor 1951), *Xantholinus* Dejean, 1821 (Scheloske 1969, probably *Megalinus* Mulsant & Rey, 1877 according to Tavares 1985), *Pseudolathra* Casey, 1905 (Rossi 1975); maybe fortuitously on Col. Carabidae like *Patrobus* Dejean, 1821 (Scheloske 1969) and *Pterostichus* Bonelli, 1810 (De Kesel & Gerstmans 2011). Widespread in **Europe** (United Kingdom, France, Switzerland, the Netherlands, Belgium, Germany, former Yugoslavia, Poland, Italy, Finland, Hungary, Spain, Latvia), **Africa** (Algeria, Morocco), **Asia** (Japan), North and South **America** (USA, Bolivia) (Majewski 2008). Recently reported also from Czech Republic (Rossi *et al.* 2010), Sweden (Huggert 2010), Ecuador (Bernardi *et al.* 2014), Greece (Goldmann & Weir 2018), and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Lathrobium brunnipes* (Fabricius, 1792) (Col. Staphylinidae Paederinae)
DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14 45.260′ E; VB81; 23 Jun. 2018; *JP 1156*; JP det.; ZMUC C-F-123681. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 648*; JP det.; ZMUC C-F-123136. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 7*; JP det.; ZMUC C-F-122479 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1243*; JP det.; ZMUC C-F-123771. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1380*; JP det.; ZMUC C-F-123922 • Rådmandshave i Næstved; 55°14.426′ N, 11°45.240′ E; PG73; 1 Sep. 2019; *JP 1481*; A.K. Hansen det.; ZMUC C-F-124066.

On *Lathrobium elongatum* (Linnaeus, 1767) (Col. Staphylinidae Paederinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 649*; JP det.; ZMUC C-F-123138 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; JP 1333; JP det.; ZMUC C-F-123872. – **Nordøstsjælland (NEZ)** • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 272*; JP det.; ZMUC C-F-122751 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 8*; JP det.; ZMUC C-F-122480.

On *Lathrobium geminum* Kraatz, 1857 (Col. Staphylinidae Paederinae)
DENMARK – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 258*; JP det.; ZMUC C-F-122738. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1381*; JP det.; ZMUC C-F-123923.

On *Lathrobium impressum* Heer, 1841 (Col. Staphylinidae Paederinae)
DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14 45.096′ E; VB80; 25 Apr. 2014; *JP 503*; JP det.; ZMUC C-F-122987. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 650*; JP det.; ZMUC C-F-123139.

On *Lathrobium lineatocolle* Scriba, 1859 (Col. Staphylinidae Paederinae)
DENMARK – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1382*; JP det.; ZMUC C-F-123924.

On *Lathrobium longulum* Gravenhorst, 1802 (Col. Staphylinidae Paederinae)
DENMARK – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 559*; JP det.; ZMUC C-F-123045 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 766*; JP det.; ZMUC C-F-123260. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1359*; JP det.; ZMUC C-F-123897 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 9 Nov. 2019; *JP 1543*; JP det.; ZMUC C-F-124303 • Østerskov ved Langebæk; 54°59.331′ N, 12°6.357′ E; UA19; 27 Mar. 2018; *JP 1019*; JP det.; ZMUC C-F-123526 • ibid.; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1299*; JP det.; ZMUC C-F-123832.

Remarks

First record from Denmark. Very variable in receptacle length and width, as well as in the number of appendages and perithecia, from one perithecium on narrow long (Fig. 4A), or narrow short (Fig. 4B) receptacles, to large and broad thalli bearing numerous perithecia (Fig. 4C). There is no relation between these thallus shapes and different species of *Lathrobium*, although at least part of the variation seems to be geographical. Further studies with more modern integrative taxonomical techniques should be carried out to reveal if there is more than one species in the genus. Antheridia simple, grouped by 2 on a short simple branchlet supported by cell VII as is seen in Fig. 4D (an, VII).

Family Laboulbeniaceae Peyr.
Subfamily Zodiomycetoideae (Thaxt.) I.I.Tav.

Genus ***Zodiomyces*** Thaxt.
MB#5872

Proceedings of the American Academy of Arts and Sciences 25: 263 (Thaxter 1891). – Type species: *Z. vorticellarius* Thaxt.

Brief description

Monoecious. The large to very large pseudoparenchymatous receptacle unmistakably defines this genus, along with other features related to perithecial morphology (Santamaria 2004).

Remarks

The genus consists of five species, of which two in Europe, one in Denmark. The most recently described species is *Z. vermiformis* (Das *et al.* 2018). *Zodiomyces* was an isolated genus in the Zodiomycetoideae (Tavares 1985) until Santamaria (2004) redefined its status when two new related genera were described.

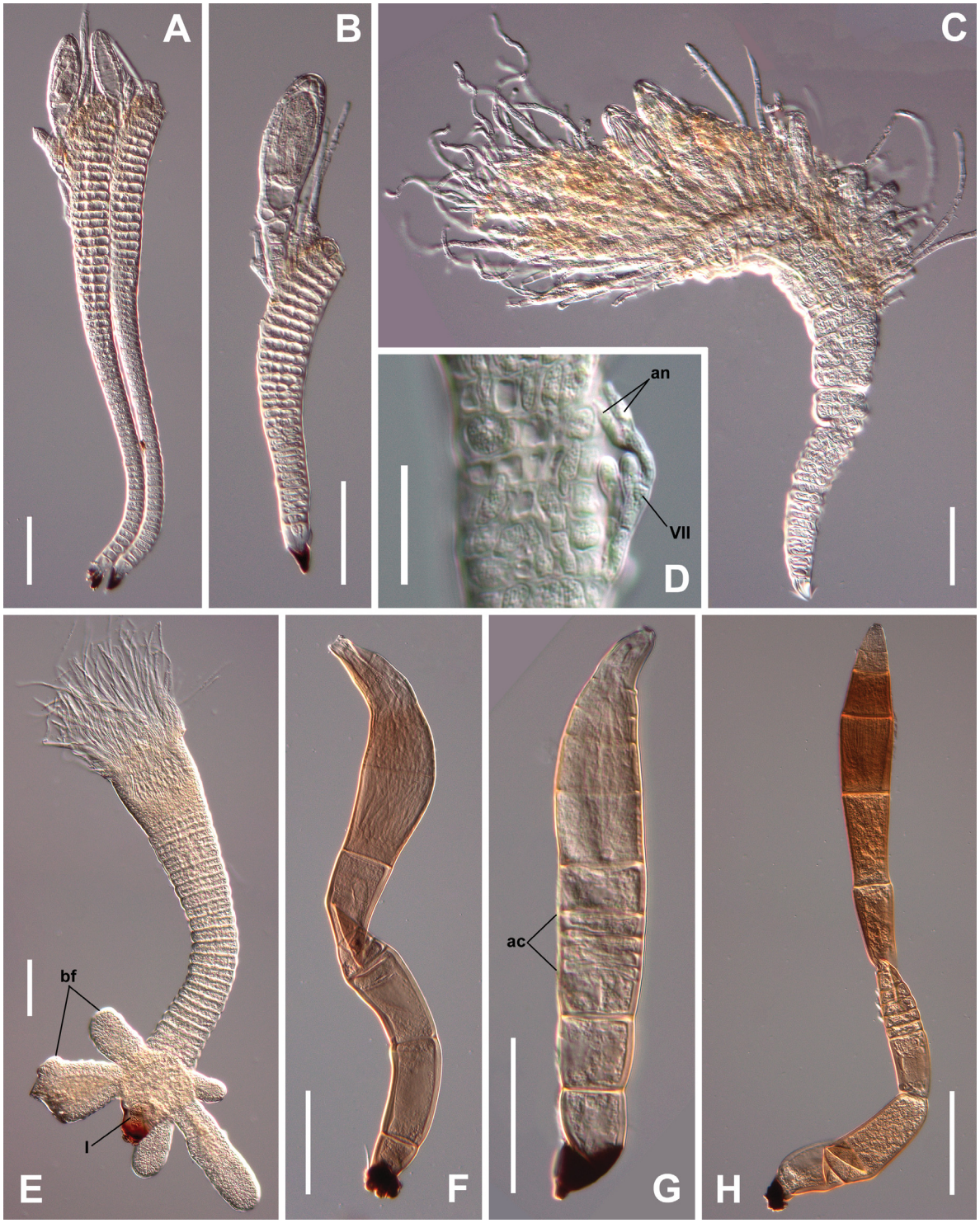

Fig. 4. A–**D**. *Euzodiomyces lathrobii* Thaxt. **A**–**B**. Reduced forms. **C**. Typical form. **D**. Labelling of a secondary axis, with antheridia (an) and perithecial initial with cell VII. – **E**. *Zodiomyces vorticellarius* Thaxt.; with labelled cell I and buffer projections (bf). – **F**. *Coreomyces arcuatus* Thaxt.; mature thallus. – **G**. *Coreomyces corixae* Thaxt.; mature thallus showing the appendiculate cells (ac). – **H**. *Coreomyces macropus* Thaxt.; mature thallus. Scale bars: A–C, E–H = 50 µm; D = 25 µm. Photographs from slides ZMUC C-F-123138 (A–B), ZMUC C-F-124066 (C), ZMUC C-F-122479 (D), ZMUC C-F-122570 (E), ZMUC C-F-124285 (F), ZMUC C-F-123723 (G), and ZMUC C-F-123722 (H).

Zodiomyces vorticellarius Thaxt.
MB#214003
Fig. 4E

Proceedings of the American Academy of Arts and Sciences 25: 263 (Thaxter 1891, as *vorticellaria*). – **Type**: USA • "Connecticut: West Haven, on *Hydrocombus lacustris* LeConte, May 1890, R. Thaxter, FH7117 [Holotype, see Santamaria 2004]"; FH.

Diagnostic features

Base of receptacle consisting only of an undivided basal cell (Fig. 4E, I). With buffer projections lateral to receptacle (Fig. 4E, bf). Perithecia bearing four thin, ligula-like protuberances. [Detailed descriptions: Thaxter 1896; Majewski 1994b]

Distribution and hosts

Hosts belong to Col. Hydrophilidae, usually *Helochares* Mulsant, 1844 in Europe, but on other continents also *Cymbiodyta* Bedel, 1881, *Hydrobiomorpha* Blackburn, 1888, *Sternolophus* Solier, 1842, and *Enochrus*. This species has been reported from few countries in **Europe**: France, Poland, Germany, Italy and Spain; **America**: USA, Cuba, Trinidad, Venezuela, Mexico, and Argentina; **Africa**: Cameroon; **Asia**: Korea (Santamaria 2004). Other records after are from Greece (Castaldo *et al.* 2004), Czech Republic (Rossi & Máca 2006), Belarus (Majewski 2008), Sweden (Huggert 2010), the Netherlands (Haelewaters *et al.* 2012), Turkey (Rossi 2016), United Kingdom (Bratton 2018), Bulgaria (Rossi *et al.* 2019a), and Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Helochares obscurus* (Müller, 1776) (Col. Hydrophilidae)
DENMARK – **Nordøstsjælland (NEZ)** • Heatherhill; 56°5.240′ N, 12°8.611′ E; UC21; 22 May 2016; *JP 95*; JP det.; ZMUC C-F-122570. – **Nordvestsjælland (NWZ)** • Klintebjerg ved Klint; 55°57.294′ N, 11°34.169′ E; PH60; 1 Apr. 2017; *JP 246*; JP det.; ZMUC C-F-122726. – **Sydsjælland (SZ)** • Bårse; 55°7.680′ N, 11°56.494′ E; PG81; 24 Aug. 2019; *JP 1502*; JP det.; ZMUC C-F-124089.

Remarks

First record from Denmark. The huge diversity of hosts and wide distribution of this species make us suspect that several cryptic species are involved.

Subfamily Laboulbenioideae s. str.
Tribe Coreomyceteae Thaxt.

Genus ***Coreomyces*** Thaxt.
MB#1243

Proceedings of the American Academy of Arts and Sciences 38: 56 (Thaxter 1902). – Type species: *C. corixae* Thaxt.

Paracoreomyces R.A.Poisson, *Compte rendu hebdomadaire des Sciences de l'Académie des sciences, Paris* 188: 826 (Poisson 1929) [MB#3697]

Brief description

Monoecious. Receptacle consisting of a series of superposed cells, with a three-celled lower receptacle (cells I, II and III), some flattened cells above (known as the appendiculate cells; Fig. 4G, ac) giving rise

to lateral slender branchlets including intercalary antheridia. Perithecium solitary, found on the top of the receptacle. Primary appendage vanishing with perithecium development.

Remarks

The genus consists of 20 described species, of which five in Europe, three in Denmark. The most recently described species is *C. javanicus* (Lee & Na 2009). This genus has recently been the subject of a Ph.D. dissertation (Sundberg 2018) and two papers generated from it (Sundberg *et al.* 2018a, 2018b) where, with the help of molecular techniques, the reliability of some European species, like those included here, has been demonstrated. Sundberg (2018) mentioned and named two more species which have not yet been formally or validly described at the moment this work was written.

Key to the Danish species (partially following Majewski 1994b and Santamaria 2003)

1. Cells III and VI flattened to isodiametric. Thalli growing on abdominal sternites..... ..... ***C. corixae*** Thaxt.
– Cells III and VI longer than broad..... 2

2. Thalli growing on inferior margin of hemielytra. Perithecium symmetric..... ***C. macropus*** Thaxt.
– Thalli growing on abdominal sternites, in middle part of 5th segment. Perithecium asymmetric .... ***C. arcuatus*** Thaxt.

Coreomyces arcuatus Thaxt.
MB#257238
Fig. 4F

Memoirs of the American Academy of Arts and Sciences 16: 324 (Thaxter 1931). – **Type**: "On the inferior surface of the abdomen near the middle, or slightly to the left, of the tip of *Centrocorixa Kollari* (Fieb.), No. 1751, Mandeville, Jamaica, B. W. I."; FH.

Diagnostic features

Cells I and II 1.5–2 times as long as broad. Terminal cell (III) 2–3 times as long as broad. Perithecium arcuate, laterally bent. [Detailed descriptions: Majewski 1973b, 1994b; De Kesel & Werbrouck 2008]

Distribution and hosts

Reported on Corixidae (Hemiptera) of the genera *Centrocorisa* Lundblad, 1928 (= *Centrocorixa*); *Callicorixa* White, 1873; and *Sigara* Fabricius, 1775 from Jamaica (type), Poland, Bulgaria (Majewski 1973b), and Belgium (De Kesel & Werbrouck 2008).

Collections examined from Denmark

On *Sigara limitata* (Fieber, 1848) (Heteroptera Corixidae)

DENMARK – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1529*; M. Holmen det.; ZMUC C-F-124285.

Remarks

First record from Denmark. Only a single thallus of this species has been found in its typical position on the host body, i.e., the middle part of 5th abdominal sternite (Majewski 1994b).

Coreomyces corixae Thaxt.
MB#183819
Fig. 4G

Proceedings of the American Academy of Arts and Sciences 38: 56 (Thaxter 1902: 56, as *corisae*). – **Type**: "On inferior surface of abdomen of *Corisa Kennicottii* Uhler, Arlington, Mass"; FH. [USA] [this is the type according to Tavares 1985 and the host is *Hesperocorixa kennicotti* (Uhler)]

Coreomyces italicus Speg. (Spegazzini 1918: 321) [MB#192011]

Diagnostic features

Cells I and II 1.5–2 times as long as broad. Terminal cell (III) flattened. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 2003]

Distribution and hosts

This species has been reported on Corixidae (Hemiptera) of the genera *Callicorixa* White, 1873, *Corixa* Geoffroy, 1762 (= *Corisa*), *Cymatia* Flor, 1860, *Hesperocorixa* Kirkaldy, 1908, *Micronecta*? Kirkaldy, 1897 (Lee *et al.* 2008), and *Sigara* from **Europe**: Bulgaria, France, Germany, Hungary, Italy, Poland, Romania, Spain; **America**: Chile, USA; and **Asia**: China, Indonesia, Japan, Taiwan (Majewski 2008). Recently reported from Denmark, Sweden, Turkey (Sundberg 2018), and Slovenia (Rossi & Christian 2020).

Collections examined from Denmark

On *Sigara distincta* (Fieber, 1848). (Heteroptera Corixidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°59.127′ N, 12°31.517′ E; UA49; 12 May 2018; *JP 1198*; M. Holmen det.; ZMUC C-F-123723. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1528*; M. Holmen det.; ZMUC C-F-124283 • ibid.; *JP 1529*; M. Holmen det.; ZMUC C-F-124286 • ibid.; *JP 1530*; M. Holmen det; ZMUC C-F-124288.

Remarks

This species is very common, although according to Majewski (1994b) less frequent than *C. macropus* which very often coexists on the same host.

Coreomyces macropus Thaxt.
MB#270152
Fig. 4H

Memoirs of the American Academy of Arts and Sciences 16: 327 (Thaxter 1931). – **Type**: "On the inferior margin of the left elytron of *Centrocorixa Kollari* (Fieb.), No. 1751, Mandeville, Jamaica (Wight)"; FH.

Diagnostic features

Cell I almost twice longer than broad. Cell II 3–4 times as long as broad. Terminal cell (III) 1.5–2 times as long as broad. [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

On the same hosts as previous species including *Centrocorixa* but excluding *Cymatia* and *Micronecta*. *Coreomyces macropus* grows on the lower outer margin of left hemielytron. It has been reported from

Jamaica, Russia, Romania, Bulgaria, Poland (Majewski 1973b), Spain (Santamaria 1989), Turkey, Denmark, and Sweden (Sundberg 2018).

Collections examined from Denmark

On *Sigara distincta* (Fieber, 1848) (Heteroptera Corixidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°59.127′ N, 12°31.517′ E; UA49; 12 May 2018; *JP 1198*; M. Holmen det.; ZMUC C-F-123722. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; JP 1528; M. Holmen det.; ZMUC C-F-124284.

On *Sigara falleni* (Fieber, 1848) (Heteroptera Corixidae)
DENMARK – **Nordvestjylland (NWJ)** • Thy, Voldum Sø (now Vullum Sø); 57°4.912′ N, 8°47.641′ E; MJ82; 1948–1965; *coll. unknown 1199*; E. W. Kaiser det.; ZMUC C-F-123725.

On *Sigara limitata* (Fieber, 1848) (Heteroptera Corixidae)
DENMARK – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1529*; M. Holmen det.; ZMUC C-F-124287.

On *Sigara scotti* (Douglas & Scott, 1868) (Heteroptera Corixidae)
DENMARK – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1527*; M. Holmen det.; ZMUC C-F-124282.

On *Sigara semistriata* (Fieber, 1848) (Heteroptera Corixidae)
DENMARK – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1530*; M. Holmen det.; ZMUC C-F-124289.

Remarks

No noteworthy variations have been observed.

Tribe Compsomyceteae Thaxt.
Subtribe Compsomycetinae s. str.

Genus ***Compsomyces*** Thaxt.
MB#1200

Proceedings of the American Academy of Arts and Sciences 29: 96 (Thaxter 1894). – Type species: *C. verticillatus* (Thaxt.) Thaxt.

Moschomyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 29: 97 (Thaxter 1894) [MB#3277]

Brief description

Monoecious. Cell II supporting secondary axes and appendages bearing simple sessile antheridia. Perithecia borne on the secondary axes; outer wall with 4–8 unequal cells in each vertical row. Asci with 4 or 8 ascospores.

Remarks

The genus consists of five or six species depending on whether *C. macropoda* is regarded as a separate species or is included among the synonyms of *C. verticillatus* (Santamaria 2003). No new species have been added after Thaxter (1931). Two in Europe, both in Denmark. This genus is remarkable because perithecia are borne on secondary instead of primary receptacle, and because there are species, like

C. verticillatus (Thaxt.) Thaxt. which show 8-spored asci instead of the usual 4-spored asci, a character exclusively shared within the Laboulbeniales with the genus *Euceratomyces* (Tavares 1985). It seems quite logical to think that this genus needs a revision and probably needs to be subdivided. Some characteristics accepted as essential to segregate genera, such as the number of perithecial wall cells is here very different from one species to the other. Indeed, the number of cells in each vertical row of wall cells in perithecium varies from four in *C. lestevae* to 6–8 in *C. verticillatus*.

Key to the Danish species (partially following Santamaria 2003)

1. Perithecium with each vertical row of outer wall cells consisting of 6–8 subequal cells (Fig. 5E, arrows). On *Astenus* (Col. Staphylinidae) ..... ***C. verticillatus*** (Thaxt.) Thaxt.
– Perithecium with each vertical row of outer wall cells consisting of four unequal cells (Fig. 5A, arrows). On *Lesteva* (Col. Staphylinidae)..... ***C. lestevae*** Thaxt.

Compsomyces lestevae Thaxt.
MB#209523
Fig. 5A–B

Proceedings of the American Academy of Arts and Sciences 35: 439 (Thaxter 1900, as *lestevi*). – **Type**: [Not designated] [Ind. loc.] "On *Lesteva sicula* Erich, British Museum, Nos. 452 and 453, Paisley and Red Hill, England. On abdomen and elytra"; FH.

Diagnostic features

Each row of perithecial outer wall cells consists of four unequal cells (Fig. 5A, arrows). Primary appendage with a base consisting of 2–3 large and inflated cells, bearing a solitary, short antheridium in the uppermost of these cells (Fig. 5A–B, an). [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 2003]

Distribution and hosts

On *Lesteva* (= *Lesta* Blackwelder, 1952) (Col. Staphylinidae Omalinae) from **Europe**: France, Italy, Poland, Spain, Sweden, United Kingdom (Santamaria *et al.* 1991), Belgium (De Kesel & Gerstmans 2011), the Netherlands (Haelewaters *et al.* 2012); and **Africa**: Algeria (Maire 1916a).

Collections examined from Denmark

On *Lesteva hanseni* Lohse, 1953 (Col. Staphylinidae Omalinae)
DENMARK – **Nordøstsjælland (NEZ)** • Eskemose ved Sydøstbredden af Sjælsø; 55°51.557′ N, 12°26.533′ E; UB49; 10 Apr. 2020; *JP 1599*; JP det.; ZMUC C-F-124357.

On *Lesteva pubescens* Mannerheim, 1830 (Col. Staphylinidae Omalinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 18 Jan. 2015; *JP 455*; JP det.; ZMUC C-F-122940.

On *Lesteva punctata* Erichson, 1839 (Col. Staphylinidae Omalinae)
DENMARK – **Nordøstsjælland (NEZ)** • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 787*; JP det.; ZMUC C-F-123282.

On *Lesteva sicula* Erichson, 1840 (Col. Staphylinidae Omalinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 18 Jan. 2015; *JP 454*; JP det.; ZMUC C-F-122939 • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; 10 Nov. 2018; *JP 1228*; JP det.; ZMUC C-F-123755 • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 533*; JP det.; ZMUC C-F-123017. – **Nordøstsjælland (NEZ)** • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 620*; JP det.; ZMUC C-F-123108. –

Fig. 5. *Compsomyces* spp. **A**–**B**. *C. lestevae* Thaxt. **A**. Mature thallus showing antheridium (an) and perithecial wall cells (arrows). **B**. Immature thallus showing antheridium (an). – **C**–**E**. *C. verticillatus* (Thaxt.) Thaxt. **C**–**D**. Mature thalli. **E**. Detail of perithecium labelling eight wall cells (arrows). Scale bars: A–D = 50 µm; E = 20 µm. Photographs from slides ZMUC C-F-122939 (A–B), and ZMUC C-F-124184 (C–E).

Nordvestjylland (NWJ) • Gammelgård på Fur; 56°50.314′ N, 8°58.971′ E; MH99; 22 Nov. 2013; *JP 420*; JP det.; ZMUC C-F-122904 • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 556*; JP det.; ZMUC C-F-123042. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 602*; JP det.; ZMUC C-F-123091. – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 969*; JP det.; ZMUC C-F-123476.

Remarks

First record from Denmark. The new finding could easily be anticipated because Denmark is in the middle of other European countries where *C. lestevae* has already been reported.

Compsomyces verticillatus (Thaxt.) Thaxt.
MB#245733
Fig. 5C–E

Proceedings of the American Academy of Arts and Sciences 29: 96 (Thaxter 1894). – **Basionym**: *Cantharomyces verticillata* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 25: 9 (Thaxter 1890) [MB#175236]. – **Type**: "On *Sunius longiusculus*, Anna, Ill. (S.A. Forbes)"; FH. [USA]

Diagnostic features

Each row of perithecial outer wall cells consists of 6–8 subequal cells (Fig. 5E, arrows). Cell II usually gives rise to 2–5 appendages which appear to be verticillate when 3–5 of such appendages are present. [Detailed descriptions: Thaxter 1896; Santamaria 2003]

Distribution and hosts

On *Astenus* (sometimes as *Sunius* Stephens, 1829 in old literature) (Col. Staphylinidae Paederinae) from USA (type), Argentina (Spegazzini 1912), Germany (Scheloske 1969), Italy (Rossi & Cesari Rossi 1981), Spain (Santamaria 1995b), and Sweden (Huggert 2010).

Collections examined from Denmark

On *Astenus gracilis* (Paykull, 1789) (Col. Staphylinidae Paederinae)
DENMARK – **Fyn (F)** • Drejø; 54°58.141′ N, 10°25.237′ E; NF99; 30 Oct. 1936; *Christiani Dry0117*; JP det.; ZMUC C-F-124184.

Remarks

First record from Denmark. Neither the host nor the fungus seem to be common in Denmark.

Subtribe Kainomycetinae I.I.Tav.

Genus ***Kainomyces*** Thaxt.
MB#2542

Proceedings of the American Academy of Arts and Sciences 37: 44 (Thaxter 1901b). – Type species: *K. isomali* Thaxt.

Brief description

Monoecious. Receptacle multiseriate, cells II and III broadening and ± divided. Perithecia borne on uniseriate multicellular stalks; with an apical rostrum (Fig. 6A–B, ro) and a subterminal outgrowth (Fig. 6C, arrow). Perithecial outer wall cells numerous (Fig. 6C), more than five in each vertical row.

Remarks

The genus consists of three species, of which two in Europe, one in Denmark. The most recently described species is *K. rehmanii* (Majewski 1990c).

Kainomyces isomali Thaxt.
MB#431753
Fig. 6A–F

Proceedings of the American Academy of Arts and Sciences 37: 44 (Thaxter 1901b). – **Type**: "On *Isomalus Conradti* Fauvel. Derema, Usambara, East Africa. Berlin Museum, Nos. 847–848"; FH. [Tanzania]

Diagnostic features

Cells in the lower receptacle darkened basally but especially towards the dorsal margins; some of them divided by longitudinal septa. The pigmentation is a consequence of merged spots in a characteristic comb-like pattern (Fig. 6F). [Detailed descriptions: Thaxter 1908; Lee & Sugiyama 1984]

Distribution and hosts

Reported on *Eleusis* Laporte, 1835 and *Isomalus* Erichson, 1839 (which now is a synonym of *Eleusis*) (Col. Staphylinidae Osoriinae) from Tanzania (type), Burundi (Thaxter 1908), Cameroon, Philippines, Sumatra, Java, Borneo (Thaxter 1931), Zaire (Collart 1947), Taiwan (Sugiyama 1978a), and Bali Island (Lee & Sugiyama 1984). Also on *Maseochara* (Col. Staphylinidae Aleocharinae) from Sumatra (Thaxter 1931) but the host identification seems incorrect according to Frank (1982); *Maseochara* is a subgenus of *Aleochara* Gravenhorst, 1802.

Collections examined from Denmark

On *Gyrohypnus angustatus* Stephens, 1833 (Col. Staphylinidae Xantholininae)
DENMARK – **Nordøstsjælland (NEZ)** • Brede; 55°47.650′ N, 12°29.951′ E; UB48; 30 Aug. 1876; *Løvendal Dry0185*; Schiødte det.; ZMUC C-F-124250 • København; 55°41.332′ N, 12°33.762′ E; UB47; 11 Apr. 1911; *O. Jacobsen Dry0187*; O. Jacobsen det.; ZMUC C-F-124252 • Malmmose; 55°48.134′ N, 12°26.364′ E; UB38; May 1899; *N.P. Jørgensen Dry0186*; N.P. Jørgensen det.; ZMUC C-F-124251. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1452*; JP det.; ZMUC C-F-124002.

Remarks

First European record. The presence of this fungus in European beetles of the genus *Gyrohypnus* Leach, 1819 was unexpected and defies any explanation. The single species of Laboulbeniales recorded hitherto on *Gyrohypnus* (as *Xantholinus*, Tavares 1985) was *Peyritschiella infecta* (Thaxt.) I.I.Tav. from USA (Thaxter 1894).

Kainomyces isomali, *K. alutellae* Thaxt. and *K. hyalinus* Terada are similar species. According to Rossi & Leonardi (2018), *K. hyalinus* should be synonymized with *K. alutellae* because the brown pigmentation in the receptacle is a variable characteristic, useless for distinguishing these taxa. *Kainomyces isomali* is separated by the vertical septa in receptacle, lacking in *K. alutellae*. *Kainomyces rehmanii* T.Majewski

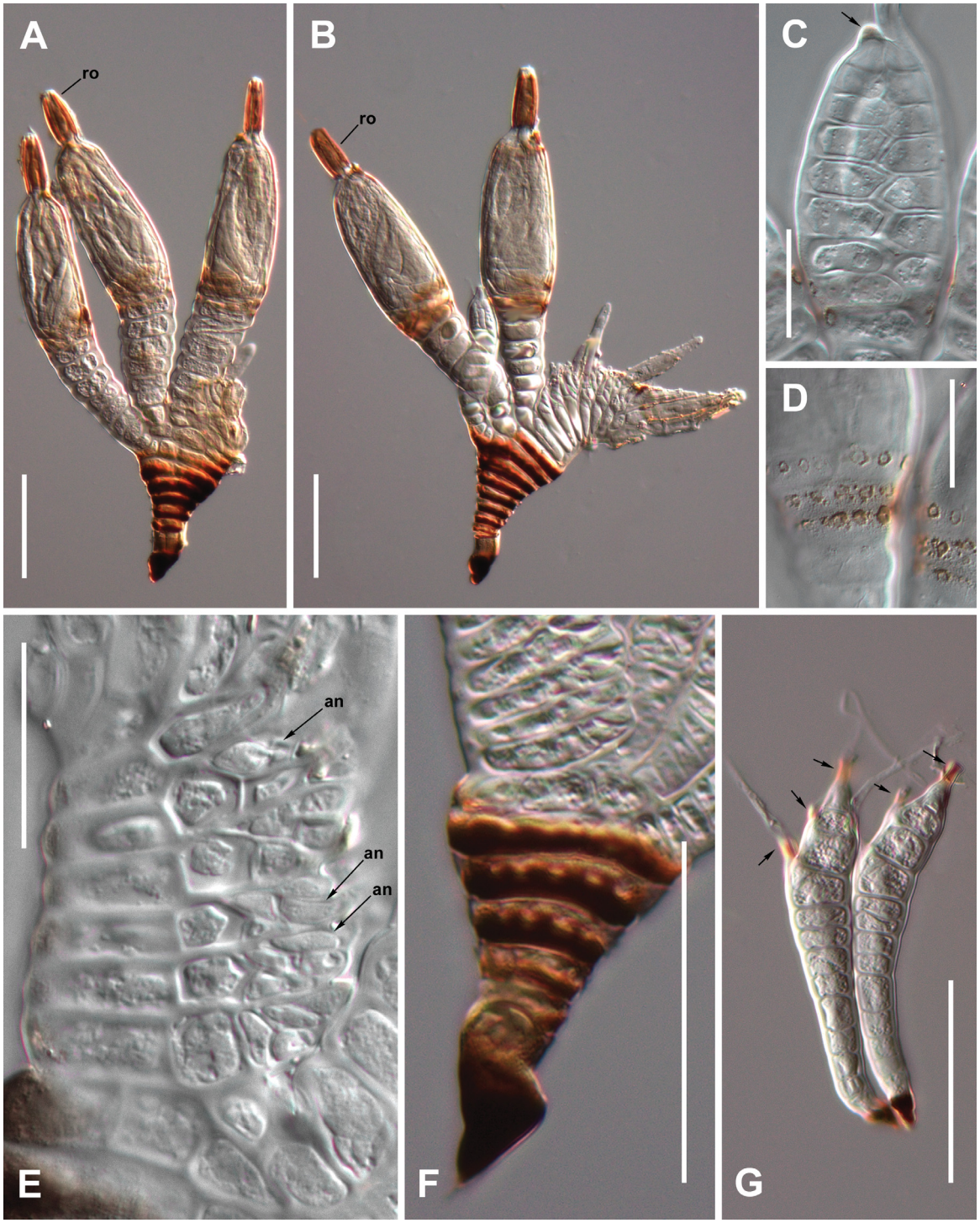

Fig. 6. A–**F**. *Kainomyces isomali* Thaxt. **A**–**B**. Mature thalli showing the rostrum (ro) on the perithecia. **C**. Detail of an immature perithecium showing numerous wall cells for each row and the subterminal outgrowth on the perithecium. **D**. Detail of basal area of perithecium showing brown spots. **E**. Detail of receptacle with antheridia (an). **F**. Detail of the lower receptacle showing comb-like pigmentation. – **G**. *Hydrophilomyces atroseptatus* T.Majewski. Young thallus where darkened septa on the base of secondary branchlets are arrowed. Scale bars: A–B, F–G = 50 µm; C–E = 20 µm. Photographs from slides ZMUC C-F-124250 (A), ZMUC C-F-124252 (B), ZMUC C-F-124002 (C–F), and ZMUC C-F-123693 (G).

which occurs on *Acrotrichis* Motschulsky, 1848 (Col. Ptiliidae) is an isolated species, well-distinguished from other species.

The basal area of perithecia appears to be variably darkened. When observed in detail with the help of DIC optics, brown round spots or circles may be distinguished (Fig. 6D). These elements recall the "stigmata" also observed in species of the genus *Monoicomyces*, *Rhachomyces* and *Stigmatomyces*. Tavares (1985) stated that determination of the exact nature of antheridia in this species was not possible but suggested that they are the terminal cells in the rows of frequently divided cells above the perithecium. We agree with this statement because numerous flask-shaped, flattened, laterally directed antheridia may be found among the tiers of cells in the massive receptacle (Fig. 6E, an).

Tribe Hydrophilomyceteae I.I.Tav.

Genus ***Hydrophilomyces*** Thaxt.
MB#2406

Memoirs of the American Academy of Arts and Sciences 13: 431 (Thaxter 1908). – Type species: *H. rhynchophorus* Thaxt.

Brief description

Monoecious. Receptacle consisting of a uniseriate multicellular axis extending into the appendage, bearing branches and antheridia born from corner cells. Unicellular buffer cells often present above the foot (Fig. 7A–C, F–G, bf). Perithecial outer wall including an elongated accessory cell on the outer side (Fig. 7D, G, acc), parallel to the longer ventral outer wall cell (w_1).

Remarks

The genus consists of 16 species, of which 11 in Europe, five in Denmark. The most recently described species are *H. deflexus* and *H. riberae* (Santamaria *et al.* 2020a). The number and origin of the perithecial basal cells in this genus is puzzling because there seems to be four rather of the typical three (i.e., m, n, and n').

Key to the Danish species (partially following Majewski 1994b and Santamaria 2003)

1. Corner cells of the appendage separated by constricted dark septa from the arising branchlets or antheridia. On *Limnebius* Leach, 1815 (Col. Hydraenidae) ..... ***H. atroseptatus*** T.Majewski
– Corner cells without dark septa 2

2. Receptacle consisting of up to 16 cells. On *Ochthebius* Leach, 1815 (Col. Hydraenidae) and *Laccobius* (Col. Hydrophilidae)..... 3
– Receptacle consisting of 18–44 cells. On *Cercyon* Leach, 1817 (Col. Hydrophilidae) 4

3. Thalli dimorphic, depending on the host sex and its specific location of growth on host body. On *Laccobius* (Col. Hydrophilidae) ..... ***H. coneglianensis*** Speg.
– Thalli not dimorphic, invariable despite host sex. On *Ochthebius* (Col. Hydraenidae)..... ..... ***H. digitatus*** F.Picard

4. Mature perithecium with a bent neck. Buffer cells present. Receptacle robust..... ..... ***H. hamatus*** T.Majewski
– Mature perithecium with a straight neck. Buffer cells absent. Receptacle slender .... ***H. gracilis*** T.Majewski

Hydrophilomyces atroseptatus T.Majewski
MB#363459
Fig. 6G

Polish Botanical Studies 7: 56 (Majewski 1994b). – **Type**: "On *Limnebius aluta* (Bedel), Sw. Smolniki, 12.8.1974, leg. A. Sarna (T.M. 1482 – Holotype)"; KRAM. [Poland]

Diagnostic features

Main appendage axis with dark constricted septa separating secondary branchlets or antheridia from corner cells (Fig. 6G, arrows); stout, not exceeding the perithecial apex, consisting of 9–12 flattened cells. [Detailed description: Santamaria 2003]

Distribution and hosts

Known from Poland (type) and Spain on *Limnebius* (Col. Hydraenidae) (Santamaria 2001a). According to Majewski (2008) the record of *Hydrophilomyces limnebii* on *L. aluta* (Balazuc 1990) from France probably belongs to *H. atroseptatus*.

Collections examined from Denmark

On *Limnebius aluta* Bedel, 1881 (Col. Hydraenidae)
DENMARK – **Nordøstsjælland (NEZ)** • Storø i Gurre Sø; 56°2.208′ N, 12°29.057′ E; UC41; 7 Apr. 2020; *JP 1628*; JP det.; ZMUC C-F-124366. – **Sydjylland (SJ)** • Brænøre Mose; 55°23.906′ N, 9°25.714′ E; NG23; 5 Aug. 2018; *JP 1168*; JP det.; ZMUC C-F-123693.

Remarks

First record from Denmark. The Danish material consists only of young thalli. Nevertheless the distinctive dark septa of this species confirm its classification (Fig. 6G, arrows). *Hydrophilomyces limnebii* also occurs on *Limnebius*, but may be easily distinguished by the absence of dark septa in corner cells and by the strongly bent perithecium. A photo of *H. atroseptatus* is given here for the first time, although in immature condition.

Hydrophilomyces coneglianensis Speg.
MB#195358
Fig. 7A–B

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 53 (Spegazzini 1915b). – *Misgomyces coneglianensis* (Speg.) Thaxt. (Thaxter 1931: 296) [MB#261637]. – **Type**: " Sobre el pecho entre las patas de los *Laccobius sinuatus* pescados en los alrededores de Conegliano, Veneto, en los veranos 1913 y 1914"; LPS. [Italy]

Hydrophilomyces elegans Speg. (Spegazzini 1915b: 54) [MB#224576]. – *Misgomyces elegans* (Speg.) Thaxt. (Thaxter 1931: 297) [MB#263859]

Diagnostic features

Thallus dimorphic depending on the host sex. Receptacle consisting of 9–11 superposed cells, strongly arcuate in female hosts (Fig. 7A) straight in males (Fig. 7B). Perithecium symmetrical and straight in female hosts (Fig. 7A), asymmetric and with a strongly arcuate neck in males (Fig. 7B). [Detailed descriptions: Scheloske 1976; Majewski 1994b; Santamaria 2003]

Distribution and hosts

Occurs on beetles of the genus *Laccobius* (Col. Hydrophilidae) in Spain, Germany, Italy (type), Poland, Greece (Majewski 2008) and Hungary (Bánhegyi *et al.* 1985).

Collections examined from Denmark

On *Laccobius minutus* (Linnaeus, 1758) (Col. Hydrophilidae)

DENMARK – **Nordøstsjælland (NEZ)** • Karlstrup Kalkbrud syd for Karlstrup; 55°32.863′ N, 12°12.385′ E; UB25; 28 May 2016; *JP 228*; JP det.; ZMUC C-F-122709. – **Sydsjælland (SZ)** • Bårse; 55°7.680′ N, 11°56.494′ E; PG81; 24 Aug. 2019; *JP 1501*; JP det.; ZMUC C-F-124088.

Remarks

First record from Denmark. Dimorphism related to sex host in this species was experimentally demonstrated by Scheloske (1976) who kept living insects and observed their mating behaviour.

Hydrophilomyces digitatus F.Picard
MB#195295
Fig. 7C

Bulletin de la Société Mycologique de France 25: 245 (Picard 1910). – *Ecteinomyces digitatus* (F.Picard) Thaxt. (Thaxter 1912a: 212) [not registered in MB]. – *Misgomyces digitatus* (F.Picard) Thaxt. (Thaxter 1931: 297) [MB#263206]. – **Type**: [Type lost!] [Ind. loc.] "Fixé, par paquets de nombreux individus, à la face inférieure de l'élytre gauche d'*Ochthebius marinus* Paykull. … Très commun à Trappes (Seine-et-Oise) dans les canaux attenant à l'étang de St.-Quentin" [France]

Diagnostic features

Receptacle consisting of 6–14 superposed cells, curved to strongly arcuate. Perithecium rather variable, straight to arcuate, broadest near the basal quarter, abruptly tapering towards a narrow, cylindrical neck, then broadened at the level of the septa between w_2 and w_3. [Detailed description: Santamaria 2003]

Distribution and hosts

Known on *Ochthebius* (Col. Hydraenidae) from France (type), Sweden, Portugal and Spain (Santamaria 2003).

Collections examined from Denmark

On *Ochthebius marinus* (Paykull, 1798) (Col. Hydraenidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Keldskov; 54°39.681′ N, 11°33.593′ E; PF66; 15 Oct. 2019; *JP 1516*; JP det.; ZMUC C-F-124271. – **Nordøstsjælland (NEZ)** • Kalvebod Fælled; 55°35.117′ N, 12°32.693′ E; UB46; 24 Mar. 2020; *JP 1638*; JP det.; ZMUC C-F-124368.

On *Ochthebius minimus* (Fabricius, 1792) (Col. Hydraenidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; *JP 1519*; JP det.; ZMUC C-F-124274.

Remarks

First record from Denmark. The classification of *Hydrophilomyces* species occurring on *Ochthebius* is difficult. Further studies using modern molecular techniques are needed. *Hydrophilomyces digitatus* is best separable from other species by the absence of any remarkable character.

Fig. 7. *Hydrophilomyces* spp., mature thalli. **A**–**B**. *H. coneglianensis* Speg. Thallus from female (A) and from male hosts (B). – **C**. *H. digitatus* F.Picard. – **D**–**E**. *H. gracilis* T.Majewski. – **F**–**G**. *H. hamatus* T.Majewski. Abbreviations: acc = accessory cell; bf = buffer cells. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122709 (A), ZMUC C-F-124088 (B), ZMUC C-F-124274 (C), ZMUC C-F-124043 (D–F), and ZMUC C-F-124042 (G).

Hydrophilomyces gracilis T.Majewski
MB#315332
Fig. 7D–E

Acta Mycologica 10: 272 (Majewski 1974). – **Type**: "On *Cercyon granarius* Er. (Col., Hydrophilidae): Kurzeszyn Nowy, Rawa Mazowiecka county, on flooded meadows near the Rawka River, 18.8.1972 leg. T. Majewski (TM. 1076 – holotype)"; KRAM. [Poland]

Diagnostic features

Receptacle slender, consisting of up to 44 flattened cells. Buffer cells absent. Perithecial neck straight. [Detailed description: Majewski 1994b]

Distribution and hosts

On *Cercyon* (Col. Hydrophilidae) from Poland (type), Greece (Castaldo *et al.* 2004), and maybe from Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Cercyon littoralis* (Gyllenhal, 1808) (Col. Hydrophilidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Tjørnebjerg ved Kramnitse; 54°41.586′ N, 11°16.980′ E; PF46; 19 May 2019; *JP 1463*; JP det.; ZMUC C-F-124043. – **Nordøstsjælland (NEZ)** • Boserup Strand; 55°40.086′ N, 12°1.806′ E; UB17; 11 May 1900; *coll. unknown Dry0031*; unknown det.; ZMUC C-F-124101. – **Nordvestsjælland (NWZ)** • Bjerge Sydstrand; 55°33.493′ N, 11°9.730′ E; PG35; 1 May 2013; *JP 300*; JP det.; ZMUC C-F-122779.

On *Cercyon marinus* Thomson, 1853 (Col. Hydrophilidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Mandemarke; 54°58.014′ N, 12°29.479′ E; UA39; 8–13 Jun. 2013; *O. Karsholt 178*; JP det.; ZMUC C-F-122657.

Remarks

First record from Denmark. According to the large quantity of *Cercyon* studied without success, this and the next species may be considered as very rare. This species grows on the tip of the elytra.

Hydrophilomyces hamatus T.Majewski
MB#315333
Fig. 7F–G

Acta Mycologica 10: 274 (Majewski 1974). – **Type**: "On *Cercyon bifenestratus* Küst. (Col., Hydrophilidae): Pomiechówek, Nowy Dwór Mazowiecki county, in mud on the left bank of the River Wkra, 13.6.1973 leg. T. Majewski (TM. 1301 – holotype)"; KRAM. [Poland]

Diagnostic features

Receptacle stout, consisting of up to 22 flattened cells. Buffer cells present (Fig. 7F–G, bf). Perithecial neck bent. [Detailed description: Majewski 1994b]

Distribution and hosts

On *Cercyon* (Col. Hydrophilidae) from Poland (type), United Kingdom (Weir & Beakes 1993), Sierra Leone (Rossi 1990), and maybe from Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Cercyon littoralis* (Gyllenhal, 1808) (Col. Hydrophilidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Tjørnebjerg ved Kramnitse; 54°41.586′ N, 11°16.980′ E; PF46; 19 May 2019; *JP 1463*; JP det.; ZMUC C-F-124042, C-F-124043.

Remarks

First record from Denmark. According to Majewski (1974), *Hydrophilomyces hamatus* is distinguished from *H. gracilis* by the presence of buffer cells, by the strongly recurved neck of the perithecium (although only seen on overmature perithecia), and by the stout receptacle, with less cells. *Hydrophilomyces hamatus* grows on the ventral side of the thorax or between coxae and the base of legs, whereas *H. gracilis* grows on the elytral apices. Majewski (1994b) considers the possibility that both species might be "growth forms of the same species".

These species may exist on the same host specimen and their position is not related to host sex as is the case for example with *H. coneglianensis* and its synonym *H. elegans*. For this reason we prefer to maintain both species separate.

Tribe Euphoriomyceteae I.I.Tav.
Subtribe Euphoriomycetinae s. str.

Genus ***Euphoriomyces*** Thaxt.
MB#1935

Memoirs of the American Academy of Arts and Sciences 16: 307 (Thaxter 1931). – Type species: *E. bilateralis* Thaxt.

Brief description

Monoecious or dioecious. Receptacle consisting of a multicellular axis extending into the primary appendage; some of the cells below the perithecium divide laterally by means of vertical septa. Antheridia terminal on any part of receptacle or appendages.

Remarks

With the two new species described here, the genus consists of 19 species, of which 10 in Europe, eight in Denmark. The most recently described species is *Euphoriomyces rugosus* (Rossi & Bernardi 2018). Eleven species occur on Col. Leiodidae. The genus was reviewed by Santamaria (1991). The genus *Euphoriomyces* belongs to the tribe Euphoriomyceteae I.I.Tav. (Tavares 1985), together with genera *Phaulomyces* and *Siemaszkoa*, well-characterized because the walls of the perithecial basal cells and cell VII almost vanish with maturity, being hardly distinguishable. Another particular character of the tribe refers to the number of perithecial wall cells in each vertical row, with three in three of the rows and four in the remaining, where the extra 4th cell is visible as a small protruding cell near the perithecial apex (Fig. 9C, w_4).

Key to the Danish species (partially following Majewski 1994b and Santamaria 2003)

1. Perithecia ovate. Receptacle cells below perithecia divided laterally to form unicellular or multicellular secondary appendages. Sometimes, thalli appearing flattened on the host body surface (similar to *Rickia* species) 2
– Perithecia slender. Receptacle cells below perithecia not or rarely laterally divided. Thalli not flattened. On Col. Staphylinidae..... ***E. huggertii*** T.Majewski

2. Perithecial neck inconspicuous. Perithecial basal cells (m, n, n') and secondary stalk cell (VII) fully indistinguishable in mature thalli. On Col. Leiodidae 3
– Perithecial neck conspicuous, abruptly distinguished. Trichogyne scar persistent as an outgrowth. Some of the perithecial basal cells and secondary stalk cell (VII) ± visible at maturity. On Col. Ptiliidae of the genus *Smicrus* Matthews, 1872 ..... ***E. smicri*** Santam. sp. nov.

3. One of the upper axial cells next to the perithecium distinctly elongate. Cell VI triangular in section, forming a strongly oblique base for perithecium. On Col. Leiodidae of the genus *Hydnobius* Schmidt, 1841 ..... ***E. magnicellulatus*** Santam.
– All cells of receptacle similar each other or cell VI different 4

4. Thalli without long branches (i.e., secondary appendages) below the perithecia (rarely one such appendages in *E. unilateralis* just below the lowermost perithecium) 5
– Thalli with few to many long branches (i.e., secondary appendages) below or between the perithecia 6

5. Thalli very small, up to 85 µm from foot to perithecial tip; with a receptacle consisting of 3–6 superposed cells. Typically on *Cyrtusa* Erichson, 1842 and *Colenis* Erichson, 1842 (Col. Leiodidae) ..... ***E. gillerforsii*** (Huggert) I.I.Tav.
– Thalli measuring more than 85 µm from foot to perithecial tip, with a receptacle consisting of 8–12 superposed cells. On *Agathidium* Panzer, 1797 (Col. Leiodidae) .. ***E. unilateralis*** T.Majewski

6. Secondary appendages ± darkened, with the upper ones remarkably longer and darker. On *Leiodes rugosa* (Col. Leiodidae) ..... ***E. enghoffii*** Santam. sp. nov.
– Secondary appendages entirely hyaline 7

7. Thallus flattened like a sheet, consisting of several superposed tiers of few to several cells separated from each other by vertical septa. All perithecia developing from the same side of the thallus; antheridia and the variably elongated secondary appendages present in both margins of the receptacle. On *Leiodes* Latreille, 1797 (Col. Leiodidae) ..... ***E. liodivorus*** (Huggert) I.I.Tav.
– Characters not as above. On *Agathidium*, *Amphicyllis* Erichson, 1845 and *Cyrtusa* (Col. Leiodidae) ..... ***E. agathidii*** (Maire) I.I.Tav.

Euphoriomyces agathidii (Maire) I.I.Tav.
MB#105308
Fig. 8A

Mycologia Memoirs 9: 218 (Tavares 1985). – **Basionym**: *Ecteinomyces agathidii* Maire, *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 11(8): 156 (Maire 1920) [MB#183944]. – *Asaphomyces agathidii* (Maire) Scheloske (1969: 92) [MB#326502]. – **Type**: [Type lost?!] "En fascicules apprimés sur les élytres d'*Agathidium laevigatum* Er., M. Rabat, 1918 (Théry in coll. Peyerimhoff)". [Morocco]

Diagnostic features

Thalli up to 150 µm long from foot to apex of furthest perithecia. Receptacle consisting of 4–8 superposed cells, dividing bilaterally into secondary appendages or perithecia. Perithecia stout, less than three times long than broad. [Detailed descriptions: Scheloske 1969; Santamaria 1991, 2003; Majewski 1994b]

Distribution and hosts

Occurs on *Agathidium*, *Amphicyllis* and *Cyrtusa* (Col. Leiodidae). Known from Morocco (type), Spain, Germany, Poland, Sweden (Majewski 2008), South Korea (Lee *et al.* 2007), Russia (Huldén 1983), Bulgaria, Italy (Rossi *et al.* 2019a), Czech Republic (Rossi *et al.* 2019b) and the Netherlands (Haelewaters & De Kesel 2020).

Collections examined from Denmark

On *Agathidium convexum* Sharp, 1866 (Col. Leiodidae)

DENMARK – **Østjylland (EJ)** • Mols; 56°13.340′ N, 10°33.441′ E; NH93; 25 Aug. 1940; *Johs. Andersen Dry0169*; Johs. Andersen det.; ZMUC C-F-124235 • Rye Nørreskov; 56°6.065′ N, 9°41.814′ E; NH41; ca 1870; *Schiødte Dry0172*; Schiødte det.; ZMUC C-F-124238. – **Nordøstjylland (NEJ)** • Lundby Bakker; 56°59.043′ N, 9°59.874′ E; NJ61; Sep. 1887; *J.P. Johansen Dry0171*; J.P. Johansen det.; ZMUC C-F-124237. – **Vestjylland (WJ)** • Esbjerg Strandskov; 55°29.094′ N, 8°25.956′ E; MG64; 24 Nov. 1928; *A. West Dry0170*; A. West det.; ZMUC C-F-124236.

On *Agathidium laevigatum* Erichson, 1845 (Col. Leiodidae)

DENMARK – **Nordøstjylland (NEJ)** • Restrup; 57°0.308′ N, 9°46.586′ E; NJ41; Jul. 1890; *J.P. Johansen Dry0173*; J.P. Johansen det.; ZMUC C-F-124239. – **Nordøstsjælland (NEZ)** • Tisvilde; 56°3.629′ N, 12°5.777′ E; UC11; 3 Aug. 1886; *N.P. Jørgensen Dry0174*; N.P. Jørgensen det.; ZMUC C-F-124240.

On *Agathidium rotundatum* (Gyllenhal, 1827) (Col. Leiodidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Østerskoven; 54°50.689′ N, 12°8.811′ E; UA18; 6 Jul. 1935; *Johs. Andersen Dry0175*; Johs. Andersen det.; ZMUC C-F-124241. – **Nordøstjylland (NEJ)** • Hals Nørreskov; 57°2.012′ N, 10°15.653′ E; NJ72; 15 Jun. 1932; *A. West Dry0178*; A. West det.; ZMUC C-F-124244 • Høstemark Skov; 56°56.064′ N, 10°13.758′ E; NJ71; 12 May 1990; *V. Mahler Dry0177*; V. Mahler det.; ZMUC C-F-124243 • Lerbæk Skov, Vendsyssel; 57°5.505′ N, 10°0.219′ E; NJ62; 7 Apr. ca 1870; *Schiødte Dry0176*; Schiødte det.; ZMUC C-F-124242 • Rold Skov; 56°48.933′ N, 9°50.218′ E; NH59; 1–30 Jun. 2017; *J. Heilmann-Clausen et al. 1141*; A.K. Hansen det.; ZMUC C-F-123664.

On *Agathidium varians* Beck, 1817 (Col. Leiodidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Roden Skov; 54°40.539′ N, 11°49.087′ E; PF86; 5 Sep. 1883; *N.P. Jørgensen Dry0179*; N.P. Jørgensen det.; ZMUC C-F-124245.

Remarks

First record from Denmark. Distinctiveness of the three species of *Euphoriomyces* described on beetles of the genus *Agathidium* (*E. agathidii*, *E. bilateralis* and *E. unilateralis*) was analyzed by Rossi *et al.* (2019a). *Euphoriomyces agathidii* and *E. unilateralis* seem to be well-separable because the latter only bears secondary appendages and perithecia on the same side of the thallus. The presence of *Euphoriomyces bilateralis* in Europe and its distinctiveness from *E. agathidii* is questionable; it was described from Sumatra (Thaxter 1931) but the later Spanish record (Santamaria 1991) probably belongs to *E. agathidii*.

Euphoriomyces enghoffii Santam. sp. nov.
MB#840600
Fig. 8B–F

Diagnosis

Similar to *E. liodivorus* (Huggert) I.I.Tav., but differing by the darkish brown appendages, especially the primary appendage which, moreover, is very elongated.

Fig. 8. *Euphoriomyces* spp. **A**. *E. agathidii* (Maire) I.I.Tav. Paired mature thalli. – **B**–**F**. *E. enghoffii* Santam. sp. nov. **B**. The peduncle of primary appendage is labelled (*). **F**. Brown basis of appendages are pointed with arrows. Abbreviations: a = primary septum; a = antheridia; pa = primary appendage; sa = secondary appendage; VI = cell VI. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124241 (A), ZMUC C-F-124142 (holotype) (B–C), and ZMUC C-F-124143 (D–F).

Etymology

Named after the Danish scientist Henrik Enghoff, who studies millipedes and its fungi and has also actively collaborated so that this project could be carried out.

Type material

Holotype

DENMARK – **Nordøstsjælland (NEZ)** • Malmmosevej; 55°47.974′ N, 12°26.512′ E; UB38; on *Leiodes rugosa* Stephens, 1829 (Col. Leiodidae); 22 Oct. 1916; *A. West Dry0076*; A. West det.; ZMUC C-F-124142.

Paratypes

DENMARK – **Fyn (F)** • Svendborg; 55°3.943′ N, 10°37.118′ E; PG00; on *L. rugosa*; 10 Oct. 1935; *Christiani Dry0078*; Christiani det.; ZMUC C-F-124144. – **Nordøstsjælland (NEZ)** • Rude Skov; 55°49.861′ N, 12°28.241′ E; UB49; on *Leiodes calcarata* Erichson, 1845 (Col. Leiodidae); 25 Jun. 1911; *A. West Dry0093*; A. West det.; ZMUC C-F-124159 • Holte; 55°48.802′ N, 12°28.125′ E; UB48; on *L. rugosa*; 1 Oct. 1916; *V. Hansen Dry0075*; V. Hansen det.; ZMUC C-F-124141 • Sanddalen; 55°51.080′ N, 12°30.727′ E; UB49; on *L. rugosa*; 14 Oct. 1917; *A. West Dry0077*; A. West det.; ZMUC C-F-124143.

Description

Thallus hyaline, except for the blackened foot and brown appendages. Receptacle axis consisting of (7–)9(–11) superposed cells which are broader than long, those of the basal area being especially flattened, cells gradually elongated towards the distal region. Basal cell of the receptacle (I) longer than broad, tapering towards the foot. Most cells of the receptacle, except the 2–4 lower ones, dividing obliquely at one or both sides into one to more cells to form perithecia, secondary appendages, or antheridia (Fig. 8D, an). These lateral cells remain in contact with cells above and below in such a way that the whole thallus gives the impression of a unilayered sheet.

Primary appendage unbranched, entirely dark brown, continuing the main receptacle axis, consisting of rather elongated and apparently rigid cells (this can be verified with the manipulation that we do with a needle to detach the thallus from the host cuticle) (Fig. 8B–E, pa). The uppermost receptacular axis consists of two superposed cells which form a peduncle for the primary appendage (Fig. 8B, *) below the primary septum (Fig. 8B, D, a), and sometimes bear some additional secondary branches which grow upwards parallel to the primary appendage (Fig. 8D, sa).

Perithecial stalk cell (VI) inconspicuous, subtriangular (Fig. 8C, VI). Perithecia symmetrical, ovoidal, broadest near the middle height, then gradually tapering towards an indistinct neck and a blunt apex; 1–6 per thallus, unilaterally arranged.

Length from foot to apex of uppermost perithecium (86–)100–149(–190) µm. Perithecium (37–)48–74(–94) × (19–)22–31(–38) µm. Length of primary appendage from primary septum (when undamaged) 158–233 µm.

Thalli were found mostly on elytra but also on other body parts of the hosts. Nothing is known about the collecting circumstances of the hosts.

Remarks

Euphoriomyces enghoffii sp. nov. is similar to *E. liodivorus*, from which it could easily be distinguished at first sight by the darkish brown appendages, and especially for the primary appendage which, if unbroken, may be very long (up to three times as long as the thallus from foot to uppermost perithecium)

(Fig. 8B–E, pa). The thallial appearance may vary substantially according to maturity and position on the host body. Thalli bearing only a single mature perithecium (but with some initials below) could be considered mostly typical (Fig. 8B–C) and have been found on elytra apices.

Overmature damaged thalli, with broken appendages, may be difficult to separate from *E. liodivorus*. Nevertheless, in these circumstances, the brown basis of appendages can help to distinguish them (Fig. 8F, arrows). The precise arrangement of cells explained by Santamaria (2003: 266) for *E. liodivorus* also applies to *E. enghoffii*.

Euphoriomyces gillerforsii (Huggert) I.I.Tav.
MB#105309
Fig. 9A–C

Mycologia Memoirs 9: 218 (Tavares 1985). – **Basionym**: *Asaphomyces gillerforsii* Huggert, *Svensk Botanisk Tidskrift* 67: 245 (Huggert 1973) [MB#309030]. – **Type**: "Gtl, Etelhem, 6.VII.1971, L. Huggert (L.H. 1202), on *Colenis immunda* Sturm. (Holotype)"; UME. [Sweden]

Diagnostic features

Thallus up to 85 µm long from foot to perithecial apex. Receptacle consisting of 3–6 superposed cells; only the uppermost of these cells, below the perithecium, isolates a unicellular secondary appendage (Fig. 9B, sa). Perithecium about twice longer than broad. [Detailed description: Santamaria 2003]

Distribution and hosts

Known from Sweden on *Colenis* (type), *Cyrtusa*, and *Xanthosphaera* Fairmaire, 1859 (Col. Leiodidae) (Huggert 2010), and only on *Colenis* from Spain, France, Hungary (Santamaria 1995b), Italy and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Colenis immunda* (Sturm, 1807) (Col. Leiodidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 19 Aug. 2019; *JP 1493*; JP det.; ZMUC C-F-124079 • Søholt; 54°44.613′ N, 11°32.479′ E; PF66; 28 Jul. 2001; *JP Dry0062*; JP det.; ZMUC C-F-124128. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.481′ N, 11°47.823′ E; PG73; 1 Jul. 1999; *JP Dry0064*; JP det.; ZMUC C-F-124130 • Strandegård Dyrehave; 55°11.799′ N, 12°7.953′ E; UB12; 23 May 2000; *JP Dry0063*; JP det.; ZMUC C-F-124129.

Remarks

First record from Denmark. The new find is not surprising given the geographical proximity of the Swedish type record.

Euphoriomyces huggertii T.Majewski
MB#103298
Fig. 9D–E

Acta Mycologica 19: 185 (Majewski 1986a). – **Type**: "On *Proteinus brachypterus* F. (Col. Staphylinidae): Bieszczady Mts., Wetlina (Krosno voiv.), under bark of overthrown trunks of *Fagus sylvatica* in *Fagetum* on the eastern mountain-side of Jawornik, about 700 m above sea level, 2.6.1974 (holotype, TM. 1418)"; KRAM. [Poland]

Diagnostic features

Thalli with 1–2 perithecia, if two, then borne on opposite sides of the 5th receptacular cell. Fourth cell of the receptacle larger than others above and below. Secondary appendages ± branched, continuing the six- to eight-celled receptacle. Primary appendage two-celled, concealed, lateral to the distal cell of receptacle (Fig. D, pa). [Detailed descriptions: Santamaria 1991, 2003; Majewski 1994b]

Distribution and hosts

Only known from Poland on *Acrulia* Thomson, 1858 and *Proteinus* Latreille, 1796 and also from Spain on *Baptolinus affinis* (Paykull, 1789) (Santamaria 1989). All hosts belong to Col. Staphylinidae.

Collections examined from Denmark

On *Acrulia inflata* (Gyllenhal, 1813) (Col. Staphylinidae Omalinae)

DENMARK – **Østjylland (EJ)** • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 799*; JP det.; ZMUC C-F-123294. – **Sydsjælland (SZ)** • Havnen i Næstved; 55°13.583′ E, 11 45.278′ E; PG72; 6 Jan. 1999; *JP Dry0097*; JP det.; ZMUC C-F-124163. – **Vestjylland (WJ)** • Estrup Skov; 55°29.601′ N, 9°4.608′ E; NG05; 5 Aug. 1928; *Johs. Andersen Dry0098*; Johs. Andersen; ZMUC C-F-124164.

Remarks

First record from Denmark. According to Tavares (in litt.) this species may belong to the genus *Carpophoromyces*. Thalli from *Acrulia* represent a reduced form where the second perithecium is shown at the one-celled initial stage (cell d), and maybe it never develops beyond that (Majewski 1994b).

Euphoriomyces liodivorus (Huggert) I.I.Tav.
MB#105310
Fig. 9F–G

Mycologia Memoirs 9: 218 (Tavares 1985). – **Basionym**: *Amphimyces liodivorus* Huggert, *Svensk Botanisk Tidskrift* 67: 240 (Huggert 1973) [MB#308662]. – **Type**: "Tl, Kiruna, Kurravaara village, 12.VIII.1971, S.-O. Ulefors (L.H. 761), on *Liodes* (sic) *puncticollis* Th. (Holotype)"; UME. [Sweden]

Diagnostic features

Thalli up to 200 µm long from foot to apex of furthest perithecia. Receptacle consisting of 7–12 superposed cells, dividing bilaterally into secondary appendages, some of them giving rise to antheridia, or up to 8 perithecia, the later on the same side. [Detailed descriptions: Santamaria 1991, 2003]

Distribution and hosts

Occurs on *Leiodes* (Col. Leiodidae) from Sweden (type), Spain (Santamaria 1989), United Kingdom (Weir & Beakes 1993), Slovakia (Rossi & Máca 2006), Italy and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Leiodes badia* (Sturm, 1807) (Col. Leiodidae)

DENMARK – **Østjylland (EJ)** • Ladegårds Å; 55°55.861′ N, 10°5.009′ E; NG69; ca 1870; *No data coll. & det. Dry0070*; ZMUC C-F-124136. – **Lolland, Falster, Møn (LFM)** • Høvblege; 54°57.826′ N, 12°30.574′ E; UA49; 2 Jun. 1934; *Johs. Andersen Dry0068*; Johs. Andersen det.; ZMUC C-F-124134 • ibid.; 27 Aug. 1951; *F. Larsen Dry0069*; F. Larsen det.; ZMUC C-F-124135.

Fig. 9. *Euphoriomyces* spp. **A**–**C**. *E. gillerforsii* (Huggert) I.I.Tav. **A**–**B**. Paired mature thalli, with unicellular secondary appendage labelled in B (sa). **C**. Detail of perithecial apex with labelled extra cell w_4. – **D**–**E**. *E. huggertii* T.Majewski. **D**. Mature thallus with labelled primary appendage (pa). **E**. Paired mature thalli. – **F**–**G**. *E. liodivorus* (Huggert) I.I.Tav. Mature thalli. Scale bars: A–C = 20 µm; D–G = 50 µm. Photographs from slides ZMUC C-F-124079 (A–C), ZMUC C-F-123294 (D–E), ZMUC C-F-124158 (F), and ZMUC C-F-124138 (G).

On *Leiodes calcarata* Erichson, 1845 (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Boller; 55°50.269′ N, 9°53.826′ E; NG58; 30 Jun. 1927; *Høeg Dry0091*; Høeg det.; ZMUC C-F-124157. – **Fyn (F)** • Engene ved Svendborg; 55°2.937′ N, 10°34.301′ E; PG00; 15 Sep. 1940; *Christiani Dry0095*; Christiani det.; ZMUC C-F-124161. – **Nordøstsjælland (NEZ)** • Ågesholm; 55°40.456′ N, 12°14.542′ E; UB27; 25 Jul. 1916; *A. West Dry0092*; A. West det.; ZMUC C-F-124158 • Boserup; 55°39.746′ N, 12°2.173′ E; UB17; ca 1870; *No data coll. & det. Dry0096*; ZMUC C-F-124162 • Jægerspris Nordskov; 55°54.438′ N, 11°58.702′ E; PH80; 15 Aug. 1973; *F. Bangsholt Dry0094*; F. Bangsholt det.; ZMUC C-F-124160.

On *Leiodes ciliaris* (Schmidt, 1841) (Col. Leiodidae)
DENMARK – **Nordøstjylland (NEJ)** • Kettrupgård; 57°19.131′ N, 9°40.669′ E; NJ45; 15 Jul. 1900; *F. de Tengnagel Dry0071*; F. de Tengnagel det.; ZMUC C-F-124137.

On *Leiodes ferruginea* (Fabricius, 1787) (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Rugballegård ved Vejle; 55°43.981′ N, 9°27.852′ E; NG49; Jun. 1883; *F. de Tengnagel Dry0083*; F. de Tengnagel det.; ZMUC C-F-124149. – **Lolland, Falster, Møn (LFM)** • Lindeskov; 54°44.747′ N, 11°53.917′ E; PF87; 6 Jun. 1911; *A. West Dry0085*; A. West det.; ZMUC C-F-124151. – **Nordøstsjælland (NEZ)** • Sjælland, North; without coordinates; ca 1870; *No data coll. & det. Dry0084*; ZMUC C-F-124150.

On *Leiodes furva* (Erichson, 1845) (Col. Leiodidae)
DENMARK – **Nordøstjylland (NEJ)** • Hvorup, Nørresundby; 57°5.130′ N, 9°55.659′ E; NJ52; Sep. 1891; *No data coll. & det. Dry0073*; ZMUC C-F-124139.

On *Leiodes gallica* Reitter, 1884 (Col. Leiodidae)
DENMARK – **Nordøstsjælland (NEZ)** • Holte; 55°48.802′ N, 12°28.125′ E; UB48; 3 Sep. 1916; *V. Hansen Dry0074*; V. Hansen det.; ZMUC C-F-124140.

On *Leiodes longipes* (Schmidt, 1841) (Col. Leiodidae)
DENMARK – **Nordøstjylland (NEJ)** • Hvorup, Nørresundby; 57°5.130′ N, 9°55.659′ E; NJ52; 21 Oct. 1891; *J.P. Johansen Dry0082*; V. Hansen det.; ZMUC C-F-124148.

On *Leiodes picea* (Panzer, 1797) (Col. Leiodidae)
DENMARK – **Nordøstjylland (NEJ)** • Hvorup, Nørresundby; 57°5.130′ N, 9°55.659′ E; NJ52; Oct. 1888; *J.P. Johansen Dry0072*; J.P. Johansen det.; ZMUC C-F-124138.

On *Leiodes rufipennis* (Paykull, 1798) (Col. Leiodidae)
DENMARK – **Fyn (F)** • Fåborg; 55°5.897′ N, 10°14.474′ E; NG70; ca 1870; *No data coll. & det. Dry0090*; ZMUC C-F-124156. – **Nordøstjylland (NEJ)** • Hvorup, Nørresundby; 57°5.130′ N, 9°55.659′ E; NJ52; 21 Oct. 1891; *V. Hansen Dry0089*; J.P. Johansen det.; ZMUC C-F-124155. – **Nordøstsjælland (NEZ)** • Ørholm; 55°47.916′ N, 12°30.502′ E; UB48; 15 Sep. 1918; *Rosenberg Dry0088*; Rosenberg det.; ZMUC C-F-124154 • Ravnehom Grusgrav; 55°48.353′ N, 12°31.055′ E; UB48; 12 Aug. 1923; *Rosenberg Dry0087*; Rosenberg det.; ZMUC C-F-124153. – **Sydjylland (SJ)** • Tørning; 55°14.262′ N, 9°22.426′ E; NG22; 23 Jul. 1898; *Johs. Andersen Dry0086*; Johs. Andersen; ZMUC C-F-124152.

On *Leiodes triepkei* (Schmidt, 1841) (Col. Leiodidae)
DENMARK – **Nordøstjylland (NEJ)** • Hvorup, Nørresundby; 57°5.130′ N, 9°55.659′ E; NJ52; Sep. 1891; *J.P. Johansen Dry0080*; J.P. Johansen det.; ZMUC C-F-124146. – **Vestjylland (WJ)** • Esbjerg; 55°29.375′ N, 8°26.363′ E; MG64; 13 Aug. 1920; *Rosenberg Dry0079*; Rosenberg det.; ZMUC C-F-124145.

Remarks

First record from Denmark. The precise description of some so-called "curious thalli" (Santamaria 2003: 265–266) corresponds to what, according to Danish thalli studied, seems to be the most typical for this species. These larger forms are found on legs and tarsi whereas the smaller thalli are from elytra.

Euphoriomyces magnicellulatus Santam.
MB#128408
Fig. 10A

Revista Iberoamericana de Micología 8: 48 (Santamaria 1991). – **Type**: "España. Girona: Riells i Viabrea, 16-I-88, DG62, leg. S. Santamaría, sobre los élitros y pronoto de *Hydnobius multistriatus* Gyll. [SS777a] (Holotypus)"; FH.

Diagnostic features

Receptacle consisting of 6–9 superposed cells. All cells flattened except for the upper cell of the receptacle which is rectangular, twice or more times as long as broad, and laterally bears the perithecium (Fig. 10A, *). All cells of the receptacle, except for cell I and 1–2 cells above, dividing bilaterally to form secondary appendages, some of them giving rise to terminal, short antheridia. Cell VI triangular in section, forming an oblique base for the perithecium. [Detailed descriptions: Santamaria 2003; Majewski 2006]

Distribution and hosts

Only known from Spain (type), Poland (Majewski 2006), and Bulgaria (Rossi *et al.* 2019a), typically on *Hydnobius*, but also reported on *Leiodes* (Col. Leiodidae).

Collections examined from Denmark

On *Hydnobius multistriatus* (Gyllenhal, 1813) (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Hestehave; 56°17.015′ N, 10°28.162′ E; NH93; 6 Sep. 1922; *V. Hansen Dry0066*; V. Hansen det.; ZMUC C-F-124132 • Silistria; 56°7.023′ N, 10°13.638′ E; NH72; 5 Sep. 1922; *V. Hansen Dry0067*; V. Hansen det.; ZMUC C-F-124133.

On *Hydnobius punctatus* (Sturm, 1807) (Col. Leiodidae)
DENMARK – **Nordøstjylland (NEJ)** • Hvorup, Nørresundby; 57°5.130′ N, 9°55.659′ E; NJ52; Sep. 1891; *J.P. Johansen Dry0065*; J.P. Johansen det.; ZMUC C-F-124131.

Remarks

First record from Denmark. The distribution of this species is patchy, from Southern to Northern Europe, probably by lack of exploration, but the record from Denmark is not surprising because of its previous record from neighbouring Poland.

Euphoriomyces smicri Santam. sp. nov.
MB#840601
Fig. 10B–F

Diagnosis

Thallus short, stout. Perithecium flask-shaped with a well-distinguished and narrow neck. Trichogyne stump remaining as an outgrowth on the outer side of the perithecium (Fig. 10D–E, ts).

Etymology

The species epithet is based on the host genus *Smicrus*.

Type material

Holotype

DENMARK – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.469′ N, 11°23.147′ E; PG47; on *Smicrus filicornis* (Fairmaire & Laboulbène, 1855) (Col. Ptiliidae); 18 Feb. 2017; *JP 342*; JP det.; ZMUC C-F-122821.

Isotypes

DENMARK • same data as for holotype; ZMUC C-F-122822, C-F-122823, C-F-122824.

Description

Thallus hyaline, except for the blackened foot and yellowish perithecium. Receptacle axis consisting of 6–10 superposed cells which are broader than long, those of the basal area being especially flattened. Basal cell of the receptacle (I) slightly longer than broad, obtriangular. Two to four of the lower cells of the receptacle remain undivided; cells above dividing at one or both sides into cells giving rise to perithecium, secondary appendages, or antheridia. The latter broad, short, stout, sessile, on any of the two sides of thallus, usually only well-distinguished on immature thalli (Fig. 10B–C, arrows). Secondary appendages (Fig. 10C, sa) similar to the primary appendage.

Primary appendage unbranched, continuing the main receptacle axis, consisting of up to eight elongated cells (Fig. 10B–C, pa). The uppermost receptacular axis cell longer than broad, forming a peduncle for the primary appendage (Fig. 10C, *). Primary septum constricted (Fig. 10C, a).

Perithecium solitary (only one thallus shows a second perithecial initial; Fig. 10F, arrow), flask-shaped, with a broad venter and a narrow, abruptly distinguished neck. Apex blunt to flat. Trichogyne stump apparent, resulting into an outgrowth around cell w_4 (Fig. 10D–E, ts).

Length from foot to apex of perithecium 70–95 µm. Perithecium 40–63 × 17–27 µm. Maximum length of primary appendage from primary septum (when undamaged) 121 µm.

Thalli were found on the elytra of the hosts. The hosts were sifted from semi-dry, mouldy and rotten straw with many mice-tracks on sun-exposed grazed meadow.

Remarks

This is the first species of the genus described on a member of Ptiliidae, *Smicrus filicornis*, a rarely collected beetle usually found in fermenting, warm compost piles. The fungus does not seem to be related to any other known species of the genus. Although the material is scarce, we have not been able to resist describing it, given its exceptional nature. Some of the perithecial basal cells are barely apparent (Fig. 10D) which does not quite fit the genus description. Nevertheless, receptacle and other characteristics are seamlessly those described for the genus.

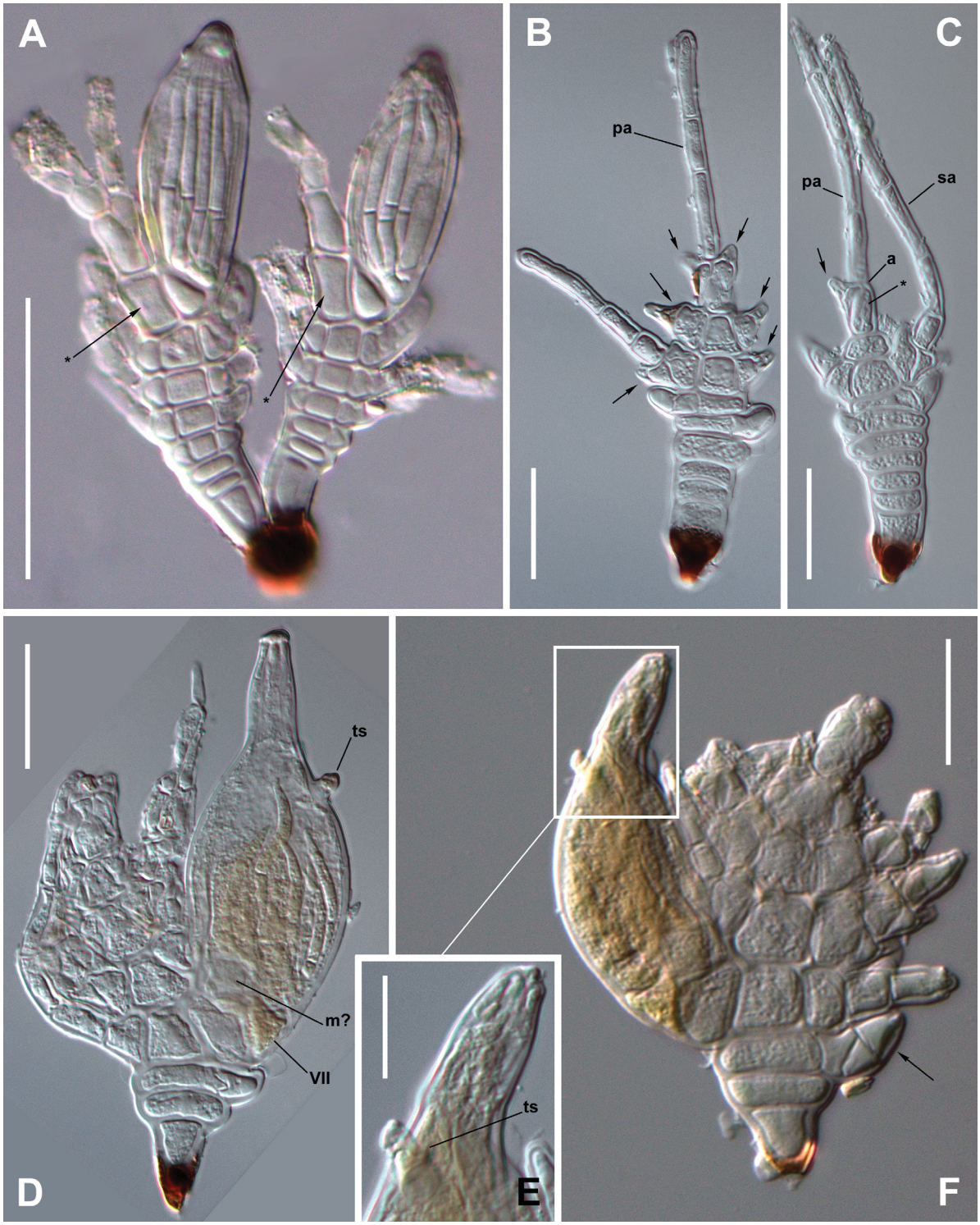

Fig. 10. *Euphoriomyces* spp. **A**. *E. magnicellulatus* Santam. Paired mature thalli, with elongated cell of receptacle (*). – **B**–**F**. *E. smicri* Santam. sp. nov. **B**–**C**. Immature thalli showing antheridia (arrows), primary appendage (pa), primary septum (a), and uppermost receptacular axial cell (*). **D**. Mature thallus showing cells VII, probably m (m?) and trichogyne stump (ts). **E**. Detail of the perithecial apex from F, with trichogyne stump (ts). **F**. Mature thallus with a labelled perithecial initial (arrow). Scale bars: A = 50 µm; B–D, F = 20 µm; E = 10 µm. Photographs from slides ZMUC C-F-124132 (A), and ZMUC C-F-122821 (holotype) (B–F).

Euphoriomyces unilateralis T.Majewski
MB#459691
Fig. 11A–B

Acta Mycologica 34: 13 (Majewski 1999). – **Type**: "On *Agathidium atrum* (Paykull) (Col. Leiodidae): Bialowieza Forest, sect. 638D, *Circaeo-Alnetum*, in litter, 24.7.1997, leg. T. Majewski (TM 7734, -holotype-)"; KRAM. [Poland]

Diagnostic features

All the cells of receptacle (except the lower 4–7) divide unilaterally to form single sterile cells and perithecia. Antheridia borne distally on short branches of the appendage which continues the receptacle axis. [Detailed description: Santamaria 2003]

Distribution and hosts

On *Agathidium* (Col. Leiodidae) from Poland (type) and Spain (Santamaria 2001a).

Collections examined from Denmark

On *Agathidium atrum* (Paykull, 1798) (Col. Leiodidae)
DENMARK – **Nordøstsjælland (NEZ)** • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 1 Dec. 2019; *JP 1567*; JP det.; ZMUC C-F-124327.

On *Agathidium seminulum* (Linnaeus, 1758) (Col. Leiodidae)
DENMARK – **Nordøstsjælland (NEZ)** • Geelskov; 55°48.269′ N, 12°28.343′ E; UB48; 10 Dec. 2018; *M. Kofoed-Hansen 1270*; M. Kofoed-Hansen det.; ZMUC C-F-123798.

Remarks

First record from Denmark. In our opinion, *E. unilateralis* is a good species, well recognizable and distinguished from the similar *E. agathidii* by the narrow receptacle and by the absence of appendages and perithecia on one side.

Genus ***Phaulomyces*** Thaxt.
MB#3983

Memoirs of the American Academy of Arts and Sciences 16: 259 (Thaxter 1931). – Type species: *P. corylophodis* Thaxt.

Adelomyces Thaxt., *Memoirs of the American Academy of Arts and Sciences* 16: 306 (Thaxter 1931) [MB#79]

Brief description

Probably all species are monoecious. Lower receptacle two-celled. Antheridia sessile or subsessile, on the basal cell of the primary appendage (Fig. 11E, an); proliferating into branches in older thalli.

Remarks

The genus consists of 14 species, of which eight in Europe, two in Denmark. The most recently described species are *P. mediterraneus* (Santamaria & Rossi 1999), and *P. ptilii* (Majewski 1999). In this genus we find some of the smallest species of Laboulbeniales, with thalli not reaching 50 µm of length, like *P. perparvus* Santam. (Santamaria 1992a).

Fig. 11. A–**B**. *Euphoriomyces unilateralis* T.Majewski. **A**. Paired thalli. **B**. Thallus with two perithecia, the lower immature, the upper overmature. – **C**. *Phaulomyces euaestheti* (Thaxt.) I.I.Tav., mature thallus with two perithecia and with the probable cell III labelled (III?). – **D**–**E**. *Phaulomyces octotemni* (T.Majewski) I.I.Tav. **D**. Paired thalli. **E**. Five thalli with a labelled antheridium (an) on the right immature thallus. Scale bars: A–B = 20 µm; C–E = 50 µm. Photographs from slides ZMUC C-F-123798 (A–B), ZMUC C-F-122484 (C), ZMUC C-F-124330 (D), ZMUC C-F-124329 (E).

Key to the Danish species

1. Third cell of the receptacle slightly flattened to isodiametric. Appendage ramified with rather long branches; up to 250 µm long. Perithecium bent towards the appendage. On Col. Ciidae ..... ***P. octotemni*** (T.Majewski) I.I.Tav.
– Third cell of the receptacle elongate, about twice longer than broad. Appendage unbranched; up to 180 µm long. Perithecium straight, or if bent, pointing towards the opposite direction of the appendage. On Col Staphylinidae Euaesthetinae ..... ***P. euaestheti*** (Thaxt.) I.I.Tav.

Phaulomyces euaestheti (Thaxt.) I.I.Tav.
MB#105669
Fig. 11C

Mycologia Memoirs 9: 274 (Tavares 1985). – **Basionym**: *Corethromyces euaestheti* Thaxt., *Memoirs of the American Academy of Arts and Sciences* 16: 196 (Thaxter 1931, as *euaesthetae*) [MB#264284]. – **Type**: "On the abdomen of *Euaesthetus americanus* Er., No. 1794, Sharon, Mass"; FH. [USA]

Diagnostic features

Third cell of the receptacle elongate, about twice longer than broad. One or two perithecia for each thallus. Appendage consisting of a basal cell supporting a simple branch and 1–2 elongated flask-shaped antheridia. [Detailed description: Majewski 1994b]

Distribution and hosts

Described from USA, it has been also reported from Germany (Scheloske 1969) and Poland (Majewski 1994a). Infects species of the genus *Euaesthetus* Gravenhorst, 1806 (Col. Staphylinidae Euaesthetinae).

Collections examined from Denmark

On *Euaesthetus ruficapillus* (Lacordaire, 1835) (Col. Staphylinidae Euaesthetinae)
DENMARK – **Østjylland (EJ)** • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 532*; JP det.; ZMUC C-F-123016. – **Lolland, Falster, Møn (LFM)** • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; *JP 1521*; JP det.; ZMUC C-F-124276. – **Nordøstsjælland (NEZ)** • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1220*; JP det.; ZMUC C-F-123747 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 11*; JP det.; ZMUC C-F-122483, C-F-122484 • ibid.; 19 Mar. 2017; *JP 674*; JP det.; ZMUC C-F-123163 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 866*; JP det.; ZMUC C-F-123362 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1031*; JP det.; ZMUC C-F-123543 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1049*; JP det.; ZMUC C-F-123565. – **Sydsjælland (SZ)** • Brænøre Mose; 55°23.906′ N, 9°25.714′ E; NG23; 5 Aug. 2018; *JP 1166*; JP det.; ZMUC C-F-123691 • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 496*; JP det.; ZMUC C-F-122980 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1414*; JP det.; ZMUC C-F-123960.

Remarks

First record from Denmark. The position of the primary septum is not well understood. The first perithecium develops from the cell II but the second perithecium is born from the elongated 3rd cell of the receptacle which, therefore, cannot be the cell III. Probably, cell III corresponds to the 4th cell of the receptacle (Fig. 11C, III?). A photo of this species is given here for the first time.

Phaulomyces octotemni (T.Majewski) I.I.Tav.
MB#105670
Fig. 11D–E

Mycologia Memoirs 9: 273 (Tavares 1985). – **Basionym**: *Euphoriomyces octotemni* T.Majewski, *Acta Mycologica* 9(2): 232 (Majewski 1973c) [MB#313989]. – **Type**: "On *Octotemnus glabriculus* Gyll. (Col., Cisidae): Berezki, Ustrzyki Dolne county (Bieszczady Mts.), in small polypores on lying trunks of trees in a beech wood on the right bank of Wolosaty stream (650 m), 12.9.1972 leg. T. Majewski (TM. … 1040 – holotype)"; KRAM. [Host family is a Ciidae, not Cisidae]

Diagnostic features

Third cell of the receptacle ± isodiametric, sometimes slightly flattened. One, more rarely two, perithecia for each thallus; bent towards the appendage. Appendage very elongate if undamaged, up to 250 µm long, 3–4 times as long as thalli. [Detailed description: Majewski 1994b]

Distribution and hosts

Only known on the species type host from Poland (type) and Spain (Santamaria 1995b).

Collections examined from Denmark

On *Octotemnus glabriculus* (Gyllenhal, 1827) (Col. Ciidae)
DENMARK – **Østjylland (EJ)** • Almose i Fjeld Skov; 56°24.698′ N, 10°27.948′ E; NH95; 23 Nov. 2019; *JP 1569*; JP det.; ZMUC C-F-124329, C-F-124330. – **Lolland, Falster, Møn (LFM)** • Keldskov; 54°39.977′ N, 11°33.286′ E; PF66; 15 Oct. 2019; *JP 1515*; JP det.; ZMUC C-F-124270. – **Nordøstsjælland (NEZ)** • Hørsholm Arboret; 55°52.017′ N, 12°30.373′ E; UB49; 13 Nov. 2019; *JP 1544*; JP det.; ZMUC C-F-124304, C-F-124305.

Remarks

First record from Denmark. Although the host is common and widespread in Denmark, the fungus seems to be quite rare. Exactly as occurs with *P. euaestheti* there are problems with understanding where the primary septum is located. The successive formation of first and second perithecia if any, is driven likewise in both species. According to literature, antheridia are unknown in *P. octotemni*. Nevertheless at least in one of the studied immature thalli we suspect the presence of one flask-shaped antheridium on the first cell of the appendage (Fig. 11E, an), similarly to described for *P. euaestheti*.

Genus ***Siemaszkoa*** I.I.Tav. & T.Majewski
MB#5028

Mycotaxon 3: 202 (Tavares & Majewski 1976). – Type species: *S. flexa* (T.Majewski) I.I.Tav. & T.Majewski

Brief description

Monoecious. Receptacle uniseriate, unbranched, consisting of three or more superposed cells supporting cell VI and the perithecium. Antheridia are sessile, short phialides, on appendages.

Remarks

The genus consists of seven species, of which six in Europe, four in Denmark. The most recently described species are *S. ramificans* and *S. valida* (Majewski 1991). All the species have diminutive thalli and occur on Ptiliidae beetles. In the species descriptions, when we describe the receptacle, it refers to cells from foot to the cell subtending cell VI; this is because the primary septum cannot be identified with certainty.

Key to the Danish species (partially following Majewski 1994b)

1. The perithecium is a continuation of the receptacle axis 2
– The perithecium is lateral to the axis which is formed by the receptacle and the appendage. Perithecium narrowly elongate. Round black spot on the foot ..... ***S. ptenidii*** (Scheloske) I.I.Tav.

2. Appendage unbranched, strongly bent backward in mature thalli; bearing broad sessile antheridia near its base..... ***S. flexa*** (T.Majewski) I.I.Tav.
– Appendage branched or, if unbranched, antheridia are the cells of appendage axis themselves which bear lateral short efferent necks 3

3. Appendage directed upwards, unbranched or sparsely branched. Perithecium ovate .... ***S. fennica*** Huldén
– Appendage branched and directed backwards in mature thalli. Antheridia flask-shaped, borne on the appendage branches. Lower cells of appendage variably inflated and with strongly constricted septa ..... ***S. ramificans*** T.Majewski

Siemaszkoa fennica Huldén
MB#108513
Fig. 12A–E

Karstenia 23: 63 (Huldén 1983). – **Type**: "Slide L. Huldén 25. On *Ptenidium laevigatum* Erichson (Coleoptera, Ptiliidae). Collecting data of the host: Finland. Ab: Uusikaupunki, leg. Söderman (holotype)"; MZH.

Diagnostic features

Receptacle consisting of 8–12 superposed cells (cell I included). Appendage simple or sparsely branched (usually broken with age); the 2–4 lower cells are antheridia showing a short lateral efferent neck on their upper, inner corners (Fig. 12D, arrows). Perithecium seems to be terminal on the receptacle axis. Perithecial apex asymmetric, showing a protruding lip. [Detailed descriptions: Majewski 1991, 1994b; Huggert 2010]

Distribution and hosts

Siemaszkoa fennica was described from Finland and later found in Poland (Majewski 1991), United Kingdom (Weir 1996), Spain, Italy (Santamaria & Rossi 1999), Sweden (Huggert 2010), and the Netherlands (Haelewaters *et al.* 2014). It occurs on species of *Ptenidium* Erichson, 1845 (Col. Ptiliidae).

Collections examined from Denmark

On *Ptenidium intermedium* Wankowiez, 1869 (Col. Ptiliidae)

DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 754*; JP det.; ZMUC C-F-123248. – **Fyn (F)** • Kohaveskov ved Landkildegård; 55°22.750′ N, 10°27.979′ E; NG93; 21 Nov. 2013; *JP 182*; JP det.; ZMUC C-F-122661 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1065*; JP det.; ZMUC C-F-123582. – **Sydsjælland (SZ)** • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; 17 Feb. 2019; *JP 1392*; JP det.; ZMUC C-F-123935.

On *Ptenidium laevigatum* Erichson, 1845 (Col. Ptiliidae)

DENMARK – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *JP 295*; JP det.; ZMUC C-F-122774 • Toftlund; 55°11.779′ N, 9°3.837′ E; NG01; 8 Mar. 2020; *JP 1602*; JP det.; ZMUC C-F-124358. – **Sydsjælland (SZ)** • Enemærket ved Næsbyholm; 55°22.429′ N, 11°36.776′ E; PG63;

Fig. 12. *Siemaszkoa* spp. **A**–**E**. *S. fennica* Huldén. **A**–**B**. Mature thalli. **C**. Unusual thallus with two perithecia. **D**. Detail of a mature thallus showing antheridia (arrows). **E**. Short thallus from legs. – **F**–**I**. *S. flexa* (T.Majewski) I.I.Tav. & T.Majewski. **F**–**G**. Mature thalli. **H**. Detail of foot. **I**. Detail of an immature thallus showing antheridia (arrows). Scale bars: A–C, E–G = 50 µm; D, H–I = 20 µm. Photographs from slides ZMUC C-F-122949 (A), ZMUC C-F-123248 (B), ZMUC C-F-123466 (C), ZMUC C-F-123309 (D), ZMUC C-F-123582 (E), ZMUC C-F-123632 (F–G), ZMUC C-F-123583 (H–I).

17 Nov. 2019; *JP 1561*; JP det.; ZMUC C-F-124321 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 23 Sep. 2018; *JP 1178*; JP det.; ZMUC C-F-123702.

On *Ptenidium pusillum* (Gyllenhal, 1808) (Col. Ptiliidae)

DENMARK – **Østjylland (EJ)** • Almose i Fjeld Skov; 56°24.698′ N, 10°27.948′ E; NH95; 23 Nov. 2019; *JP 1550*; JP det.; ZMUC C-F-124311 • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 793*; JP det.; ZMUC C-F-123288 • Kjellerup; 56°17.589′ N, 9°26.117′ E; NH23; 21 Oct. 2017; *JP 584*; JP det.; ZMUC C-F-123070 • ibid.; 56°17.614′ N, 9°26.106′ E; NH23; 18 Nov. 2017; *JP 815*; JP det.; ZMUC C-F-123309. – **Lolland, Falster, Møn (LFM)** • Busene Have syd for Busene; 54°56.738′ N, 12°31.666′ E; UA49; 8 Oct. 2017; *JP 579*; JP det.; ZMUC C-F-123065 • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 464*; JP det.; ZMUC C-F-122949. – **Nordøstsjælland (NEZ)** • Kalvehave i Gribskov; 56°0.411′ N, 12°20.660′ E; UC31; 23 Mar. 2019; *JP 1430*; JP det.; ZMUC C-F-123977 • Klinten ved Selsø; 55°44.158′ N, 11°59.634′ E; PG88; 11 Mar. 2007; *JP 517*; JP det.; ZMUC C-F-123000 • Skærød; 56°0.673′ N, 12°9.646′ E; UC21; 14 Jan. 2018; *JP 960*; JP det.; ZMUC C-F-123466 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 791*; JP det.; ZMUC C-F-123286 • ibid.; 23 Mar. 2017; *JP 465*; JP det.; ZMUC C-F-122950 • ibid.; 55°48.367′ N, 12°33.322′ E; UB48; 24 Feb. 2019; *JP 1345*; JP det.; ZMUC C-F-123884. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 601*; JP det.; ZMUC C-F-123090. – **Sydjylland (SJ)** • Sølsted Mose; 55°1.829′ N, 8°50.351′ E; MF89; 2 Jun. 2013; *JP 484*; JP det.; ZMUC C-F-122968. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1376*; JP det.; ZMUC C-F-123917 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1422*; JP det.; ZMUC C-F-123968 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 15 Aug. 2013; *JP 395*; JP det.; ZMUC C-F-122878 • Villa Gallina i Hesede Skov; 55°16.335′ N, 11°56.850′ E; PG82; 8 Mar. 2015; *JP 481*; JP det.; ZMUC C-F-122965.

On *Ptenidium turgidum* Thomson, 1855 (Col. Ptiliidae)

DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.282′ N, 9°26.197′ E; NH23; 16 Oct. 2014; *JP 322*; JP det.; ZMUC C-F-122800.

Remarks

First record from Denmark. Extremely reduced thalli with only two cells above cell I have been found growing on legs of its hosts (Fig. 12E). A photo of this species is given here for the first time.

Siemaszkoa flexa (T.Majewski) I.I.Tav. & T.Majewski
MB#323554
Fig. 12F–I

Mycotaxon 3: 204 (Tavares & Majewski 1976). – **Basionym**: *Misgomyces flexus* T.Majewski, *Acta Mycologica* 9(1): 119 (Majewski 1973a) [MB#317765]. – **Type**: "On *Ptenidium fuscicorne* Er. (Ptiliidae): Kielpin, Nowy Dwór Mazowiecki county, in litter at foot of alder next to small pond, 22.12.1971 leg. T. Majewski (TM 899 – holotype)"; KRAM. [Poland]

Diagnostic features

Receptacle consisting of 8–9 superposed cells (cell I included); strongly curved in mature thalli. Appendage unbranched, long, strongly bent outward in relation to the receptacle axis, bearing broad, conical, short, 1–3 antheridia in some lower cells (Fig. 12I, arrows). Perithecium appears to be terminal on the receptacle axis. Perithecial apex obtuse, slightly asymmetric. [Detailed descriptions: Majewski 1991, 1994b]

Distribution and hosts

Only known from the Polish type on species of *Ptenidium* (Col. Ptiliidae).

Collections examined from Denmark

On *Ptenidium fuscicorne* Erichson, 1845 (Col. Ptiliidae)

FDENMARK – **yn (F)** • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1066*; JP det.; ZMUC C-F-123583. – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1113*; JP det.; ZMUC C-F-123632. – **Nordøstjylland (NEJ)** • Vandplasken ved Kærsgård Strand; 57°31.199′ N, 9°53.070′ E; NJ57; 21 Nov. 2017; *JP 805*; JP det.; ZMUC C-F-123300. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 734*; JP det.; ZMUC C-F-123227 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 21*; JP det.; ZMUC C-F-122494 • ibid.; 19 Mar. 2017; *JP 682*; JP det.; ZMUC C-F-123170 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 790*; JP det.; ZMUC C-F-123285. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Apr. 2019; *JP 1426*; JP det.; ZMUC C-F-123972 (2 slides).

On *Ptenidium intermedium* Wankowiez, 1869 (Col. Ptiliidae)

DENMARK – **Sydsjælland (SZ)** • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1431*; JP det.; ZMUC C-F-123978.

On *Ptenidium pusillum* (Gyllenhal, 1808) (Col. Ptiliidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 840*; JP det.; ZMUC C-F-123335.

Remarks

First record from Denmark and the first after it was originally described. This species has rarely been found as mature in Denmark, but the immature thalli showing broad, lateral antheridia on appendage, may be easily classified. The foot consists of a lateral darker spot surrounded by a paler area (Fig. 12H).

Siemaszkoa ptenidii (Scheloske) I.I.Tav. & T.Majewski
MB#323555
Fig. 13A–C

Mycotaxon 3: 204 (Tavares & Majewski 1976). – **Basionym**: *Misgomyces ptenidii* Scheloske, *Parasitologische Schriftenreihe* 19: 135 (Scheloske 1969) [MB#334359]. – **Type**: "In einzelnen Exemplaren auf Halsschild und Elytren von *Ptenidium* sp. (*Pt. fuscicorne*?) (Col. Ptiliidae). – Die Funde stammen aus dem Gesiebe (Bodenstreu) aus Erlenbruchwäldern bei Schwand/Nürnberg und aus Genist an Weihern bei Dechsendorf/Erlangen. Deutschland. Holotypus Abb. 36". [Germany]

Diagnostic features

Receptacle consisting of 5–9 superposed cells (cell I included). Appendage unbranched, seeming like a prolongation of the receptacle axis. Antheridia unknown. Perithecium narrow and elongate, lateral to the thallial axis. Perithecial apex asymmetric, showing a protruding lip (Fig. 13A, *). [Detailed descriptions: Majewski 1991, 1994b]

Distribution and hosts

Only known from Germany (type), Poland (Majewski 1973c), and Belgium (De Kesel *et al.* 2020). Occurs on *Ptenidium* (Col. Ptiliidae).

Collections examined from Denmark

On *Ptenidium fuscicorne* Erichson, 1845 (Col. Ptiliidae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 684*; JP det.; ZMUC C-F-123172 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1066*; JP det.; ZMUC C-F-123583. – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1113*; JP det.; ZMUC C-F-123633 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1341*; JP det.; ZMUC C-F-123880. – **Nordøstjylland (NEJ)** • Syd for Krogsagergård; 56°37.534′ N, 9°45.551′ E; NH47; 24 Nov. 2019; *JP 1551*; JP det.; ZMUC C-F-124312. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 734*; JP det.; ZMUC C-F-123227 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 682*; JP det.; ZMUC C-F-123170 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 870*; JP det.; ZMUC C-F-123366 • Mølleå ved Farum Lillevang; 55°49.093′ N, 12°18.496′ E; UB38; 24 Feb. 2018; *JP 993*; JP det.; ZMUC C-F-123500 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 790*; JP det.; ZMUC C-F-123285. – **Nordvestjylland (NWJ)** • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 768*; JP det.; ZMUC C-F-123262. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 887*; JP det.; ZMUC C-F-123385. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Apr. 2019; *JP 1426*; JP det.; ZMUC C-F-123972 (2 slides) • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1453*; JP det.; ZMUC C-F-124003. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1269*; JP det.; ZMUC C-F-123797.

On *Ptenidium intermedium* Wankowiez, 1869 (Col. Ptiliidae)

DENMARK – **Sydsjælland (SZ)** • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1431*; JP det.; ZMUC C-F-123978.

On *Ptenidium pusillum* (Gyllenhal, 1808) (Col. Ptiliidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 840*; JP det.; ZMUC C-F-123335.

Remarks

First record from Denmark. Sometimes coexists with *S. flexa* on the same host specimen. Although many immature thalli have been studied, we have not detected the presence of antheridia. A well-distinguished trichogyne stump may be seen on the outer side of the perithecium (Fig. 13B, arrow), which suggests the existence of antheridia. Rarely, some thalli bear a second mature perithecium (Fig. 13B). Thalli from host underside show inflated receptacular cells with constricted septa (Fig. 13B).

Siemaszkoa ramificans T.Majewski
MB#363463
Fig. 13D–G

Polish Botanical Studies 2: 224 (Majewski 1991). – **Type**: "On *Ptenidium turgidum* Thomson. Bt. Bialowieza National Park, sect. 256, 18.6.1989 (4489 – holotype)"; KRAM. [Poland]

Diagnostic features

Receptacle consisting of (4–)5–6 superposed cells (cell I included). Appendage ramified into several branches above 2nd–5th cell; some of the branches bear narrowly elongated, flask-shaped antheridia (Fig. 13E–F, arrows). Cells of the base of the appendage typically inflated (Fig. 13D, *). Perithecium

Fig. 13. *Siemaszkoa* spp. **A**–**C**. *S. ptenidii* (Scheloske) I.I.Tav. & T.Majewski. Mature thalli showing protruding lip in A (*), and a trichogyne stump in B (arrow). Thallus in B has developed two mature perithecia. – **D**–**G**. *S. ramificans* T.Majewski. **D**. Mature thallus showing cells of the base of the appendage typically inflated (*). **E**–**F**. Immature thalli showing antheridia (arrows). **G**. Mature thallus. Scale bars: A, D = 20 µm; B–C, E–G = 50 µm. Photographs from slides ZMUC C-F-123285 (A), ZMUC C-F-123972 (B), ZMUC C-F-123227 (C), ZMUC C-F-122719 (D), ZMUC C-F-122797 (E–F), ZMUC C-F-124322 (G).

appears to be terminal on the receptacle axis. Perithecial apex asymmetric, with a protruding lip. [Detailed description: Majewski 1994b]

Distribution and hosts

Only known from Poland (type) on species of the genus *Ptenidium* (Col. Ptiliidae).

Collections examined from Denmark

On *Ptenidium turgidum* Thomson, 1855 (Col. Ptiliidae)

DENMARK – **Nordøstjylland (NEJ)** • Vesterskoven i Tofte Skov; 56°50.346′ N, 10°13.361′ E; NJ70; 7 Aug. 2013; *JP 318*; JP det.; ZMUC C-F-122797. – **Nordøstsjælland (NEZ)** • Stampeskov ved Rådvad; 55°48.367′ N, 12°33.322′ E; UB48; 23 Mar. 2017; *JP 239*; JP det.; ZMUC C-F-122719. – **Sydsjælland (SZ)** • Enemærket ved Næsbyholm; 55°22.429′ N, 11°36.776′ E; PG63; 17 Nov. 2019; *JP 1562*; JP det.; ZMUC C-F-124322.

Remarks

First record from Denmark and first since it was originally described. Unusual short thalli have been collected under the head of one host specimen, and we have decided to assign them to *S. ramificans* because of characters of the perithecial apex and the base of the appendage (Fig. 13D). A photo of this species is given here for the first time.

Tribe Teratomyceteae Thaxt.
Subtribe Teratomycetinae s. str.

Genus ***Idiomyces*** Thaxt.
MB#2481

Proceedings of the American Academy of Arts and Sciences 28: 162 (Thaxter 1893). – Type species: *I. peyritschii* Thaxt. (by monotypy)

Brief description

Monoecious. Receptacle asymmetric, multicelled, with a subdivided cell II giving rise to a lateral row of cells supporting a mass of secondary appendages, some of them fertile and consisting of several superposed antheridia with the efferent necks pointing laterally. Perithecia (one to a few for each thallus) with well-developed basal cells and an outer wall with four unequal wall cells for each vertical row.

Remarks

Monotypic. Related to *Diplomyces*, *Sandersoniomyces*, *Symplectromyces* and *Teratomyces*, Benjamin (1983) did a complete study of this genus.

Idiomyces peyritschii Thaxt.
MB#233231
Fig. 14A–B

Proceedings of the American Academy of Arts and Sciences 28: 162 (Thaxter 1893). – **Type**: "On abdomen of *Deleaster dichrous* Grav., Germany"; FH.

Diagnostic features

See genus description. [Detailed descriptions: Thaxter 1896; Benjamin 1983; Majewski 1994b; Santamaria 2003]

Distribution and hosts

On species of *Deleaster* (Col. Staphylinidae Oxytelinae). Known in **Europe**: Austria, France, Germany, the Netherlands, Hungary, Italy, Poland, Spain, Switzerland, United Kingdom, Russia, former Yugoslavia (Santamaria *et al.* 1991), Belgium (De Kesel & Rammeloo 1992), Greece (Castaldo *et al.* 2004), Bulgaria, Romania (Rossi *et al.* 2019a), and Austria (Rossi & Christian 2020). Also in USA and Japan (Santamaria *et al.* 1991).

Collections examined from Denmark

On *Deleaster dichrous* (Gravenhorst, 1802) (Col. Staphylinidae Oxytelinae)
DENMARK – **Bornholm (B)** • Borrelyng; 55°15.170′ N, 14 45.240′ E; VB82; 30 Jun. 1988; *E. Palm Dry0104*; JP det.; ZMUC C-F-124170. – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.958′ N, 12°32.210′ E; UA49; 18–24 Sep. 2005; *O. Karsholt Dry0102*; JP det.; ZMUC C-F-124168. – **Nordøstsjælland (NEZ)** • København Ø.; 55°42.152′ N, 12°33.572′ E; UB47; 25–27 Jun. 2001; *O. Karsholt Dry0103*; JP det.; ZMUC C-F-124169. – **Sydsjælland (SZ)** • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 4 Aug. 2014; *JP 32*; JP det.; ZMUC C-F-122507 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 20 Jun. 1984; *M. Hansen Dry0105*; M. Hansen det.; ZMUC C-F-124171.

Remarks

First record from Denmark. The new record from Denmark is not surprising because it was already reported from several European countries, including nearby Germany and Poland.

Genus ***Symplectromyces*** Thaxt.
MB#5319

Memoirs of the American Academy of Arts and Sciences 13: 314 (Thaxter 1908). – Type species: *S. vulgaris* Thaxt. (by monotypy)

Brief description

Monoecious. Receptacle multicelled, ± symmetric, with cell II subdivided by horizontal septa into cells IIa, IIb, and a distal cell III (Fig. 14C) which divides repeatedly by oblique septa forming a secondary receptacle bearing many appendages and one to a few perithecia. Antheridia seriated in the appendages, with variably elongated efferent necks (Fig. 14F); sometimes replaced by sterile branchlets.

Remarks

Monotypic. The development of its single species was studied by Benjamin (1968, 1983). Shares the subtribe Teratomycetinae with *Diplomyces*, *Idiomyces*, *Sandersoniomyces*, and *Teratomyces*.

Symplectromyces vulgaris (Thaxt.) Thaxt.
MB#236353
Fig. 14C–L

Memoirs of the American Academy of Arts and Sciences 13: 315 (Thaxter 1908). – **Basionym**: *Teratomyces vulgaris* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 35: 431 (Thaxter 1900)

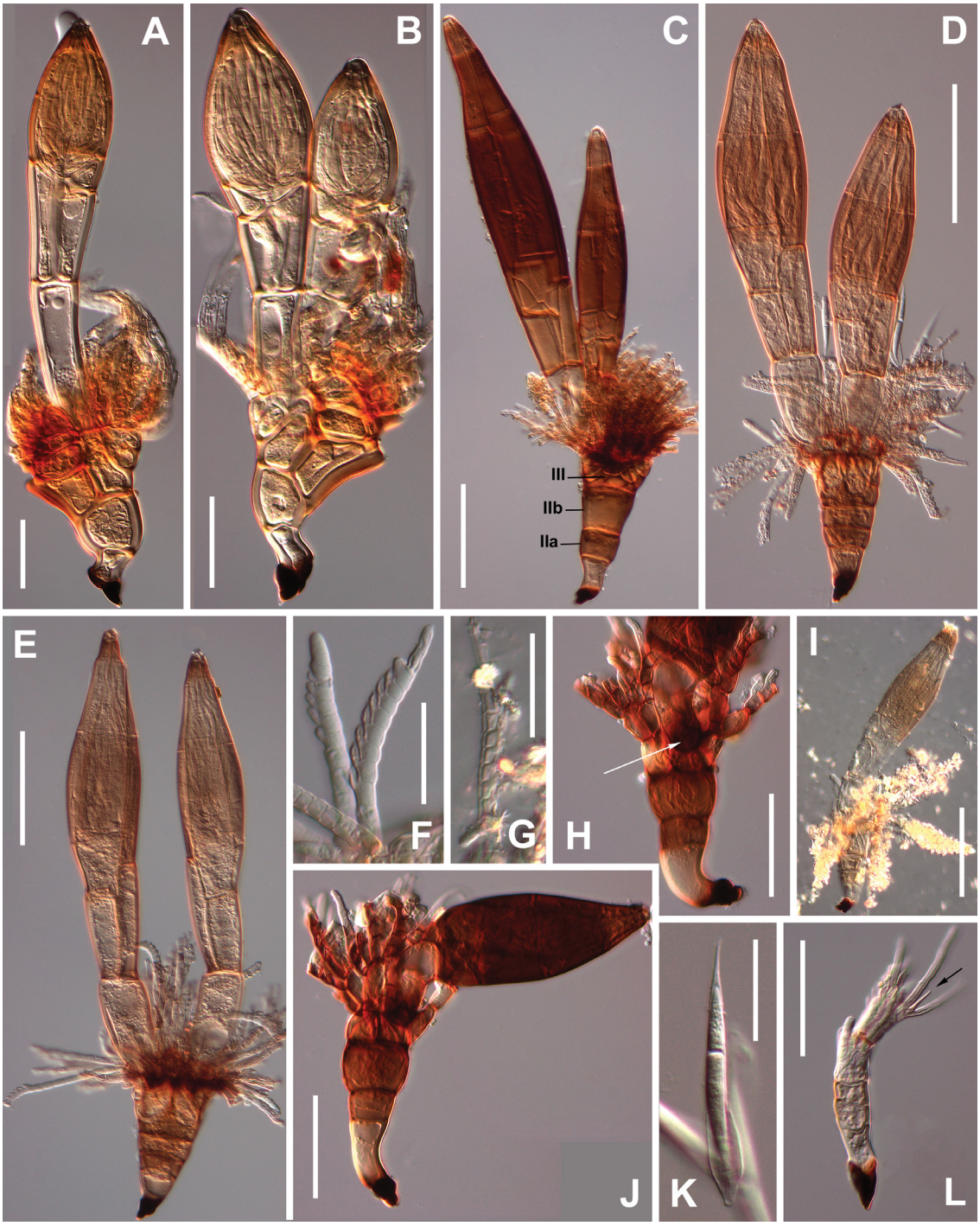

Fig. 14. A–**B**. *Idiomyces peyritschii* Thaxt. Mature thalli. – **C**–**L**. *Symplectromyces vulgaris* (Thaxt.) Thaxt. **C**. Mature thallus from *Quedius umbrinus* with labelled cells IIa, IIb, and III. **D**. Mature thallus from *Quedius xanthopus*. **E**. Mature thallus from *Quedius mesomelinus*. **F**–**G**. Details of appendages with seriated antheridia (G, in poor condition is from lectotype). **H**–**J**. Thalli from *Quedius boopoides*, with detail of dark cell VI in H (arrow). I. Mature thallus from lectotype slide. **K**. Ascospore. **L**. Very young thallus showing ascospore original spinous apex, the sx (arrow). Scale bars: A–B, G–H, J, L = 50 µm; C–E, I = 100 µm; F, K = 25 µm. Photographs from slides ZMUC C-F-122507 (A–B), ZMUC C-F-122498 (C), ZMUC C-F-122679 (D, K), ZMUC C-F-123742 (E–F), FH6581 (lectotype) (G, I), ZMUC C-F-123075 (H, J), ZMUC C-F-123521 (L).

[MB#140379]. – **Type**: "On *Quedius fulgidus* Fabr., Kiel, Schleswig Holstein (Germany), British Museum no. 354, R.Thaxter det. Harvard University Herbaria Barcode 00313732. Slide label no. 6581"; lectotype: FH[00313732], **here designated** (MycoBank: MBT10002234) (Fig. 14G, I).

Symplectromyces lapponicus Huldén (Huldén 1983: 69) [MB#108579]
Symplectromyces rarus Huldén (Huldén 1983: 69) [MB#108580]

Diagnostic features

See genus description. [Detailed descriptions: Benjamin 1968, 1983; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Infects species of *Quedius* Stephens, 1829 (Col. Staphylinidae Staphylininae). Records on *Philonthus* Stephens, 1829 require confirmation. Very common in **Europe** (Belgium, Finland, France, Germany, the Netherlands, Hungary, Italy, Poland, Portugal, Spain, Sweden, United Kingdom, Russia, former Yugoslavia), **America** (Canada, USA), and **Asia** (India, Burma) (Santamaria *et al.* 1991). Subsequently recorded from Czech Republic (Rossi *et al.* 2010), Armenia, Bulgaria, and China (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Quedius boopoides* Munster, 1923 (Col. Staphylinidae Staphylininae)
DENMARK – **Fyn (F)** • Knudshoved Marina; 55°17.781′ N, 10°50.542′ E; PG12; 18 Oct. 2017; *JP 588*; JP det.; ZMUC C-F-123075, C-F-123076, C-F-123077.

On *Quedius cinctus* (Paykull, 1790) (Col. Staphylinidae Staphylininae)
DENMARK – **Sydsjælland (SZ)** • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 1–15 Aug. 2013; *JP 526*; JP det.; ZMUC C-F-123010.

On *Quedius fuliginosus* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Dollerup Bakker; 56°21.897′ N, 9°19.716′ E; NH24; 17 May 2013; *H. Liljehult 161*; JP det.; ZMUC C-F-122640.

On *Quedius longicornis* Kraatz, 1857 (Col. Staphylinidae Staphylininae)
DENMARK – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 374*; JP det.; ZMUC C-F-122857.

On *Quedius maurorufus* (Gravenhorst, 1806) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Serup Skov; 56°14.504′ N, 9°28.051′ E; NH23; 26 Mar. 2017; *JP 244*; JP det.; ZMUC C-F-122724. – **Nordøstsjælland (NEZ)** • Damhusengen; 55°41.246′ N, 12°28.287′ E; UB49; 23 Apr. 2013; *H. Liljehult 201*; JP det.; ZMUC C-F-122680. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 561*; JP det.; ZMUC C-F-123047. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 498*; JP det.; ZMUC C-F-122982. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1263*; JP det.; ZMUC C-F-123791.

On *Quedius mesomelinus* (Marsham, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.614′ N, 9°26.106′ E; NH23; 18 Nov. 2017; *JP 817*; JP det.; ZMUC C-F-123311. – **Nordøstsjælland (NEZ)** • Islev; 55°42.351′ N, 12°26.211′ E; UB37; 20 Oct. 2018; *JP 1215*; JP det.; ZMUC C-F-123742 • **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1014*; JP det.; ZMUC C-F-123521.

On *Quedius persimilis* Mulsant & Rey, 1876 (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.301′ N, 12°16.244′ E; UB20; 25 Sep. 2016; *JP 146*; JP det.; ZMUC C-F-122625.

On *Quedius semiobscurus* (Marsham, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Nordøst for Bispebjerg Station; 55°42.508′ N, 12°32.786′ E; UB47; 22 Aug. 2016; *JP 118*; JP det.; ZMUC C-F-122595.

On *Quedius truncicola* Fairmaire & Laboulbène, 1856 (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Dyrehaven; 55°47.347′ N, 12°33.957′ E; UB47; 15 Jun. 2017; *H. Liljehult 441*; JP det.; ZMUC C-F-122926 • Gribskov, Fændriksvang; 56°1.005′ N, 12°21.245′ E; UC30; 2 Jul. 2017; *J. Heilmann-Clausen et al. 1234*; A.K. Hansen det.; ZMUC C-F-123761.

On *Quedius umbrinus* Erichson, 1839 (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 750*; JP det.; ZMUC C-F-123244 • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 20 May 2013; *JP 369*; JP det.; ZMUC C-F-122852 • ibid.; 14 Feb. 2019; *JP 1350*; JP det.; ZMUC C-F-123889. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1337*; JP det.; ZMUC C-F-123876. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 3 Apr. 2015; *H. Liljehult 25*; JP det.; ZMUC C-F-122498 • ibid.; 19 Mar. 2017; *JP 676*; JP det.; ZMUC C-F-123165. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1383*; JP det.; ZMUC C-F-123925.

On *Quedius xanthopus* Erichson, 1839 (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 843*; JP det.; ZMUC C-F-123338. – **Nordøstsjælland (NEZ)** • Dyrehaven; 55°47.347′ N, 12°33.957′ E; UB47; 24 Feb. 2014; *H. Liljehult 200*; JP det.; ZMUC C-F-122679.

Other material examined

Lectotype of *Symplectromyces vulgaris* (here designated)
"*Symplectromyces vulgaris*, slide from FH, #6581, barcode 00313732, **type**, on *Quedius fulgidus* Fabr., from Schleswig-Holstein (Germany), ex British Museum coll. no. 354"; lectotype: FH[00313732], **here designated** (MycoBank: MBT10002234). [slide includes eight mature thalli and three broken portions in very poor condition (Fig. 14G, I)]

Remarks

First record from Denmark. The species was described as *Teratomyces vulgaris* from no less than seven localities without mentioning a type (Thaxter 1900). Here, we designate a lectotype from the single slide received from FH (see above under other material examined) which is labelled as the type (although never explicitly published as such). According to Botanical Databases from Harvard University Herbaria (https://huh.harvard.edu/) this is the only slide labelled as *Symplectromyces* or *Teratomyces vulgaris* kept in that herbarium. This slide includes thalli in poor condition, full of crystals that completely cover and hide parts of them; we reproduce here two photographs from the lectotype for its documentary interest (Fig. 14G, I).

Symplectromyces vulgaris may be thought as a very variable species, following Majewski (1994b) who considered it in a broad sense. Majewski synonymized *S. lapponicus* and *S. rarus* with *S. vulgaris* because characteristics such as the length of cell VI and the number or length of secondary appendages have been regarded of little importance. We have had the opportunity to study abundant material of this species from the Danish samples as well as many others that we have from Canada (unpublished). It is difficult

to separate species among the mess of morphs we have, but we are almost convinced that this would be possible and *S. vulgaris* should be regarded as a species complex. Further studies, with the help of more modern tools, probably will lead us to this conclusion. The study of a type slide from FH does not help us for splitting the species. From a conservative point of view, currently, we prefer to follow Majewski's thoughts.

We want to highlight the thalli found on *Quedius boopoides* (ZMUC C-F-123075) that have very outstanding characteristics that would well deserve their segregation as a new species (Fig. 14H, J). As a more notorious feature, the darkening and constriction of the base of cell VI warrants mention (Fig. 14H, arrow).

Genus ***Teratomyces*** Thaxt.
MB#5374

Proceedings of the American Academy of Arts and Sciences 28: 182 (Thaxter 1893). – Type species: *T. mirificus*

Brief description

Monoecious. Receptacle multicelled, symmetric, with cell II subdivided by horizontal septa into cells IIa, IIb, and a distal cell III which divides repeatedly by oblique septa forming a secondary receptacle bearing numerous appendages and one to a few perithecia. Antheridia seriated and intercalated with lateral efferent necks, or free, flask-shaped and terminal on the appendages. Acute sterile branchlets present.

Remarks

The genus consists of ten species, of which four in Europe, two in Denmark. The most recently described species is *T. cylindrocarpus* (Rossi & Bernardi 2018). With the same thallial structure as *Symplectromyces*, it can be distinguished from it by the pointed branchlets and antheridia present on the appendages.

Key to the Danish species

1. Perithecium with slight elevations at the septa separating the wall cells tiers; w_1 and w_3 brownish alternating with paler w_2 and w_4. On *Gabrius* Stephens, 1829 and allied genera (Col. Staphylinidae) ..... ***T. philonthi*** Thaxt.
– Perithecium without elevations at wall cells septa, smooth in outline, uniform in colour. On *Erichsonius* Fauvel, 1874 and related genera (Col. Staphylinidae)..... ***T. actobii*** Thaxt.

Teratomyces actobii Thaxt.
MB#140205
Fig. 15A–B

Proceedings of the American Academy of Arts and Sciences 29: 98 (Thaxter 1894). – **Type**: "USA, Maine, Kittery Point, 18 August 1893, [R. Thaxter], on *Erichsonius nanus* (Horn, 1884) [as *Actobius*], slide FH 00313507"; FH. [lectotype designated by Haelewaters *et al.* 2015b: 471]

Teratomyces brevicaulis Thaxt. (Thaxter 1894: 99) [MB#140281]
Teratomyces atropurpureus Maire (1920: 145) [MB#140504]

Diagnostic features

Cells I, IIa, IIb and III variably pigmented, sometimes blackened or entirely pale. Pointed branchlets on secondary appendages variably curved. Perithecium uniformly tinged with brown, smooth in outline,

without elevations on septa separating the wall cell tiers. [Detailed descriptions: Thaxter 1896; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Occurs on *Erichsonius* and allied genera like *Parerichsonius* Coiffait, 1961 and *Neobisnius* Ganglbauer, 1895 (Col. Staphylinidae Staphylininae). *Teratomyces actobii* is found in **Europe** (Spain, United Kingdom, France, Italy, Germany, Poland, Finland, Russia), **Africa** (Algeria), **Asia** (Sri Lanka), and **America** (USA)

Fig. 15. *Teratomyces* spp. **A**–**B**. *T. actobii* Thaxt. Immature and mature thalli showing variability in receptacle pigmentation. – **C**. *T. philonthi* Thaxt. Mature thallus with labelled wall cell tiers (w_{1-4}), pointed and arcuate secondary appendages (arrows), and cells IIa–b of receptacle. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122481 (A), ZMUC C-F-123544 (B), ZMUC C-F-122832 (C).

(Majewski 2008). Reported later from Sweden (Huggert 2010), Bulgaria (Rossi *et al.* 2019a), and Hungary (Rossi & Christian 2020). The record of *T. brevicaulis* on *Acylophorus* Nordmann, 1837 from France by Duverger (1995) might be referred to *Teratomyces mirificus* according to the identity of the host. Records of *T. actobii* reported and illustrated on *Gabrius* from Belgium by De Kesel *et al.* (2020: pl. 81) belong to *T. philonthi*, but those reported and illustrated as *T. philonthi* on the same host genus (De Kesel *et al.* 2020: pl. 82) might belong to *T. actobii*.

Collections examined from Denmark

On *Erichsonius cinerascens* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°58.979′ N, 12°32.281′ E; UA49; 2 May 2018; *A.K. Hansen 1100*; A.K. Hansen det.; ZMUC C-F-123618. – **Nordøstsjælland (NEZ)** • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1218*; JP det.; ZMUC C-F-123745 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 9*; JP det.; ZMUC C-F-122481 • Sjælland, North; without coordinates; ca 1870; *Schiødte Dry0190*; M. Uhlig det.; ZMUC C-F-124255 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1032*; JP det.; ZMUC C-F-123544. – **Nordvestsjælland (NWZ)** • Kattrup Haveskov; 55°36.707′ N, 11°23.065′ E; PG56; 6 Feb. 1990; *E. Palm Dry0189*; JP det.; ZMUC C-F-124254. – **Sydsjælland (SZ)** • Sorø Sø; 55°26.315′ N, 11°32.726′ E; PG64; 12 May 1896; *F. de Tengnagel Dry0188*; F. de Tengnagel det.; ZMUC C-F-124253.

Remarks

First record from Denmark. The darkening of cells IIa and IIb is variable and may be totally absent; therefore, this feature cannot be used to separate species such as *T. brevicaulis*, which was synonymized with *T. actobii* according to molecular sequencing (Haelewaters *et al.* 2015b).

Teratomyces philonthi Thaxt.
MB#140683
Fig. 15C

Proceedings of the American Academy of Arts and Sciences 35: 432 (Thaxter 1900, as *T. philonothi*). – **Type**: "On *Philonthus* sp. indet., British Museum, No. 365, Hungary"; FH.

Diagnostic features

Cell IIa entirely blackened, cell IIb ± darkened, at least in the lower region (Fig. 15C, IIa, IIb). Pointed branchlets on secondary appendages strongly arcuate to coiled (Fig. 15C, arrows). Perithecium with w_1 and w_3 tiers tinged with brown contrasting with paler w_2 and w_4 tiers, showing elevations in outline where septa separate the wall cell tiers (Fig. 15C, $w_{1–4}$). [Detailed descriptions: Thaxter 1896; Santamaria 1989; Majewski 1994b]

Distribution and hosts

This species has been reported from **Europe**: Finland, France, Germany, the Netherlands, Hungary, Italy, Poland, Spain (Santamaria *et al.* 1991). It has been reported later also from Belgium (De Kesel & Rammeloo 1992), United Kingdom (Weir 1994), and Austria (Rossi & Christian 2020). The epithet of this species is misleading because the hosts actually belong to the genus *Gabrius* (Col. Staphylinidae Staphylininae). Also recorded in **Africa** on the related genus *Gabronthus* Tottenham, 1955 from Zaire (Rossi & Santamaria 1992). De Kesel *et al.* (2020) reported this species also on *Quedius*, which however is the host genus of *Symplectromyces* (see above).

Collections examined from Denmark

On *Gabrius breviventer* (Sperk, 1835) (Col. Staphylinidae Staphylininae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; *JP 1524*; JP det.; ZMUC C-F-124279 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1336*; JP det.; ZMUC C-F-123875. – **Sydsjælland (SZ)** • Holtug Kalkbrud; 55°20.470′ N, 12°26.678′ E; UB33; 21 Sep. 2013; *JP 350*; JP det.; ZMUC C-F-122832.

Remarks

First record from Denmark. Distinguishing this species from *T. actobii* may be difficult depending on the collections, as was pointed out by Rossi *et al.* (2019a). Perhaps this is why De Kesel *et al.* (2020), according to their drawings, seemed to have confused the two species.

Subtribe Rhachomycetinae (Thaxt.) I.I.Tav.

Genus ***Microsomyces*** Thaxt.
MB#3190

Memoirs of the American Academy of Arts and Sciences 16: 184 (Thaxter 1931). – Type species: *M. psammoechi* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cell I continues in a branched rhizoidal haustorium that penetrates the host. Cell II becomes ± corticated by small cells, some of which giving rise to perithecia or secondary appendages bearing flask-shaped antheridia. Cell III supports a simple primary appendage ending in a solitary spinose flask-shaped antheridium. Perithecium outer wall with four cells for each vertical row.

Remarks

The genus consists of two species, of which one in Europe. Benjamin (1985) studied the morphology of the genus, especially of the second species, *Microsomyces telephani*, and emended the generic description. This work is a must to understand the complicate morphological structure of thalli in this unusual genus.

Microsomyces psammoechi Thaxt.
MB#275376
Fig. 16A–F

Memoirs of the American Academy of Arts and Sciences 16: 185 (Thaxter 1931). – **Type**: "On the superior surface of the abdomen of *Psammoechus orbicollis* Gr. No. 2199, Type, Kamerun, West Africa"; FH.

Diagnostic features

Lower receptacle consisting of a thick-walled basal cell. The corticating cells (Fig. 16D, cc) bear one to several long-stalked perithecia. Primary appendage consisting of 1–2 elongated cells terminated by a spinose antheridium (Fig. 16D, an, sx). [Detailed description: Majewski 1988]

Distribution and hosts

On *Psammoechus* Boudier, 1834 (Col. Silvanidae). This is a rare species on a common host. Only known from Sumatra, Cameroon (Thaxter 1931), Japan (Majewski 1988), and recently found in Europe from Bulgaria (Rossi *et al.* 2019a).

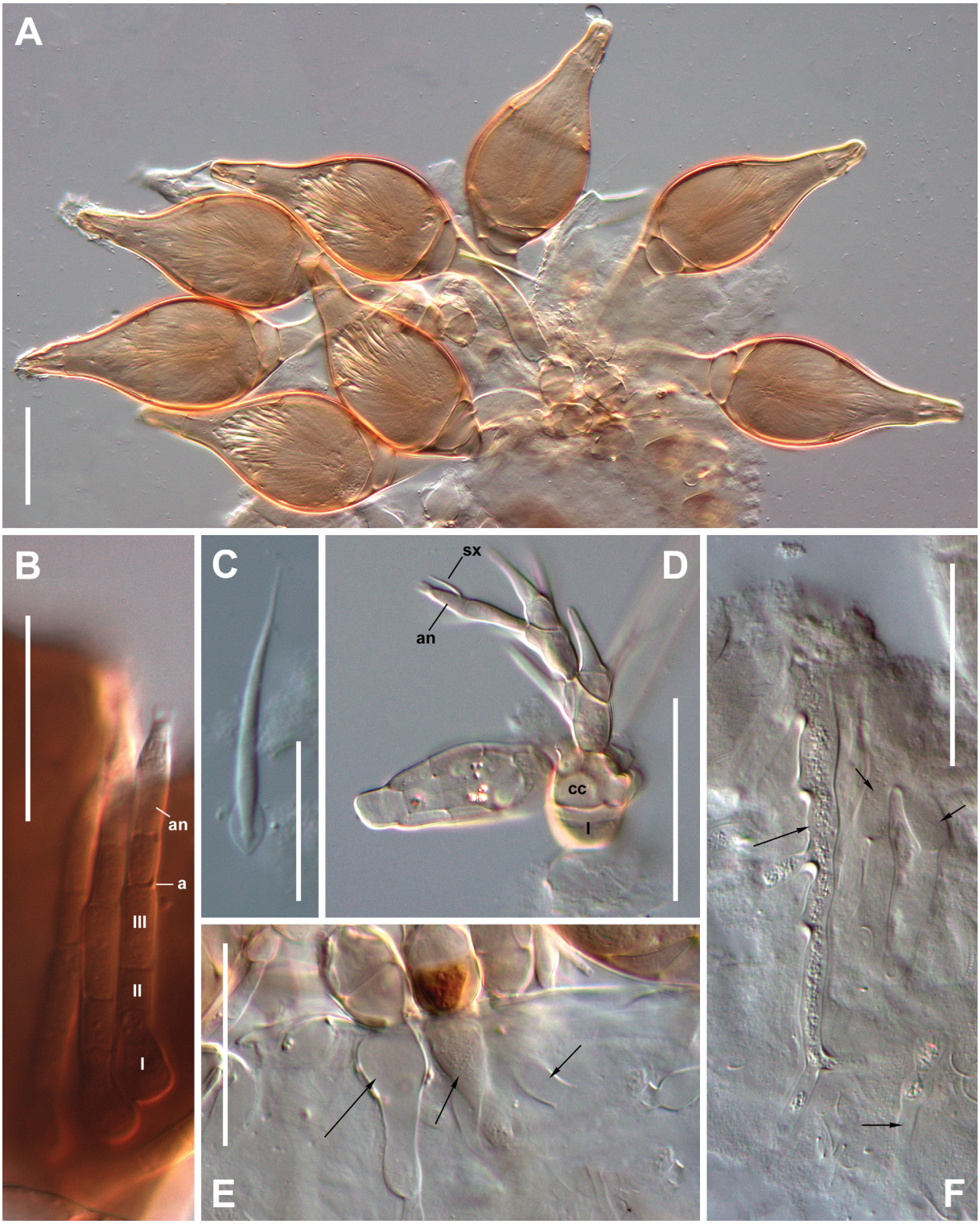

Fig. 16. *Microsomyces psammoechi* Thaxt. **A**. General habitus with several thalli corticating on host integument. **B**. Three sporelings with labelled receptacle cells (I, II, and III), the primary septum (a), and a primary antheridium (an). **C**. Ascospore. **D**. Young thallus showing cell I, one corticated cell (cc), and the primary antheridium (an) with spinose remaining of ascospore apex (sx). **E**–**F**. Haustoria penetrating the host body (arrows). Scale bars: A, D–F = 50 µm; B = 20 µm; C = 25 µm. Photographs from slides ZMUC C-F-124046 (A, C–F), ZMUC C-F-123679 (B).

Collections examined from Denmark

On *Psammoecus bipunctatus* (Fabricius, 1792) (Col. Silvanidae)

DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14 45.260′ E; VB81; 23 Jun. 2018; *JP 1155*; JP det.; ZMUC C-F-123679, C-F-123680. – **Nordøstsjælland (NEZ)** • Strødam; 55°58.056′ N, 12°16.273′ E; UC20; 4 Oct. 2014; *JP 33*; JP det.; ZMUC C-F-122508. – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 17 May 2019; *JP 1466*; JP det.; ZMUC C-F-124046. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Jun. 2019; *JP 1476*; JP det.; ZMUC C-F-124056 • Østerskov ved Langebæk; 54°59.421′ N, 12°6.435′ E; UA19; 19 Aug. 2019; *JP 1498*; JP det.; ZMUC C-F-124085.

Remarks

First record from Denmark and second from Europe. Probably rare in Denmark and considering the large number of specimens of the widespread and very common host that were examined without finding any infections, it might even be very rare. This species, like its congener, should be considered a true parasite because of the highly developed and branched haustorium which deeply penetrates into the host body (Fig. 16E–F, arrows).

Genus ***Rhachomyces*** Thaxt.

MB#4686

Proceedings of the American Academy of Arts and Sciences 30: 468 (Thaxter 1895). – Type species: *R. lasiophorus* (Thaxt.) Thaxt.

Acanthomyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 27: 36 (Thaxter 1892) [MB#11]

Brief description

Monoecious. Thallus consisting of a primary two-celled receptacle (cells I + II), a secondary receptacle or main axis formed by cell II derivatives, and a tertiary receptacle or tertiary axis consisting of a row of cells, lateral alongside the main axis and giving rise to appendages. The main axis bears up to three different types of appendages, named "a" (in the lower receptacle), "b" (in the upper receptacle, below perithecia), and "c" (supporting the antheridia) (see Santamaria & Faille 2007).

Remarks

The genus consists of 90 species, of which 32 in Europe, six in Denmark. The most recently described species are *R. insolitus* (Rossi & Christian 2020), *R. spinosus* (Santamaria *et al.* 2020a), and *R. neoproliferans* (Buyck *et al.* 2021). This genus has attracted the attention of several authors, especially for the species parasitizing cave-dwelling beetles (Rossi 2006; Santamaria & Faille 2007).

Key to the Danish species

1. Primary appendage very different from the other appendages. Secondary receptacle or main axis consists of three superposed cells. On *Syntomus* Hope, 1838 (Col. Carabidae)..... ***R. spinosus*** Santam. & Cuesta-Segura
– Primary appendage similar to the other appendages. Secondary receptacle or main axis consists of more than five superposed cells..... 2

2. Some appendages are very long, far exceeding in length the perithecial apex. Main axis, under the perithecium, much shorter than the perithecium length. On *Lathrobium* (Col. Staphylinidae Paederinae) ..... ***R. pilosellus*** (C.P. Robin) Thaxt.
– Appendages usually not exceeding the perithecial apex. More than five cells under the perithecium in the main axis; longer than the perithecium length..... 3

3. Appendages of type "c" very abundant among those of the type "a", bearing a terminal falcate and pointed antheridium or its derived sterile cell; thus giving the thallus a comb-like appearance. On *Philonthus* and allied genera (Col. Staphylinidae Staphylininae) ..... ***R. philonthinus*** Thaxt.
– Appendages of type "c" uncommon, typically on the upper region of the main axis, under or near the perithecium. Neither falcate antheridia nor with a comb-like appearance 4

4. Main axis of the receptacle continuing as a ± elongated branch (up to 250 µm in length), as long or longer than half of the length of the main axis below the perithecium. On *Othius* Stephens, 1829 (Col. Staphylinidae Staphylininae) ..... ***R. furcatus*** (Thaxt.) Thaxt.
– This branch is much shorter. On Col. Carabidae 5

5. Septa separating perithecial outer wall cell tiers w_1 from w_2, and w_2 from w_3 marked with elevations. Perithecium uniformly coloured. On *Trechus* Clairville, 1806 and related genera (Col. Carabidae)..... ***R. canariensis*** Thaxt.
– Septa separating perithecial outer wall cell tiers not clearly marked. Perithecium rounded in outline, subapically darkened. On *Acupalpus* Latreille, 1829, *Badister* Clairville, 1806 or related genera (Col. Carabidae)..... ***R. lasiophorus*** (Thaxt.) Thaxt.

Rhachomyces canariensis Thaxt.

MB#189311
Fig. 17A–B

Proceedings of the American Academy of Arts and Sciences 35: 436 (Thaxter 1900). – **Type**: "On *Trechus flavomarginatus* Woll., British Museum., No. 419. Teneriffe. On elytra"; FH. [Canary Islands]

Rhachomyces bolivarii Gonz. Fragoso (González Fragoso 1924: 405) [MB#189408]
Rhachomyces reymondii Lepesme (Lepesme 1942: 66, as *reymondi*) [MB#290453]
Rhachomyces vayssierei Lepesme (Lepesme 1942: 65) (sensu Balazuc 1971e: 114) [MB#290455]

Diagnostic features

Main receptacle axis consisting of 6–23 cells. Appendages of type "a" and "b" very similar, consisting of 3–5 brownish cells. Those of type "b" mostly abundant, surrounding ± the base of the perithecium. Appendages of type "c" consisting of a solitary flask-shaped, somewhat falcate antheridium, above a darkened supporting cell, which is separated from cells of the tertiary receptacle by a dark and constricted septum (Fig. 17A, *). Perithecium rather stout; septa between wall cells slightly prominent. [Detailed descriptions: Thaxter 1908; Santamaria 1989; Majewski 1994b; De Kesel 2002]

Distribution and hosts

Occurs on species of the genus *Trechus* and *Epaphius* Leach, 1819 (Col. Carabidae), including cave-inhabiting and surface species. According to Santamaria *et al.* (1991) appears to be widespread in **Europe** (Austria, Bulgaria, France, Germany, Hungary, Italy, Poland, Portugal, Spain, Sweden, Russia), Canary Islands, Madeira, Morocco and Turkey. Also from Bosnia-Herzegovina (Balazuc 1971d). Reported later from Belgium (De Kesel & Rammeloo 1992), United Kingdom (Weir 1994), Czech Republic (Rossi &

Máca 2006), Denmark (Høier 2009), Switzerland (Hoess & Senn-Irlet 2009), and the Netherlands (Haelewaters & De Kesel 2020).

Collections examined from Denmark

On *Epaphius secalis* (Paykull, 1790) (Col. Carabidae)

DENMARK – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 941*; JP det.; ZMUC C-F-123444 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 937*; JP det.; ZMUC C-F-123438.

On *Trechus obtusus* Erichson, 1837 (Col. Carabidae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 703*; JP det.; ZMUC C-F-123192 • Knudshoved Marina; 55°17.781′ N, 10°50.542′ E; PG12; 18 Oct. 2017; *JP 587*; JP det.; ZMUC C-F-123073. – **Lolland, Falster, Møn (LFM)** • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 550*; JP det.; ZMUC C-F-123036 • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 7 May 2017; *JP 398*; JP det.; ZMUC C-F-122881. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 927*; JP det.; ZMUC C-F-123426, C-F-123442 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 936*; JP det.; ZMUC C-F-123436 • Havgranerne i Tofte Skov; 56°50.576′ N, 10°15.552′ E; NJ70; 5–19 Sep. 2013; *I. Aggerholm 925*; JP det.; ZMUC C-F-123423 • Knarmod i Tofte Skov; 56°51.824′ N, 10°15.470′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 948*; JP det.; ZMUC C-F-123453 • Toftgården i Tofte Skov; 56°50.789′ N, 10°12.918′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 945*; JP det.; ZMUC C-F-123449. – **Nordøstsjælland (NEZ)** • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB47; 19 Sep. 2013; *H. Liljehult 1397*; JP det.; ZMUC C-F-123940. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 879*; JP det.; ZMUC C-F-123377 • Maglesø Plantage; 55°38.136′ N, 11°41.186′ E; PG66; 18 Feb. 2017; *JP 286*; JP det.; ZMUC C-F-122765.

On *Trechus quadristriatus* (Schrank, 1781) (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB50; 13 Nov. 2016; *JP 139*; JP det.; ZMUC C-F-122616.

Remarks

There are no important differences between thalli found on surface beetles (type specimens) and those collected on cave beetles (described as *R. bolivarii*, *R. reymondii* and *R. vayssierei*). The species is very common in Denmark.

Rhachomyces furcatus (Thaxt.) Thaxt.
MB#186405
Figs 17C–D, 102A

Proceedings of the American Academy of Arts and Sciences 30: 467 (Thaxter 1895). – **Basionym**: *Acanthomyces furcatus* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 28: 177 (Thaxter 1893) [MB#581133]. – **Type**: "On abdomen of *Othius fulvipennis* Fab., Germany"; FH.

Diagnostic features

Thallus variably bent to flexuous. Main receptacle axis continuing into a rather conspicuous lateral branch above the perithecium, even exceeding in length its apex. Appendages type "a" and "b" inseparable, long and very abundant, deeply darkened. Appendages of type "c" consisting of a supporting cell and one

antheridium, only visible on the upper lateral branch in mature thalli (Fig. 17D, *). [Detailed descriptions: Thaxter 1896; Santamaria 1989; Majewski 1994b; De Kesel 2002]

Distribution and hosts

Occurs on species belonging to the genus *Othius* (Col. Staphylinidae Staphylininae). Known from **Europe** (Finland, France, Germany, Hungary, Italy, Poland, Romania, Spain, Sweden, United Kingdom, Russia, former Yugoslavia), **Africa** (Algeria, Uganda), and **Asia** (Turkey) (Santamaria *et al.* 1991). More recently it has been recorded from Belgium (De Kesel & Haghebaert 1991), Czech Republic (Rossi & Máca 2006), Denmark (Rostrup 1935), Slovakia (Rossi *et al.* 2010), the Netherlands (Haelewaters *et al.* 2012), Armenia, Switzerland, and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Othius angustus* Stephens, 1833 (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Lille Lyngby Mose; 55°40.831′ N, 12°29.094′ E; UC20; 28 Jan. 2018; *J. Søgaard Hansen 999*; J. Søgaard Hansen det.; ZMUC C-F-123506.

On *Othius punctulatus* (Goeze, 1777) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 795*; JP det.; ZMUC C-F-123290 • Hestehave ved Rønde; 56°17.015′ N, 10°28.162′ E; NH93; 19 May 1994; *N. Scharff 391*; JP det.; ZMUC C-F-122874 • Kjellerup; 56°17.589′ N, 9°26.117′ E; NH23; 21 Oct. 2017; *JP 580*; JP det.; ZMUC C-F-123066 • Stidsmølle i Mattrup Skov; 55°55.455′ N, 9°33.811′ E; NG39; 19 Nov. 2017; *JP 807*; JP det.; ZMUC C-F-123302. – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 841*; JP det.; ZMUC C-F-123336 • Siesø i Klinteskoven; 54°57.830′ N, 12°32.494′ E; UA49; 15 May 2017; *Mo. Hansen Dry0146*; Mo. Hansen det.; ZMUC C-F-124214. – **Nordøstsjælland (NEZ)** • Gribskov, Fændriksvang; 56°1.005′ N, 12°21.245′ E; UC30; 1–31 May 2014; *J. Heilmann-Clausen et al. 49*; P. Jørum det.; ZMUC C-F-122524 • ibid.; *J. Heilmann-Clausen et al. 163*; P. Jørum; ZMUC C-F-122642 • ibid.; 1–30 Jun. 2014; *J. Heilmann-Clausen et al. 50*; P. Jørum; ZMUC C-F-122525 • Gribskov, Kageruphus; 55°59.428′ N, 12°16.478′ E; UC30; 1–31 May 2014; *J. Heilmann-Clausen et al. 47*; P. Jørum det.; ZMUC C-F-122522 • ibid.; 55°59.358′ N, 12°16.566′ E; UC30; 1–31 May 2014; *J. Heilmann-Clausen et al. 164*; P. Jørum det.; ZMUC C-F-122643 • Gribskov, Kalvehave; 56°0.359′ N, 12°20.339′ E; UC30; 1–31 May 2014; *J. Heilmann-Clausen et al. 48*; P. Jørum det.; ZMUC C-F-122523 • ibid.; *J. Heilmann-Clausen et al. 165*; P. Jørum det.; ZMUC C-F-122644 • ibid.; 56°0.419′ N, 12°20.564′ E; UC30; 1–31 May 2014; *J. Heilmann-Clausen et al. 166*; P. Jørum det.; ZMUC C-F-122645 • Gribskov, Kistrupvang; 56°1.612′ N, 12°19.959′ E; UC31; 1–31 May 2014; *J. Heilmann-Clausen et al. 167*; P. Jørum; ZMUC C-F-122646 • ibid.; 56°1.602′ N, 12°20.048′ E; UC31; 1–31 May 2014; *J. Heilmann-Clausen et al. 168*; P. Jørum det.; ZMUC C-F-122647 • Gribskov, Nederste Koppel; 56°2.865′ N, 12°19.999′ E; UC31; 1–31 May 2014; *J. Heilmann-Clausen et al. 46*; P. Jørum det.; ZMUC C-F-122521 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 29 Apr. 2017; *JP 402*; JP det.; ZMUC C-F-122885 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 783*; JP det.; ZMUC C-F-123278. – **Nordvestsjælland (NWZ)** • Eriksminde syd for Korshage; 55°57.744′ N, 11°46.504′ E; PH70; 27 Oct. 2019; *JP 1537*; JP det.; ZMUC C-F-124297. – **Sydjylland (SJ)** • Draved Skov; 55°0.964′ N, 8°58.395′ E; MF99; 1 Jun. 2013; *JP 305*; JP det.; ZMUC C-F-122784 • Kollund Skov; 54°50.219′ N, 9°25.411′ E; NF27; 8 May 2004; *H. Liljehult 79*; H. Liljehult det.; ZMUC C-F-122554. – **Sydsjælland (SZ)** • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 1–15 Aug. 2013; *JP 525*; JP det.; ZMUC C-F-123009.

On *Othius subuliformis* Stephens, 1833 (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 749*; JP det.; ZMUC C-F-123243 • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 796*; JP det.; ZMUC C-F-123291 • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP*

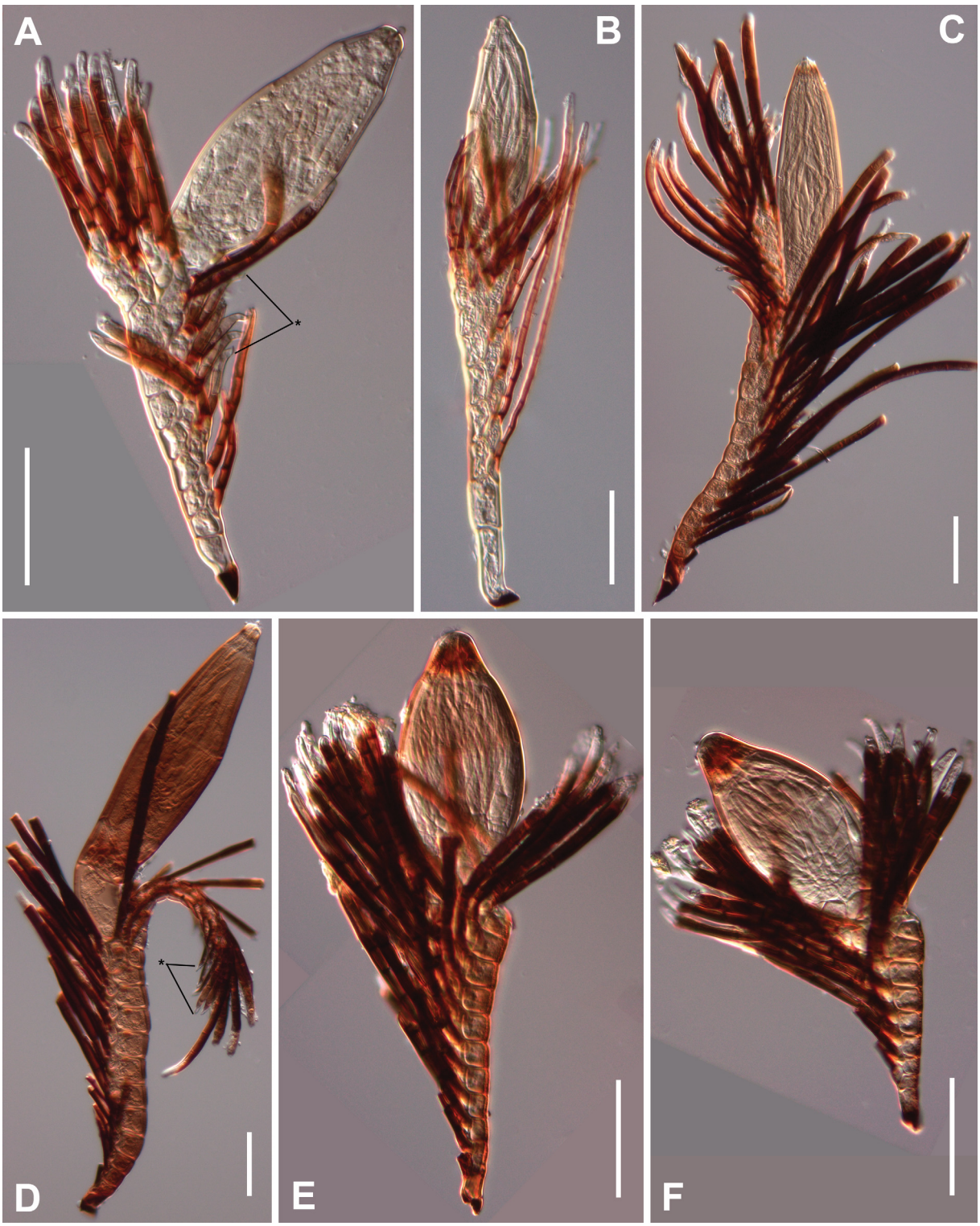

Fig. 17. *Rhachomyces* spp. **A**–**B**. *R. canariensis* Thaxt. Mature thalli from *Trechus obtusus* (A) and *Epaphius secalis* (B). Appendages type "c" are labelled in A (*). – **C**–**D**. *R. furcatus* (Thaxt.) Thaxt. Mature thalli with appendages of type "c" labelled in D (*). – **E**–**F**. *R. lasiophorus* (Thaxt.) Thaxt. Mature thalli. **F**. Short form from tarsi. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122765 (A), ZMUC C-F-123438 (B), ZMUC C-F-122521 (C–D), ZMUC C-F-122906 (E–F).

438; JP det.; ZMUC C-F-122923 • Kjellerup; 56°17.589′ N, 9°26.117′ E; NH23; 21 Oct. 2017; *JP 581*; JP det.; ZMUC C-F-123067 • Stidsmølle i Mattrup Skov; 55°55.455′ N, 9°33.811′ E; NG39; 19 Nov. 2017; *JP 808*; JP det.; ZMUC C-F-123303 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 988*; JP det.; ZMUC C-F-123495 • Vingsted; 55°40.512′ N, 9°23.500′ E; NG27; 6 Oct. 2019; *JP 1532*; JP det.; ZMUC C-F-124291. – **Lolland, Falster, Møn (LFM)** • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 552*; JP det.; ZMUC C-F-123038. – **Nordøstjylland (NEJ)** • Bøgebakken i Tofte Skov; 56°50.540′ N, 10°11.850′ E; NJ70; 17 May 2013; *H. Liljehult 198*; JP det.; ZMUC C-F-122677 • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 19 May 2013; *JP 314*; JP det.; ZMUC C-F-122793 • ibid.; 8–22 Aug. 2013; *I. Aggerholm 932*; JP det.; ZMUC C-F-123432. – **Nordøstsjælland (NEZ)** • Bognæs Storskov; 55°41.242′ N, 12°1.678′ E; UB17; 1 Aug. 2013; *JP 362*; JP det.; ZMUC C-F-122845 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 270*; JP det.; ZMUC C-F-122749 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 784*; JP det.; ZMUC C-F-123279. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 889*; JP det.; ZMUC C-F-123387 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 19 Feb. 2017; *H. Liljehult 366*; JP det.; ZMUC C-F-122849 • Sonnerup Skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 256*; JP det.; ZMUC C-F-122736. – **Sydjylland (SJ)** • Nord for Vråby Plantage; 55°6.640′ N, 8°30.239′ E; MG60; 21 Apr. 2000; *H. Liljehult 199*; JP det.; ZMUC C-F-122678. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 28 Feb. 2015; *JP 444*; JP det.; ZMUC C-F-122929.

Remarks

Perhaps one of the most common species of Laboulbeniales in Denmark, where it is infrequent to find specimens of *Othius* free of this fungus. Also remarkable is the observation of severely infected hosts.

Rhachomyces lasiophorus (Thaxt.) Thaxt.
MB#186325
Fig. 17E–F

Proceedings of the American Academy of Arts and Sciences 30: 468 (Thaxter 1895). – **Basionym**: *Acanthomyces lasiophora* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 29: 37 (Thaxter 1892) [MB#431393]. – **Type**: "On *Atranus pubescens*, Connecticut"; FH. [USA]

Diagnostic features

Main receptacle axis not continuing into a lateral branch above the perithecium. Appendages types "a" and "b" inseparable, very abundant, deeply darkened. Perithecium broadly oval, very inflated, up to 60 µm in width, showing a ± conspicuous preapical darkened ring. [Detailed descriptions: Thaxter 1896; Majewski 1994b; De Kesel 2002]

Distribution and hosts

On species of Col. Carabidae belonging to the genera *Acupalpus*, *Agonum*(?) Bonelli, 1810, *Anthracus* Motschulsky, 1850, *Atranus* LeConte, 1848, *Badister*, and *Dromius* Bonelli, 1810. Known from **Europe** (France, Belgium, United Kingdom, Italy, Germany and Poland), USA and Korea (Majewski 2008). Also from the Netherlands (Haelewaters & De Kesel 2010), Czech Republic (Rossi *et al.* 2010), Turkey (Rossi 2016), Bulgaria (Rossi *et al.* 2019a), and Hungary (Rossi & Christian 2020).

Collections examined from Denmark

On *Acupalpus dubius* Schilsky, 1888 (Col. Carabidae)

DENMARK – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 21 May 2017; *JP 422*; JP det.; ZMUC C-F-122906.

On *Acupalpus exiguus* Dejean, 1829 (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 28 Feb. 2017; *H. Liljehult 359*; JP det.; ZMUC C-F-122841 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1030*; JP det.; ZMUC C-F-123542. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1281*; JP det.; ZMUC C-F-123813.

On *Acupalpus flavicollis* (Sturm, 1825) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Dyrehaven; 55°47.347′ N, 12°33.957′ E; UB48; 20 Apr. 2017; *H. Liljehult 275*; JP det.; ZMUC C-F-122754 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1028*; JP det.; ZMUC C-F-123540.

On *Anthracus consputus* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14 45.096′ E; VB80; 25 Apr. 2014; *JP 509*; JP det.; ZMUC C-F-122992. – **Lolland, Falster, Møn (LFM)** • Gedesby; 54°35.290′ N, 11°58.199′ E; 6–14 Jun. 2013; *E. Vesterhede 188*; JP det.; ZMUC C-F-122667.

Remarks

First record from Denmark. Balazuc (1971a) described *R. lasiophorus* subsp. *demauxii* on *Acupalpus exiguus* from France, differing from typical forms by the reduced thalli, with few cells on the receptacle. We have found this form on tarsi of several studied hosts (Fig. 17F) and it may be considered a growth form of the nominal subspecies.

Rhachomyces philonthinus Thaxt.

MB#191909
Figs 18A–B, 102B

Proceedings of the American Academy of Arts and Sciences 35: 435 (Thaxter 1900). – **Type**: [Not designated] [Ind. loc.] "On *Philonthus longicornis* Steph., British Museum, No. 408, Island of St. Helena; on *Philonthus* sp. indet., Hope Coll., No. 225, British Isles. On abdomen and elytra"; FH.

Diagnostic features

Medium to large thalli, up to 700 µm long. Main receptacle axis continuing into a rather conspicuous lateral branch above the insertion of the perithecium, consisting of up to 20 squarish, isodiametric cells (Fig. 18B, arrow). Appendages of the three types deeply darkened, scattered unilaterally to the main axis in a comb-like appearance. Those of type "c" with an acute and somewhat uncinate apex. Venter and neck of perithecia usually abruptly distinguished (Fig. 18B). [Detailed descriptions: Thaxter 1908; Sugiyama 1973; Santamaria 1989; Majewski 1994b; De Kesel 2002]

Distribution and hosts

Occurs on *Philonthus* and related genera (*Bisnius* Stephens, 1829, *Gabrius*, *Spatulonthus* Tottenham, 1955, etc.) mostly collected in horse and cow dung. A very common and widespread species that has been reported from Europe, Africa, America and Asia (Santamaria *et al.* 1991; Majewski 2008). Recent records are from Ecuador, Kenya and South Africa (Proaño Castro & Rossi 2008), Denmark (Høier 2009), Slovakia and Czech Republic (Rossi *et al.* 2010).

Collections examined from Denmark

On *Bisnius fimetarius* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Sakskøbing, Tårsvej 35; 54°50.433′ N, 11°39.106′ E; PF78; 2–20 May 2018; *P.N. Buhl 1175*; JP det.; ZMUC C-F-123699. – **Nordøstsjælland (NEZ)** • Albertslund

Golfbane; 55°40.750′ N, 12°19.190′ E; UB37; 6 Jan. 2018; *JP 952*; JP det.; ZMUC C-F-123458 • Bognæs Storskov; 55°41.242′ N, 12°1.678′ E; UB17; 18 Aug. 2013; *H. Liljehult 202*; JP det.; ZMUC C-F-122681 • ibid.; 14 Sep. 2013; *H. Liljehult 204*; JP det.; ZMUC C-F-122683 • Dyrehaven; 55°47.347′ N, 12°33.957′ E; UB47; 7 May 2000; *H. Liljehult 203*; JP det.; ZMUC C-F-122682. – **Sydjylland (SJ)** • Kruså; 54°50.594′ N, 9°23.797′ E; NF27; 25 Apr. 2003; *H. Liljehult 205*; JP det.; ZMUC C-F-122684. – **Sydsjælland (SZ)** • Haslev; 55°19.669′ N, 11°58.206′ E; PG83; 19 Jun. 2016; *JP 324*; JP det.; ZMUC C-F-122802 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 15 Aug. 2013; *JP 393*; JP det.; ZMUC C-F-122876.

On *Philonthus confinis* Strand, 1941 (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Tibirke Bakker; 56°1.885′ N, 12°5.295′ E; UC11; 24 Apr. 2020; *JP 1653*; JP det.; ZMUC C-F-124375.

On *Philonthus coprophilus* Jarrige, 1949 (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°59.171′ N, 12°31.954′ E; UA49; 2 May 2018; *JP 1097*; JP det.; ZMUC C-F-123615.

On *Philonthus cruentatus* (Gmelin, 1790) (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Høvblege; 54°57.826′ N, 12°30.574′ E; UB20; 10 Jun. 2017; *JP 432*; JP det.; ZMUC C-F-122917 • ibid.; 6 Sep. 2019; *JP 1513*; JP det.; ZMUC C-F-124268 • Jydelejet, Møns Klint; 54°59.171′ N, 12°31.954′ E; UA49; 2 May 2018; *JP 1098*; JP det.; ZMUC C-F-123616.

On *Philonthus fumarius* (Gravenhorst, 1806) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 20 May 2013; *JP 370*; JP det.; ZMUC C-F-122853. – **Fyn (F)** • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1069*; JP det.; ZMUC C-F-123586. – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°58.979′ N, 12°32.281′ E; UA49; 2 May 2018; *A.K. Hansen 1099*; A.K. Hansen det.; ZMUC C-F-123617 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 651*; JP det.; ZMUC C-F-123140 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1114*; JP det.; ZMUC C-F-123634. – **Nordøstsjælland (NEZ)** • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 598*; JP det.; ZMUC C-F-123087 • Helvigstrup Skov; 55°33.131′ N, 11°52.949′ E; PG86; 24 Apr. 2007; *H. Liljehult 1459*; JP det.; ZMUC C-F-124010 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 13*; JP det.; ZMUC C-F-122486 • ibid.; 19 Mar. 2017; *JP 675*; JP det.; ZMUC C-F-123164. – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 257*; JP det.; ZMUC C-F-122737. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1410*; JP det.; ZMUC C-F-123956.

On *Philonthus marginatus* (Müller, 1764) (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.806′ N, 12°32.340′ E; UA49; 25 Jul.–15 Aug. 2013; *O. Karsholt 105*; JP det.; ZMUC C-F-122580.

On *Philonthus parvicornis* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Høvblege; 54°57.826′ N, 12°30.574′ E; UB20; 10 Jun. 2017; *JP 431*; JP det.; ZMUC C-F-122916.

On *Philonthus varians* (Paykull, 1789) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Saltholm; 55°39.546′ N, 12°45.864′ E; UB57; 13 Sep. 2006; *H. Liljehult 1460*; JP det.; ZMUC C-F-124011 • Vaserne; 55°49.129′ N, 12°26.343′ E; UB38; 20 Jan. 2018; *M. Kofoed-Hansen 1000*; JP det.; ZMUC C-F-123507. – **Nordvestsjælland (NWZ)** • Klintebjerg ved Klint; 55°57.351′ N, 11°34.463′ E; PH60; 1 May 2016; *JP 54*; JP det.; ZMUC C-F-122529 • ibid.; 1 Apr.

2017; *JP 245*; JP det.; ZMUC C-F-122725 • Nordbredden af Skarresø; 55°39.469′ N, 11°23.147′ E; PG47; 21 Apr. 2018; *JP 1058*; JP det.; ZMUC C-F-123575. – **Sydjylland (SJ)** • Margrethe Kog; 54°55.711′ N, 8°40.149′ E; MF78; 1 Jun. 2013; *JP 206*; JP det.; ZMUC C-F-122685. – **Sydsjælland (SZ)** • Bimose i Broby Overdrev; 55°23.921′ N, 11°35.499′ E; PG64; 30 Jun.–2 Jul. 2013; *JP 207*; JP det.; ZMUC C-F-122686 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1302*; JP det.; ZMUC C-F-123836.

Remarks

One of the most common species in Denmark.

Rhachomyces pilosellus (C.P.Robin) Thaxt.
MB#192158
Fig. 18C–D

Proceedings of the American Academy of Arts and Sciences 30: 467 (Thaxter 1895). – **Basionym**: *Laboulbenia pilosella* C.P.Robin, *Traité du Microscope:* 912 (Robin 1871) [MB#566983]. – **Type**: [Not designated] "On *Lathrobium* from an unknown locality in France". [According to Santamaria *et al.* 1991, the type is an "iconotype", i.e., the illustration given by Robin, which agrees with the ICNAFP – International Code of Nomenclature for Algae, Fungi and Plants (Turland *et al.* 2018)]

Acanthomyces brevipes Thaxt. (Thaxter 1893: 177) [MB#581132]. – *Rhachomyces brevipes* (Thaxt.) Saccardo (Saccardo 1895: 454) [MB#188964]

Diagnostic features

Main axis short, consisting of 4–5 cells, continuing to a 3–4 celled lateral branch. A blackish diagonal strip is seen traversing from cell I to cell II (Fig. 18C–D, arrows). Appendages "a" and "b" darkened, very elongated, yet coiled if undamaged (Fig. 18C). Type "c" appendages clustered below the perithecium. Perithecium very large, longer than main receptacle axis. [Detailed descriptions: Thaxter 1896; Majewski 1994b; De Kesel 2002]

Distribution and hosts

Grows on *Lathrobium* (Col. Staphylinidae Paederinae). An uncommon species only reported from France (type), Germany (Thaxter 1893), Poland, Ukraine (Siemaszko & Siemaszko 1932), Belgium (Collart 1945), Italy (Rossi 1975), and Hungary (Bánhegyi *et al.* 1985).

Collections examined from Denmark

On *Lathrobium fulvipenne* (Gravenhorst, 1806) (Col. Staphylinidae Paederinae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 687*; JP det.; ZMUC C-F-123175. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1300*; JP det.; ZMUC C-F-123833.

Remarks

First record from Denmark. This is one of the earliest described species of Laboulbeniales.

Fig. 18. *Rhachomyces* spp. **A**–**B**. *R. philonthinus* Thaxt. Mature thalli. In B, the lateral branch from the primary axis (a diagnostic character) is labelled (arrow). – **C**–**D**. *R. pilosellus* (C.P.Robin) Thaxt. Mature thalli with labelled blackened diagonal strip traversing cells I and II (arrows). – **E**–**F**. *R. spinosus* Santam. & Cuesta-Segura. Mature thalli. In E, primary septum (a) and spinous original spore apex (sx) are labelled. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122681 (A), ZMUC C-F-122685 (B), ZMUC C-F-123833 (C–D), ZMUC C-F-123296 (E), ZMUC C-F-123062 (F).

Rhachomyces spinosus Santam. & Cuesta-Segura
MB#834607
Fig. 18E–F

Nova Hedwigia 110(3–4): 362 (Santamaria *et al.* 2020a). – **Type**: "Spain, León, Redipuertas, Valdelugueros, Riopinos valley, 43°01′30″ N, 5°26′26″ W, 1346 m a.s.l., 22.V.2016, A.D. Cuesta-Segura, on *Syntomus foveatus* (Geoffroy) (Coleoptera Carabidae), det. A.D. Cuesta-Segura, slide BCB–SS2743n (HOLOTYPE)"; BCB.

Diagnostic features

Thallus small, up to 220 µm. Primary appendage three-celled. Primary septum constricted and darkened, with the dark brown pigmentation extending to the lower quarter of the basal cell of the primary appendage (Fig. 18E, a). Second cell of the primary appendage bearing a stout spinous process on the margin (Fig. 18E, sx). Apical cell of the primary appendage rounded distally, as long as the two lower cells together. Secondary axis three-celled, bearing five antheridial appendages.

Distribution and hosts

On *Syntomus* (Col. Carabidae). Only known from Spain (original description) and Belgium (Haelewaters & De Kesel 2020: pl. 71, as *Rhachomyces sciakyi* W.Rossi).

Collections examined from Denmark

On *Syntomus foveatus* (Geoffroy, 1785) (Col. Carabidae)

DENMARK – **Fyn (F)** • Flyvesandet ved Agernæs; 55°37.294′ N, 10°18.251′ E; NG86; 19 Apr. 2018; *JP 1043*; JP det.; ZMUC C-F-123559. – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.301′ N, 12°16.244′ E; UB20; 25 Sep. 2016; *JP 144*; JP det.; ZMUC C-F-122623. – **Nordøstjylland (NEJ)** • Sandmilen; 57°41.793′ N, 10°31.717′ E; NJ99; 21 Nov. 2017; *JP 801*; JP det.; ZMUC C-F-123296. – **Nordøstsjælland (NEZ)** • Asserbo Plantage; 56°1.794′ N, 12°1.589′ E; UC11; 15 Oct. 2017; *JP 576*; JP det.; ZMUC C-F-123062 • Liseleje; 56°1.048′ N, 11°58.454′ E; PH81; 30 Oct. 2016; *JP 132*; JP det.; ZMUC C-F-122608. – **Nordvestsjælland (NWZ)** • Sandflugtsplantage ved Rørvig; 55°57.126′ N, 11°43.060′ E; PH60; 4 Nov. 2017; *JP 712*; JP det.; ZMUC C-F-123203.

Remarks

First record from Denmark, third record after the original description. This species is related to *R. sciakyi* W.Rossi and *R. lavagnei* (F.Picard) W.Rossi but may be readily separated from them by the spinous process seen on the second cell of the primary appendage (Santamaria *et al.* 2020a).

Subtribe Asaphomycetinae I.I.Tav.

Genus ***Asaphomyces*** Thaxt.
MB#342

Memoirs of the American Academy of Arts and Sciences 16: 310 (Thaxter 1931). – Type species: *A. cholevae* Thaxt. (by monotypy)

Barbariella Middelh., *Nederlandsch Kruidkundig Archief* 56: 260 (Middelhoek 1949) [MB#511]

Brief description

Monoecious. Receptacle multicelled, consisting of a series of superposed cells giving rise to lateral perithecia and secondary appendages. The primary appendage continues the main axis of the receptacle

and bears simple antheridia. Only cell m is visible amongst the perithecial basal cells (Fig. 19A, m) and above cell VI, which is usually subdivided in two cells, the additional one named cell VI′ (Fig. 19B, *). One of the perithecial wall cells of the third tier (w_3) appears characteristically enlarged (Fig. 19C, E, arrows).

Remarks

Monotypic. See remarks under *A. cholevae*.

Asaphomyces cholevae Thaxt.
MB#260559
Figs 19A–E, 102C

Memoirs of the American Academy of Arts and Sciences 16: 311 (Thaxter 1931). – **Type**: "On the elytra of *Choleva terminans* Lec. No. 1461, Cutts Island, Kittery Point, Maine: July, 1906"; FH. [Harvard University Herbaria, slide#00313725, seen! (Fig. 19E, here)] [*Choleva terminans* is now *Sciodrepoides fumatus* subsp. *terminans*] [USA]

Barbariella tubantica Middelh. & Boelens (Middelhoek 1949: 257) [MB#284508]. – *Asaphomyces tubanticus* (Middelh. & Boelens) Scheloske (Scheloske 1969: 92) [MB#326503]

Diagnostic features

See genus description. [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

Occurs on species of Col. Leiodidae like *Apocatops* Zwick, 1968, *Choleva* Latreille, 1797, *Catops* Paykull, 1798, *Catopidius* Jeannel, 1922, *Fissocatops* Zwick, 1968, *Sciodrepoides* Hatch, 1933, *Nemadus* Thomson, 1867 and *Ptomaphagus* Hellwig, 1795. Reported as *A. cholevae* or as *A. tubanticus* from several countries in **Europe**: Czech Republic, Finland, France, Germany, Italy, Poland, Russia, Slovakia, Spain, Sweden, United Kingdom (Majewski 2008), Belgium (De Kesel & Gerstmans 2011), Bulgaria, Georgia (Rossi *et al.* 2019a); **Asia**: China (Rossi *et al.* 2019a); **America**: USA (Thaxter 1931); and **Africa**: Morocco (Santamaria & Rossi 1999).

Collections examined from Denmark

On *Apocatops nigrita* (Erichson, 1837) (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 989*; JP det.; ZMUC C-F-123496. – **Nordøstsjælland (NEZ)** • Gribskov, Kalvehave; 56°0.359′ N, 12°20.339′ E; UC30; 1–30 Jun. 2014; *J. Heilmann-Clausen et al. 52*; P. Jørum det.; ZMUC C-F-122527.

On *Catops coracinus* Kellner, 1846 (Col. Leiodidae)
DENMARK – **Sydsjælland (SZ)** • Suserup Skov; 55°22.733′ N, 11°33.627′ E; PG64; 4 Sep. 2019; *JP 1480*; A.K. Hansen det.; ZMUC C-F-124065.

On *Catops fuliginosus* Erichson, 1837 (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP 439*; JP det.; ZMUC C-F-122924 • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 822*; JP det.; ZMUC C-F-123316 • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 12 Mar. 2017; *JP 279*; JP det.; ZMUC C-F-122758. – **Fyn (F)** • Lykkesholm syd for Ellested; 55°14.421′ N, 10°37.357′ E; PG02; 27 Mar. 2009; *JP 82*; JP det.; ZMUC C-F-122557. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov;

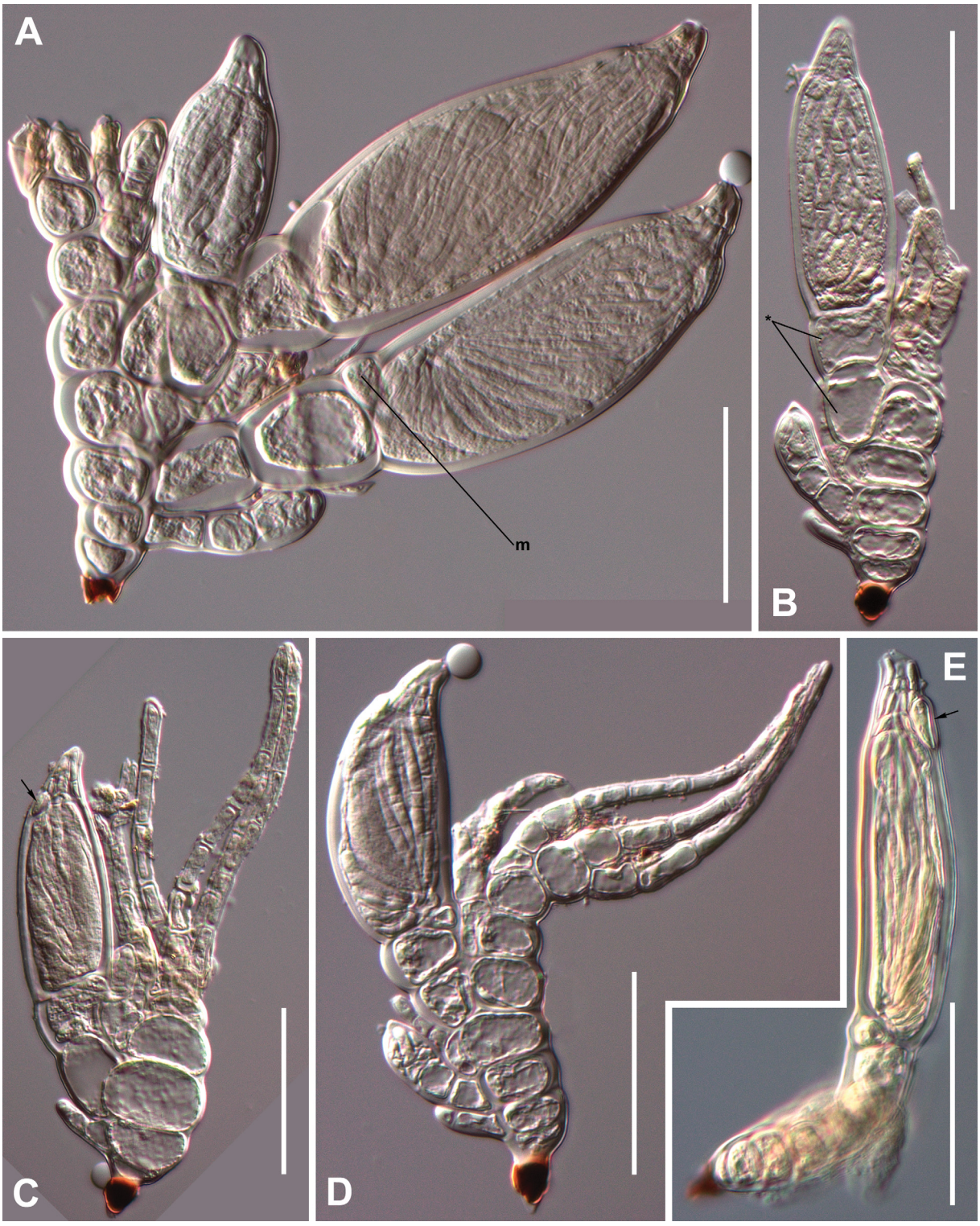

Fig. 19. *Asaphomyces cholevae* Thaxt. **A**–**E**. Mature thalli with labelled cell m in A, cells VI and VI′ (*) in B, and enlarged w_3 (arrows) in C and E. Thallus in E is from the holotype. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122758 (A), ZMUC C-F-122527 (B–C), ZMUC C-F-122654 (D), FH3980 (holotype).

54°46.408′ N, 11°39.955′ E; PF77; 7 Oct. 1993; *S. Langemark & O.E. Meyer 896*; JP det.; ZMUC C-F-123394. – **Nordøstsjælland (NEZ)** • Albertslund golfbane; 55°40.750′ N, 12°19.190′ E; UB37; 6 Jan. 2018; *JP 953*; JP det.; ZMUC C-F-123459 • Bognæs Storskov; 55°41.242′ N, 12°1.678′ E; UB17; 20 Feb. 2018; *O. Martin 1039*; JP det.; ZMUC C-F-123555 • Klinten ved Selsø; 55°44.158′ N, 11°59.634′ E; PG88; 11 Mar. 2007; *JP 522*; JP det.; ZMUC C-F-123006 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 2 Dec. 2011; *JP 472*; JP det.; ZMUC C-F-122956 • ibid.; 1 Dec. 2019; *JP 1566*; JP det.; ZMUC C-F-124326 • Stenholtsvang; 55°57.365′ N, 12°21.254′ E; UC30; 7 Apr. 2018; *JP 1024*; JP det.; ZMUC C-F-123531. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 224*; JP det.; ZMUC C-F-122705 • ibid.; *JP 376*; JP det.; ZMUC C-F-122859. – **Sydsjælland (SZ)** • Gammel Dyrehave ved Edelesminde; 55°16.930′ N, 11°58.348′ E; PG83; 27 Nov. 2016; *JP 170*; JP det.; ZMUC C-F-122649 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 537*; JP det.; ZMUC C-F-123021. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1251*; JP det.; ZMUC C-F-123779.

On *Catops fuscus* (Panzer, 1794) (Col. Leiodidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Hobyskov; 54°44.069′ N, 11°15.296′ E; PF46; 22 Dec. 2019; *M. Kofoed-Hansen 1579*; JP det.; ZMUC C-F-124340.

On *Catops morio* (Fabricius, 1787) (Col. Leiodidae)
DENMARK – **Nordøstsjælland (NEZ)** • Gundsømagle; 55°43.398′ N, 12°10.842′ E; UB27; 6 Apr. 2019; *L. Kjær-Thomsen & L. Thomas 1399*; JP det.; ZMUC C-F-123945. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.331′ N, 12°6.357′ E; UA19; 27 Mar. 2018; *JP 1023*; JP det.; ZMUC C-F-123530 • Turebyholm Dyrehave; 55°21.071′ N, 12°4.840′ E; UB13; 6 Jan. 2018; *M. Kofoed-Hansen 1106*; M. Kofoed-Hansen det.; ZMUC C-F-123624.

On *Catops nigricans* (Spence, 1815) (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.614′ N, 9°26.106′ E; NH23; 18 Nov. 2017; *JP 816*; JP det.; ZMUC C-F-123310 • Stidsmølle i Mattrup Skov; 55°55.455′ N, 9°33.811′ E; NG39; 19 Nov. 2017; *JP 812*; JP det.; ZMUC C-F-123306. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 460*; JP det.; ZMUC C-F-122945. – **Nordøstsjælland (NEZ)** • Ryegård Dyrehave; 55°40.500′ N, 11°50.851′ E; PG77; 2 Dec. 2014; *JP 343*; JP det.; ZMUC C-F-122825 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1241*; JP det.; ZMUC C-F-123768. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1293*; JP det.; ZMUC C-F-123825. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1250*; JP det.; ZMUC C-F-123778.

On *Catops nigriclavis* Gerhardt, 1900 (Col. Leiodidae)
DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 680*; JP det.; ZMUC C-F-123168.

On *Catops picipes* (Fabricius, 1787) (Col. Leiodidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 459*; JP det.; ZMUC C-F-122944. – **Nordøstsjælland (NEZ)** • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 2 Dec. 2011; *JP 473*; JP det.; ZMUC C-F-122957. – **Sydsjælland (SZ)** • Højstrup ved Rødvig; 55°14.319′ N, 12°20.234′ E; UB32; 15 Jan. 2017; *JP 176*; JP det.; ZMUC C-F-122655.

On *Catops tristis* (Panzer, 1793) (Col. Leiodidae)
DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.331′ N, 12°6.357′ E; UA19; 27 Mar. 2018; *JP 1022*; JP det.; ZMUC C-F-123529.

On *Fissocatops westi* (Krogerus, 1931) (Col. Leiodidae)
DENMARK – **Sydsjælland (SZ)** • Højstrup ved Rødvig; 55°14.319′ N, 12°20.234′ E; UB32; 15 Jan. 2017; *JP 175*; JP det.; ZMUC C-F-122654.

Other material examined

Holotype of *Asaphomyces cholevae*
UNITED STATES • "*Asaphomyces cholevae*, slide from FH, #3980, barcode 00313725, **holotype**, on elytra of *Choleva terminalis* Lec. [as *Clove terminalis*, typing error?], from Kittery Point, Maine, York County (USA), 07-1906, leg. R. Thaxter"; FH[00313725]. [consists of four mature thalli in fair condition (Fig. 19E)]

Remarks

First record from Denmark. Separation of *A. cholevae* and *A. tubanticus* has been widely discussed (Majewski 1994b; Santamaria 2003). Tavares (1985) questioned the presence of *A. cholevae* in Europe, and separated it from *A. tubanticus* because of the broad perithecium with tapering neck and slender apex of the latter species, whereas a broad apex and a ± cylindrical perithecium were reported for *A. cholevae*. Synonymy has been suggested by Rossi & Máca (2006) after examining abundant material occurring on the same host of the type series, i.e., *Sciodrepoides fumatus* subsp. *terminans* (LeConte) from the USA. We agree with this opinion because we had the opportunity to study a large series of thalli in which the morphological variation cannot be explained in terms of separate species supported by habitus, nor by habitat or distribution. At first, *A. tubanticus* was restricted to larger thalli, bearing more perithecia and appendages, but between the two extremes there is a large number of intermediate forms, without discontinuities. Also, to support this idea, we have studied the type from FH (see above under other material examined) which include small thalli (Fig. 19E).

Tribe Laboulbenieae Thaxt.
Subtribe Chitonomycetinae I.I.Tav.

Genus ***Chitonomyces*** Peyr.
MB#1002

Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1 68: 250 (Peyritsch 1873). – Type species: *C. melanurus* Peyr.

Heimatomyces Peyr., *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1* 68: 251 (Peyritsch 1873) [MB#2252]

Brief description

Monoecious. Receptacle six-celled. The primary appendage, which is subtended by cell IIIa, is two-celled and consists of a dome-shaped basal cell and a filiform distal cell. Only one antheridium for each thallus, usually also dome-shaped and mostly similar to the basal cell of the primary appendage (this corresponds to the genus *Chitonomyces* in the strict sense, see below), embedded between cell IIIa and the perithecium.

Remarks

The genus consists of 89 species, of which 13 in Europe, seven in Denmark. The most recently described species is *C. tylopus* (Santamaria 2001b). This is an isolated and well-characterized genus associated with aquatic beetles, mostly Dytiscidae, but also Haliplidae and Gyrinidae. Some species show a high degree of specialization by growing on very restricted areas of host bodies (Goldmann & Weir 2012).

Thalli show a bizarre morphology requiring a particular terminology. Thaxter (1924) divided the genus in two subgenera, *Euchitonomyces* and *Chitonomyces* s. str. for species with six or eight receptacular cells, respectively. The only further difference between the two types seems to be related to the distinctiveness of the antheridium which is, weakly distinguished in *Euchitonomyces* (e.g., *C. bidessarius*). Otherwise we see no reason to separate the two groups. The six receptacular cells are named I, Ia, II, IIa, III, and IIIa (Santamaria 2003; Goldmann & Weir 2012) (Fig. 20B). Because of the absence of a thorough study of thallus development in this genus, the exact identity of some cells has not been clearly interpreted, particularly the cells lying under the perithecium, as m, n, n′ and VII.

Key to the Danish species (partially following Santamaria 2003)

1. Species with some kind of horn-like outgrowth perithecial cell, including basal and stalk cells 2
– Species without this kind of outgrowths on or near the perithecium 4

2. A perithecial outgrowth on the top, arising from an uppermost wall cell. Thalli growing under the posterior margin of left elytron. On *Laccophilus* Leach, 1815 (Col. Dytiscidae) ..... ***C. paradoxus*** (Peyr.) Thaxt.
– Perithecial outgrowth lateral. Thalli on other locations of host body..... 3

3. A perithecial outgrowth arising from a preapical wall cell. Thalli growing under the margins of the pronotum. On *Graptodytes* Seidlitz, 1887 (Col. Dytiscidae) and *Haliplus* Latreille, 1802 (Col. Haliplidae) ..... ***C. aculeifer*** Speg.
– A perithecial outgrowth arising from the lower third of the anterior side of the perithecium, sometimes also including a bulging cell VI which resembles a second protuberance. Thalli growing on the last tarsus of left hind leg. On *Laccophilus* (Col. Dytiscidae) ..... ***C. ensifer*** Speg.

4. Cell IIIa proliferating into a lateral outgrowth. On *Laccophilus* (Col. Dytiscidae) ..... ***C. italicus*** Speg.
– Cell IIIa not proliferating into an outgrowth 5

5. Cell IIIa and basal cell of primary appendage blackened and with a hook-shaped tip. On *Laccophilus* (Col. Dytiscidae)..... ***C. melanurus*** Peyr.
– Cell IIIa and basal cell of primary appendage hyaline to pale yellowish-brown, concolorous with the remaining thallus 6

6. Cell I very elongate, 5–10 or even more longer as broad. Thalli concealed under the last abdominal sternite of *Laccophilus* (Col. Dytiscidae) ..... ***C. elongatus*** Speg.
– Cell I shorter, at most twice longer as broad. On *Hygrotus* Stephens, 1828 (Col. Dytiscidae)..... ***C. bidessarius*** (Thaxt.) Thaxt.

Chitonomyces aculeifer Speg.
MB#150989
Fig. 20A–B

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 44 (Spegazzini 1915b; as *aculeiferus*). – **Type**: “Sobre las patas del *Laccophilus virescens*, pescado en el lago de Tarzo, Veneto, Ag. 1914”; LPS. [Italy]

Chitonomyces bruchii Speg. (Spegazzini 1917: 479) [MB#166509]
Chitonomyces ceratomycetalis Thaxt. (Thaxter 1926: 517) [MB#260283]

Diagnostic features

Dimorphic. In the typical form the perithecium bears a conspicuous straight to strongly arcuate or sigmoidal darkened horn-like outgrowth arising from the preapical wall cell in the posterior margin (Fig. 20A, arrow). [Detailed descriptions: Scheloske 1969; Majewski 1994b; Santamaria 2003; De Kesel & Haelewaters 2012]

Distribution and hosts

On *Haliplus*, *Peltodytes* Régimbart, 1878 (Col. Haliplidae), *Laccophilus*? (type of *Ch. aculeiferus*) and *Graptodytes* (Col. Dytiscidae) from **Europe**: Czech Republic, Germany, Italy, Poland, Spain, Bulgaria (Rossi *et al.* 2019a), Belgium (De Kesel & Haelewaters 2012), as well as in South **America** (Argentina, type of *Ch. bruchi*) and **Asia** (China, type of *Ch. ceratomycetalis*).

Collections examined from Denmark

On *Graptodytes bilineatus* (Sturm, 1835) (Col. Dytiscidae)

DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 22 Apr. 2018; *JP 1037*; JP det.; ZMUC C-F-123553.

On *Haliplus ruficollis* (Degeer, 1774) (Col. Haliplidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Busemarke Mose; 54°57.688′ N, 12°26.619′ E; UA39; 19 Aug. 2019; *JP 1495*; JP det.; ZMUC C-F-124082, C-F-124083.

Remarks

First record from Denmark. It is broadly accepted that this species exists in two "growth forms" or "morphotypes" related to the sex of the host and growth position on the body. The typical horned form grows under the margins of the pronotum or neighbouring areas in females, and the not horned form grows between the anterior or medium claws in males.

Chitonomyces bidessarius (Thaxt.) Thaxt.
MB#166754
Fig. 20C–D

Memoirs of the American Academy of Arts and Sciences 12: 292 (Thaxter 1896). – **Basionym**: *Heimatomyces bidessarius* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 28: 185 (Thaxter 1893) [MB#147264]. – **Type**: "On elytra of *Bidessus granarius* Aube, Kittery, Maine"; FH. [USA]

Diagnostic features

Thallus slender, hyaline to yellowish-brow, with cell Ia flattened, subtending parallel cells II and IIa; cells III and IIIa overlapping, nearly parallel, separated by a strongly oblique to nearly vertical septum (Fig. 20C). [Detailed descriptions: Scheloske 1969; Sugiyama 1973; Majewski 1994b]

Distribution and hosts

On Col. Dytiscidae of the genera *Bidessus* Sharp, 1882, *Hygrotus*, *Guignotus* Houlbert, 1934, *Hyphydrus* Illiger, 1802, *Laccophilus*, *Uvarus* Guignot, 1939, *Hydrovatus* Motschulsky, 1853, *Liodessus* Guignot, 1939, and *Hydroglyphus* Motschulsky, 1853 from **Europe** (France, Poland, Germany, Finland, Hungary and Sweden), USA (type), **Asia** (China and Japan) and **Oceania** (Fiji) (Majewski 2008; Huggert 2010). Recently reported from the Netherlands (Haelewaters & De Kesel 2020).

Collections examined from Denmark

On *Hygrotus inaequalis* (Fabricius, 1777) (Col. Dytiscidae)

DENMARK – **Nordøstjylland (NEJ)** • Knarmod i Tofte Skov; 56°51.824′ N, 10°15.470′ E; NJ70; 8 Aug. 2013; *JP 337*; JP det.; ZMUC C-F-122816. – **Nordøstsjælland (NEZ)** • Heatherhill; 56°5.240′ N, 12°8.611′ E; UC21; 22 May 2016; *JP 96*; JP det.; ZMUC C-F-122571. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1477*; JP det.; ZMUC C-F-124057.

Remarks

First record from Denmark. The finding of this species in Denmark is not surprising given its presence in several neighbouring countries.

Chitonomyces elongatus Speg.

MB#163977

Fig. 20E–F

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 44 (Spegazzini 1915b). – **Type**: "Conegliano, on *Laccophilus poecilus* (as *L. virescens*), VII.1914, slide C. Spegazzini 46–1915 (LPS–61915, type)"; LPS. [according to Santamaria 2001b: 345] [Italy]

Diagnostic features

Dimorphic. Thalli on female hosts (Fig. 20E) are zigzagged, with cell I up to seven times as long as broad; cell Ia similar to I, abruptly turning back; cell IIIa laterally diverging from the perithecial axis. Thalli on male hosts (Fig. 20F) are straight, with cell I up to ten times as long as broad; cell Ia trapezoidal, ± isodiametric; cell IIIa 2–3 times as long as broad, distinctly darker than the surrounding cells. [Detailed descriptions: Santamaria 2001b, 2003]

Distribution and hosts

This species can be seen only thanks to the translucency of last abdominal sternite of its hosts, where the brownish thalli and their darkened feet can be distinguished; otherwise they would be invisible because they are nearly hidden from eye, with only the upper parts being slightly perceptible sometimes. On *Laccophilus* (Col. Dytiscidae) from Italy (type), USA? (Seymour 1967, this record should be verified), and Spain (Santamaria 2001b).

Collections examined from Denmark

On *Laccophilus minutus* (Linnaeus, 1758) (Col. Dytiscidae)

DENMARK – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1478*; JP det.; ZMUC C-F-124060, C-F-124061.

Remarks

First record from Denmark. Spegazzini (1915b) only described the form found on female hosts, without specifying its origin, mentioning the thorax as its growing location and *Laccophilus poecilus* as the host; all is quite doubtful.

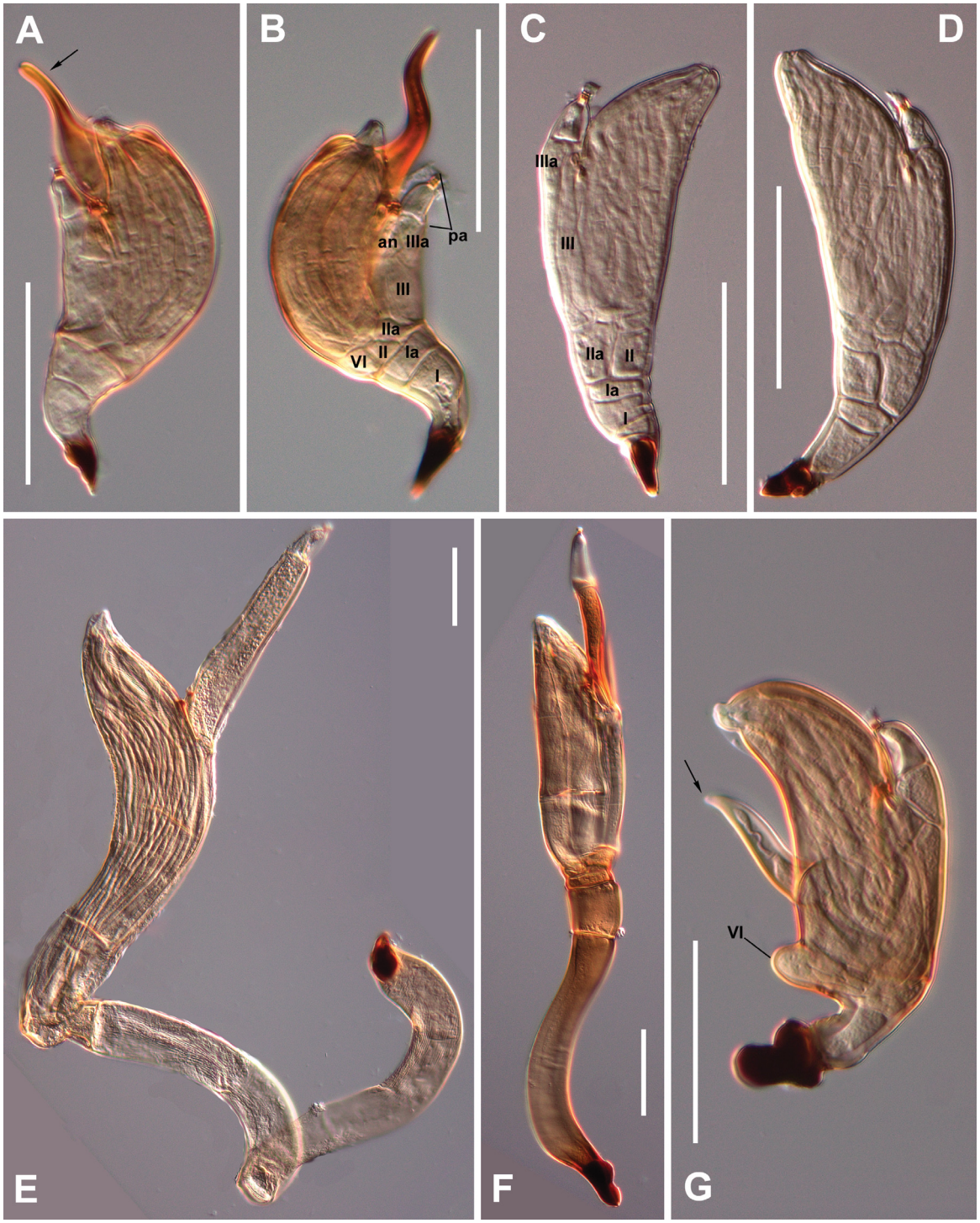

Fig. 20. *Chitonomyces* spp. **A**–**B**. *C. aculeifer* Speg. Mature thalli with labelling of cells and other parts of the thallus, i.e., cells I, Ia, II, IIa, III, IIIa, VI, antheridium (an), primary appendage (pa) and perithecial outgrowth (arrow). **A**. From *Graptodytes*. **B**. From *Haliplus*. – **C**–**D**. *C. bidessarius* (Thaxt.) Thaxt. Mature thalli with labelling of cells of the thallus, i.e., cells I, Ia, II, IIa, III, and IIIa. – **E**–**F**. *C. elongatus* Speg. **E**. Thallus from a female host. **F**. Thallus from a male host. – **G**. *C. ensifer* Speg. Mature thallus showing prominent cell VI and perithecial outgrowth (arrow). Scale bars: 50 µm. Photographs from slides ZMUC C-F-123553 (A), ZMUC C-F-124083 (B), ZMUC C-F-122816 (C–D), ZMUC C-F-124060 (E), ZMUC C-F-124061 (F), ZMUC C-F-123670 (G).

Chitonomyces ensifer Speg.
MB#177051
Fig. 20G

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 45 (Spegazzini 1915b; as *ensiferus*). – **Type**: "Sobre el abdomen y el margen de los élitros de *Laccophilus virescens*, pescado en los charcos cerca de Conegliano, Jul. y Nov. 1913"; LPS. [Italy]

Diagnostic features

The perithecium bears a nearly straight, finger-like, pointed outgrowth, up to 44 µm long, directed obliquely upwards, arising from the lower third of the perithecial wall (Fig. 20G, arrow). Cell VI sometimes inflated and prominent below the perithecium (Fig. 20G, VI). [Detailed descriptions: Majewski 1994b; Santamaria 2001b, 2003]

Distribution and hosts

Between the claws of *Laccophilus* (Col. Dytiscidae) from Italy (type), Poland (Majewski 1994b), and Spain (Santamaria 2001b).

Collections examined from Denmark

On *Laccophilus minutus* (Linnaeus, 1758) (Col. Dytiscidae)
DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1146*; JP det.; ZMUC C-F-123670. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1478*; JP det.; ZMUC C-F-124058.

Remarks

First record from Denmark. Easily overlooked because it is a tiny species which grows in a very hidden position. The new finding suggests a wider distribution than indicated by the relatively few previous records, especially when it is taken into account that the host species is very common and widespread.

Chitonomyces italicus Speg.
MB#155523
Fig. 21A–B

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 46 (Spegazzini 1915b). – **Type**: "Sobre el margen posterior de los élitros del *Laccophilus obscurus ?*, pescado en los zanjones de los alrededores de Conegliano, Nov, 1913"; LPS. [Italy]

Diagnostic features

Cell IIIa extending into a short and straight to arcuate or sigmoid, ± darkened, sometimes lobate up to 50 µm long outgrowth, which is directed upwards to outwards without exceeding the perithecial apex (Fig. 21A, arrow). [Detailed descriptions: Sugiyama 1977; Majewski 1994b; Santamaria 2001b, 2003; De Kesel & Werbrouck 2008]

Distribution and hosts

On the legs of *Laccophilus* (Col. Dytiscidae) in **Europe** (Belarus, Belgium, Germany, Italy – type –, Poland, Spain) and Japan (Majewski 2008; De Kesel & Haelewaters 2012).

Collections examined from Denmark

On *Laccophilus minutus* (Linnaeus, 1758) (Col. Dytiscidae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1146*; JP det.; ZMUC C-F-123669. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1478*; JP det.; ZMUC C-F-124059.

Remarks

First record from Denmark. The finding of this species in Denmark is not surprising because of its worldwide distribution.

Chitonomyces melanurus Peyr.
MB#169599
Fig. 21C–D

Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1 68: 250 (Peyritsch 1873). – *Heimatomyces melanurus* (Peyr.) Saccardo (Saccardo 1895: 448) [MB#250301]. – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "Diese merkwürdige Art kommt stets in Gemeinschaft der nächst folgenden auf Wasserkäfern vor. Zuerst entdeckte ich sie auf *Laccophilus minutus* Sturm, dann auf *Laccophilus hyalinus* Degeer". [Austria]

Heimatomyces melanurus (Peyr.) Saccardo (Saccardo 1895: 448) [MB#250301]

Diagnostic features

Cell IIIa blackened, supporting an elongate, dark, hooked basal cell of the primary appendage (Fig. 21D, arrow). Perithecial apex with two enlarged or lobulate lip cells formed by the uppermost wall cells from the anterior and posterior vertical rows (Fig. 21C, *). [Detailed descriptions: Thaxter 1896; Sugiyama & Hayama 1981; Majewski 1994b; Santamaria 2001b, 2003; De Kesel & Werbrouck 2008]

Distribution and hosts

A common species that can be found on the posterior lateral margin of the left elytron in *Laccophilus* (Col. Dytiscidae) from **Europe**: Austria (type), Finland, France, Germany, Hungary, Italy, Poland, Spain, United Kingdom (Santamaria *et al.* 1991), Belgium (De Kesel & Werbrouck 2008), Sweden (Huggert 2010), the Netherlands, Croatia, and Ukraine (Haelewaters & De Kesel 2020); **Africa**: Algeria (Maire 1920), Cameroon, Morocco (Santamaria *et al.* 1991); **Asia**: China, Japan, Taiwan (Santamaria *et al.* 1991), Korea (Lee & Kim 1990), Turkey (Rossi 2016), Cambodia (Try *et al.* 2017), but not found in America and Oceania.

Collections examined from Denmark

On *Laccophilus minutus* (Linnaeus, 1758) (Col. Dytiscidae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1146*; JP det.; ZMUC C-F-123671. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1478*; JP det.; ZMUC C-F-124062.

Remarks

First record from Denmark. The finding of this species is not surprising because of its cosmopolitan distribution.

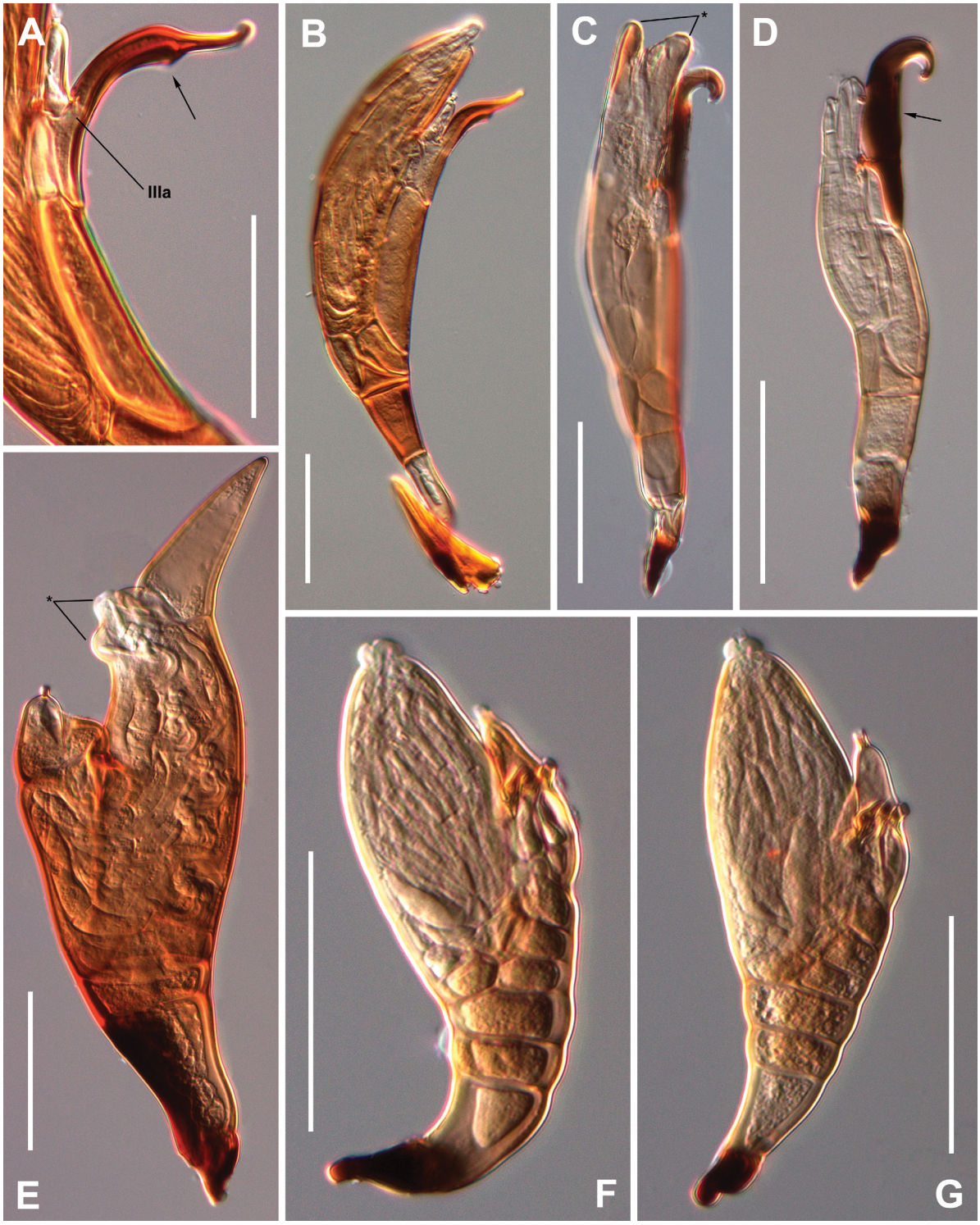

Fig. 21. A–**B**. *Chitonomyces italicus* Speg. **A**. Detail of cell IIIa and its outgrowth (arrow). **B**. Mature thallus. – **C**–**D**. *Chitonomyces melanurus* Peyr. **C**. Mature thallus showing perithecial enlarged lips (*). **D**. Young thallus with labelled cell IIIa and hooked basal cell of primary appendage (arrow). – **E**. *Chitonomyces paradoxus* (Peyr.) Thaxt. Mature thallus showing prominent perithecial lips (*). – **F**–**G**. *Hydraeomyces halipli* (Thaxt.) Thaxt. Mature thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124059 (A–B), ZMUC C-F-124062 (C), ZMUC C-F-123671 (D), ZMUC C-F-123078 (E), ZMUC C-F-122568 (F–G).

Chitonomyces paradoxus (Peyr.) Thaxt.
MB#170184
Fig. 21E

Memoirs of the American Academy of Arts and Sciences 12: 287 (Thaxter 1896: 287). – **Basionym**: *Heimatomyces paradoxus* Peyr., *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1* 68: 251 (Peyritsch 1873) [MB#249906]. – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "Mit der vorhergehenden Art auf *Laccophilus minutus* Sturm und *L. hyalinus* Degeer". [Austria]

Heimatomyces unciger Thaxt. (Thaxter 1895: 478, as *uncigerus*) [MB#245659]. – *Chitonomyces unciger* (Thaxt.) Thaxt. (Thaxter 1896: 288, as *uncigerus*) [MB#175610]
Chitonomyces truncatus Speg. (Spegazzini 1915b: 47) [MB#176303]

Diagnostic features

The ascogenous cavity inside the perithecium appears nearly horizontal, strongly curved, u-shaped. The ostiole is surrounded by obtuse, usually prominent and asymmetrical lips (Fig. 21E, *). The perithecium bears a variably elongated horn-like outgrowth arising from the upper outer wall cell of the anterior row. [Detailed descriptions: Thaxter 1916, 1924; Sugiyama 1973; Majewski 1994b; Santamaria 2001b, 2003; De Kesel & Werbrouck 2008; Goldmann & Weir 2012]

Distribution and hosts

More common than *Ch. melanurus* with which it often coexists on the same host individual, occupying a similar position but just below it. Reported on *Laccophilus* (Col. Dytiscidae) in **America**: Grenada, Jamaica, USA, Trinidad & Tobago (Santamaria *et al.* 1991), Bahamas (Haelewaters *et al.* 2017); **Asia**: Indonesia, Japan, Taiwan, Thailand (Santamaria *et al.* 1991), Korea (Lee & Kim 1990), China (Lee *et al.* 1995), Turkey (Rossi 2016), Cambodia (Try *et al.* 2017); **Africa**: Sierra Leone (Rossi & Leonardi 2018); and **Europe**: Austria (type), Finland, France, Germany, Hungary, Italy, Poland, Russia, Spain, United Kingdom, former Yugoslavia (Santamaria *et al.* 1991), Belgium (De Kesel & Werbrouck 2008), Sweden (Huggert 2010).

Collections examined from Denmark

On *Laccophilus minutus* (Linnaeus, 1758) (Col. Dytiscidae)
DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1146*; JP det.; ZMUC C-F-123668. – **Nordvestsjælland (NWZ)** • Klintebjerg ved Klint; 55°57.321′ N, 11°34.197′ E; PH60; 16 Oct. 2017; *JP 589*; JP det.; ZMUC C-F-123078. – **Vestjylland (WJ)** • Simmelmose; 55°46.299′ N, 9°3.519′ E; NG08; 2 Jun. 2019; *JP 1478*; JP det.; ZMUC C-F-124063.

Remarks

First record from Denmark. Three forms of this species may be perfectly distinguished by morphological traits, depending on the hosts, being *Laccophilus minutus*, *L. poecilus* (= *L. variegatus*) and *L. hyalinus*. These forms were described and illustrated by Majewski (1994b) and Santamaria (2001b, 2003). Further studies supported by molecular analysis might clarify the taxonomic position of these forms. Danish thalli belong to the form growing on *L. minutus*.

Genus ***Hydraeomyces*** Thaxt.
MB#2404

Memoirs of the American Academy of Arts and Sciences 12: 293 (Thaxter 1896). – Type species: *H. halipli* (Thaxt.) Thaxt. (by monotypy)

Parahydraeomyces Speg., *Anales del Museo Nacional de Historia Natural de Buenos Aires* 27: 70 (Spegazzini 1915b) [MB#3702]

Brief description

Monoecious. Receptacle consisting of 6–8 cells viz.: a basal cell (I), 2–4 cells Ia, two cells II, and one cell III. Cell III subtends two broad cells which each bear two bell-shaped antheridia. The perithecium has two adjacent vertical rows of outer wall cells with 4–5 cells, and other two rows with 7–8 cells.

Remarks

Monotypic. Closely related to *Chitonomyces* from which it can be separated by the perithecial wall cell arrangement and appendage characteristics.

Hydraeomyces halipli (Thaxt.) Thaxt.
MB#148360
Fig. 21F–G

Memoirs of the American Academy of Arts and Sciences 12: 293 (Thaxter 1896). – **Basionym**: *Heimatomyces halipli* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 29: 32 (Thaxter 1893) [MB#462738]. – **Type**: [Not designated] [Ind. loc.] "On *Haliplus ruficollis* and *Cnemidotus muticus*, Connecticut"; FH. [USA] [According to Tavares 1985, the type are the fungi from *H. ruficollis*]

Hydraeomyces cnemidoti Thaxt. (Thaxter 1908: 267) [Not registered in MycoBank]
Hydraeomyces venetus Speg. (Spegazzini 1915b: 52) [MB#187540]
Parahydraeomyces italicus Speg. (Spegazzini 1915b: 70) [MB#146173]

Diagnostic features

See genus description. [Detailed descriptions: Sugiyama 1973; Sugiyama & Hayama 1981; Weir 1994; Majewski 1994b; Santamaria 2003; De Kesel & Werbrouck 2008]

Distribution and hosts

On species of the aquatic beetles belonging to the genera *Haliplus* and *Peltodytes* (=*Cnemidotus* Illiger, 1802) (Col. Haliplidae). This fungus is widely distributed in **Europe**: Croatia, Czech Republic, Finland, France, Germany, Italy, Poland, Russia, Spain, United Kingdom (Majewski 2008), Hungary (Bánhegyi 1950), Belgium (De Kesel & Werbrouck 2008), Sweden (Huggert 2010), Bulgaria (Rossi *et al.* 2019a), Slovenia (Rossi & Christian 2020), and the Netherlands (Haelewaters & De Kesel 2020); **Africa**: Tunisia and Morocco (Maire 1916a); **America**: USA (Thaxter 1892), and Argentina (Spegazzini 1917); **Asia**: China (Thaxter 1924), Japan (Sugiyama 1973), and Taiwan (Sugiyama & Hayama 1981).

Collections examined from Denmark

On *Haliplus apicalis* Thomson, 1868 (Col. Haliplidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°3.218′ N, 12°15.801′ E; UB20; 10 Jun. 2017; *JP 427*; JP det.; ZMUC C-F-122912.

On *Haliplus immaculatus* Gerhardt, 1877 (Col. Haliplidae)

DENMARK – **Nordøstsjælland (NEZ)** • Nordhavnstippen på Københavns Nordhavn; 55°43.091′ N, 12°37.088′ E; UB57; 29 Apr. 2018; *JP 1094*; JP det.; ZMUC C-F-123611.

On *Haliplus ruficollis* (Degeer, 1774) (Col. Haliplidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Busemarke Mose; 54°57.688′ N, 12°26.619′ E; UA39; 19 Aug. 2019; *JP 1495*; JP det.; ZMUC C-F-124081 • Ulvshale; 55°2.729′ N, 12°16.354′ E; UB20; 2 May 2018; *JP 1101*; JP det.; ZMUC C-F-123619. – **Nordøstsjælland (NEZ)** • Heatherhill; 56°5.240′ N, 12°8.611′ E; UC21; 22 May 2016; *JP 93*; JP det.; ZMUC C-F-122568.

Remarks

First record from Denmark. The presence of this species in Denmark is not surprising according to its cosmopolitan distribution.

Subtribe Chaetarthriomycetinae I.I.Tav.

Genus ***Chaetarthriomyces*** Thaxt.
MB#936

Memoirs of the American Academy of Arts and Sciences 16: 319 (Thaxter 1931). – Type species: *C. flexatus*

Brief description

Monoecious. Receptacle multicelled, consisting of a series of superposed cells forming the main axis which extends into the primary appendage without apparent discontinuity. Antheridia are corner cells of appendage.

Remarks

The genus consists of four species, of which two in Europe, both in Denmark. The most recently described species is *C. spiralis* (Santamaria 2001a).

Key to the Danish species

1. Perithecial wall cells arranged in spiral ..... ***C. spiralis*** Santam.
– Perithecial walls cells arranged in vertical rows..... ***C. crassiappendicatus*** Scheloske

Chaetarthriomyces crassiappendicatus Scheloske
MB#327992
Fig. 22A–B

Parasitologische Schriftenreihe 19: 97 (Scheloske 1969; as *C. crassappendicatus*). – **Type**: [In ?] "Auf den Elytren und nahe der Basis der Schenkel der Hinterbeine von *Chaetarthria seminulum* (Col. Hydrophilidae). Die Wirte stammen von einer feuchten Wiese in Ufernähe des Hembach bei Schwand/Nürnberg sowie aus dem flachen Wasser (zwischen Pflanzen) eines Weihers bei Dechsendorf/Erlangen, Deutschland. Holotypus Abb. 10". [Germany]

Diagnostic features

Primary appendage consisting of 5–6 isodiametric cells culminated with a rounded uppermost cell; the intermediate cells separate 1–2 small and short antheridia at one or at opposite sides (Fig. 22A, arrows). Perithecium showing a short neck and a ± bent, asymmetric, subacute apex. [Detailed descriptions: Majewski 1994b; Santamaria 2003]

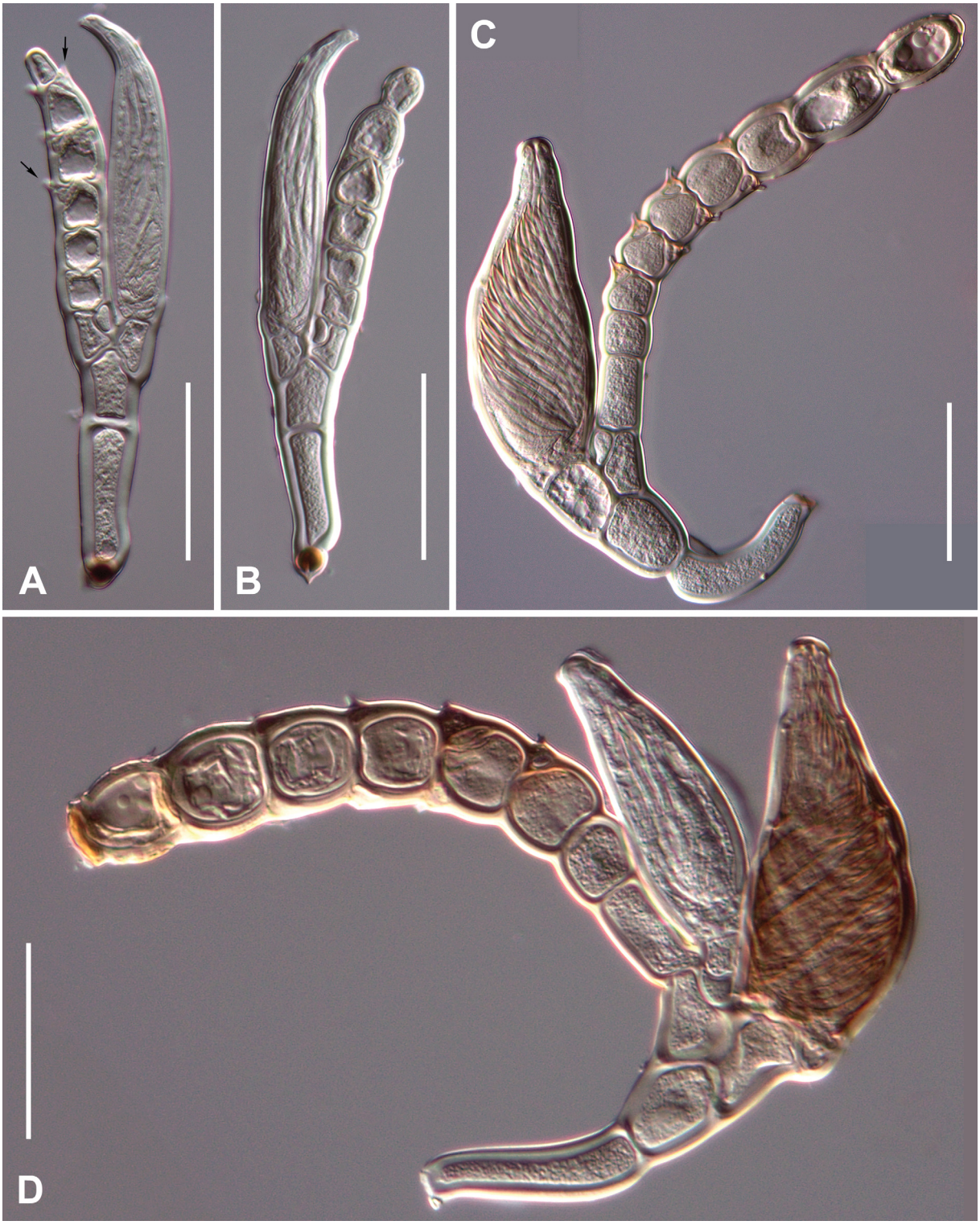

Fig. 22. *Chaetarthriomyces* spp. **A**–**B**. *C. crassiappendicatus* Scheloske. Mature thalli with labelled antheridia (arrows). – **C**–**D**. *C. spiralis* Santam. Mature thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123215 (A–B), ZMUC C-F-123214 (C–D).

Distribution and hosts

On *Chaetarthria* (Col. Hydrophilidae) from Germany (type), Poland (Majewski 1972a), Spain (Santamaria 1989), United Kingdom (Weir 1996), Sweden (Huggert 2010), and the Netherlands (Haelewaters *et al.* 2014).

Collections examined from Denmark

On *Chaetarthria seminulum* (Herbst, 1787) (Col. Hydrophilidae)

DENMARK – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 722*; JP det.; ZMUC C-F-123215.

Remarks

First record from Denmark. The finding of this species in Denmark was expected by its presence in the neighbouring countries. The thalli of this fungus can easily be overlooked due to their small size.

Chaetarthriomyces spiralis Santam.

MB#474853

Fig. 22C–D

Nova Hedwigia 72 (3–4): 379 (Santamaria 2001a). – **Type**: "Spain. Jaén: Santiago–Pontones, Parque Natural de Cazorla, Segura y Las Villas, río Aguamulas, below the head of *Chaetarthria seminulum* (Herbst) (Coleoptera, Hydrophilidae), 12.V.1990, leg. S. Santamaria, BCB–Mycotheca SS·0945 [Holotypus]"; BCB.

Diagnostic features

Primary appendage strongly arcuate, consisting of up to 12 isodiametric cells culminated with a rounded uppermost cell. Perithecium with a blunt apex, with the wall cells spirally arranged and distinctively brown-pigmented (Fig. 22D). [Detailed description: Santamaria 2003]

Distribution and hosts

Grows on the underside of the head of *Chaetarthria* (Col. Hydrophilidae) in Spain (type) and Poland (Majewski 2008).

Collections examined from Denmark

On *Chaetarthria seminulum* (Herbst, 1787) (Col. Hydrophilidae)

DENMARK – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 722*; JP det.; ZMUC C-F-123214.

Remarks

First record from Denmark. This species is much larger and significantly less frequent than *C. crassiappendicatus.* The development of two viable perithecia on the same thallus is exceptional (Fig. 22D).

Subtribe Misgomycetinae (Thaxt.) I.I.Tav.

Genus ***Misgomyces*** Thaxt.
MB#3217

Proceedings of the American Academy of Arts and Sciences 35: 443 (Thaxter 1900). – Type species: *M. dyschirii* Thaxt.

Brief description

Monoecious. Receptacle multicelled, consisting of a lower uniseriate row of superposed cells and an upper region formed by irregularly arranged cells developed from subdivision of cell III. Antheridia immersed in primary appendage.

Remarks

The genus consists of two species: *Misgomyces mastacis* Balazuc (1975b) and *M. dyschirii*, only the latter in Europe. The genus *Misgomyces* has undergone many changes since its description, with many species having gone into and out of it. Thaxter (1931) added more species and transferred some species from *Ecteinomyces* and *Hydrophilomyces*. Tavares (1985) and Tavares & Majewski (1976) redefined the limits of the genus describing some new genera: *Blasticomyces* I.I.Tav., *Botryandromyces* I.I.Tav. & T.Majewski, *Dixomyces* I.I.Tav., *Kyphomyces* I.I.Tav., *Ormomyces* I.I.Tav. and *Siemaszkoa* I.I.Tav. & T.Majewski. *Misgomyces reicheiae* (Santam.) Santam. and *M. speluncae* (Santam.) Santam. were added later (Santamaria 1995a) but their generic position should be reconsidered, especially *M. reicheiae* which is dioecious (unpublished observations by SS).

Misgomyces dyschirii Thaxt.
MB#158617
Figs 23A–B, 103A

Proceedings of the American Academy of Arts and Sciences 35: 443 (Thaxter 1900). – **Type**: [Not designated] [Ind. loc.] "On *Dyschirius globosus* Herbst., Hope Coll., No. 349, England; on *D. salinus* Schaum., British Museum, No. 582, Europe"; FH. [According to Majewski (2008), Tavares (1985) designated a lectotype but we don't see any explicit reference to this in her work]

Misgomyces lavagnei F.Picard (Picard 1913: 520) [Not registered in MycoBank]

Diagnostic features

Receptacle consisting of a lower uniseriate row of 4–25 cells derived from cell II. Cell III irregularly divided into several small cells. Primary septum constricted and darkened. Primary appendage irregular, consisting of some embedded antheridia giving rise to short efferent necks, and a variable number of cells, some of them giving rise to sterile branches. [Detailed descriptions: Thaxter 1931; Sugiyama 1973; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Occurs on species of the genera *Dyschirius* Bonelli, 1810 and *Dyschiriodes* Jeannel, 1941 (Col. Carabidae) and rarely of the genus *Bledius* Leach, 1819 (Col. Staphylinidae Oxytelinae). The fungus on *Bledius* was described as *M. lavagnei*. Widely distributed in **Europe** (Austria, Denmark, Finland, France, Germany, Greece, the Netherlands, Hungary, Ireland, Italy, Poland, Romania, Spain, Switzerland, United Kingdom, Russia), **Asia** (Iran, Israel, Japan), **Africa** (Algeria, Canary Islands) and **America** (USA) (Santamaria *et al.* 1991). Subsequent records are from Belgium (De Kesel & Rammeloo 1992), India (Kaur & Mukerji

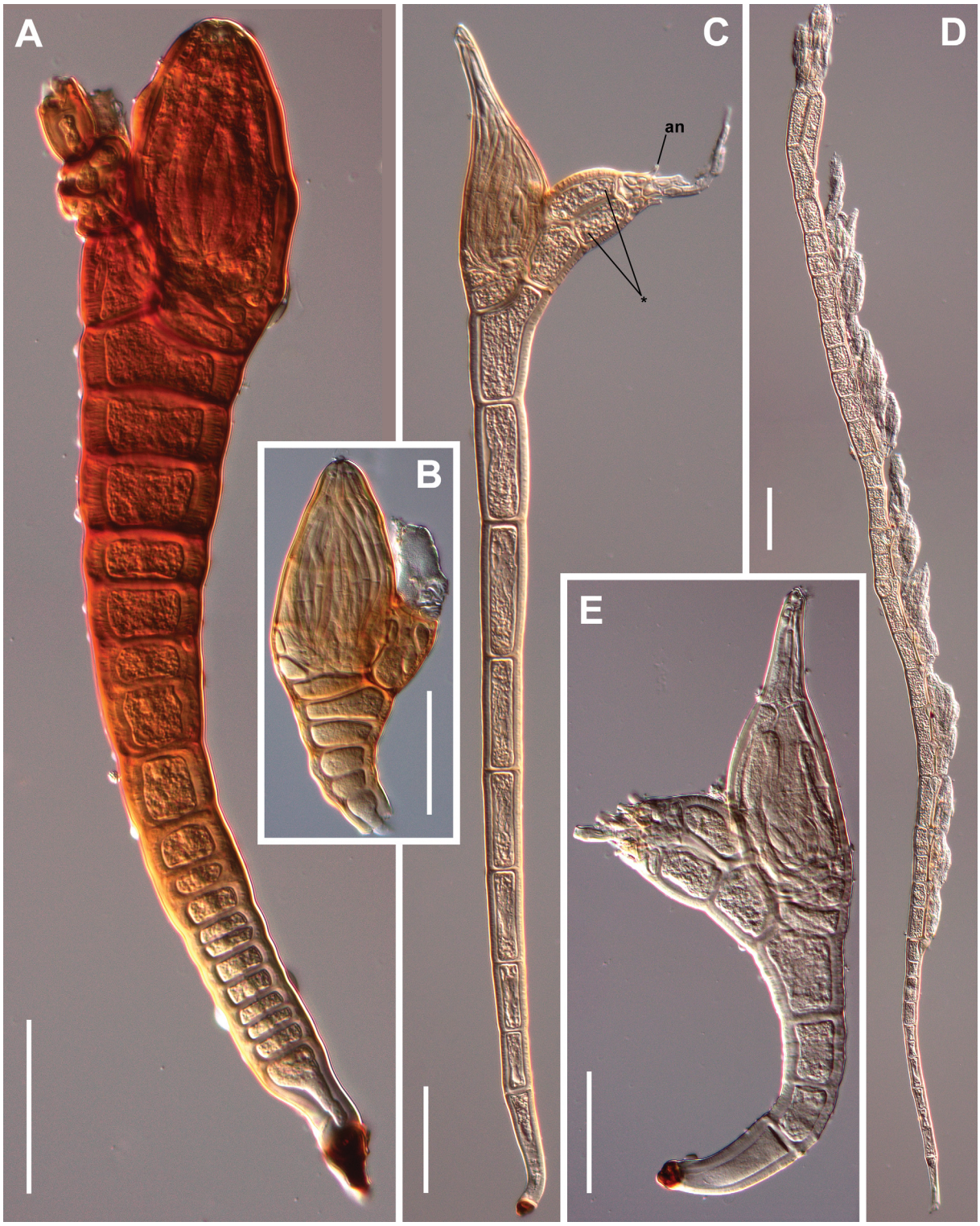

Fig. 23. A–**B**. *Misgomyces dyschirii* Thaxt. Mature thalli from pronotum (A) and tarsi (B). – **C**–**E**. *Botriandromyces heteroceri* (Maire) I.I.Tav. & T.Majewski. **C**. Mature thallus from elytra, showing two parallel cells of upper receptacle (*) and antheridia (an). **D**. Filiform thallus without perithecium, filled with clusters of antheridia on one side. **E**. Mature thallus from tarsi. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122694 (A), ZMUC C-F-123644 (B), ZMUC C-F-122594 (C–D), ZMUC C-F-122660 (E).

1996a), Korea (Lee & Na 1998), Lithuania (Markovskaja 2000), China (Shen & Ye 2006), Latvia (De Kesel & Krastina De Kesel 2006), Czech Republic, Slovakia (Rossi *et al.* 2010), Sweden (Huggert 2010), Turkey (Rossi 2016), Bulgaria, Namibia, Mongolia, Kazakhstan, Albania (Rossi *et al.* 2019a), and South Africa (Goldmann & Weir 2018).

Collections examined from Denmark

On *Dyschirius globosus* (Herbst, 1784) (Col. Carabidae)

DENMARK – **Fyn (F)** • Fyns Hoved; 55°36.736′ N, 10°35.706′ E; PG06; 4 Jan. 2015; *K.B. Nielsen 282*; JP det.; ZMUC C-F-122761. – **Lolland, Falster, Møn (LFM)** • Busemarke Mose; 54°57.459′ N, 12°27.054′ E; UA39; 28 Aug. 2019; *JP 1507*; JP det.; ZMUC C-F-124095 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1127*; JP det.; ZMUC C-F-123649 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1305*; JP det.; ZMUC C-F-123839. – **Nordøstsjælland (NEZ)** • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 623*; JP det.; ZMUC C-F-123111 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1054*; JP det.; ZMUC C-F-123571. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH08; 6 Feb. 2015; *JP 215*; JP det.; ZMUC C-F-122694 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 769*; JP det.; ZMUC C-F-123263. – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 713*; JP det.; ZMUC C-F-123204 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 636*; JP det.; ZMUC C-F-123125. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1363*; JP det.; ZMUC C-F-123902 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1441*; JP det.; ZMUC C-F-123988 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 538*; JP det.; ZMUC C-F-123022 • ibid.; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1272*; JP det.; ZMUC C-F-123801 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 962*; JP det.; ZMUC C-F-123468.

On *Dyschirius salinus* Schaum, 1843. (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.270′ N, 12°15.392′ E; UB20; 6 Jun. 2018; *JP 1122*; JP det.; ZMUC C-F-123644.

On *Dyschirius tristis* Stephens, 1827 (Col. Carabidae)

DENMARK – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1364*; JP det.; ZMUC C-F-123904.

Remarks

The length of thalli is very variable, from very short for thalli found on tarsi (Fig. 23B), to the mostly usual elongated thalli which are found on the upper rear surface of pronotum of their hosts (Figs 23A, 103A). Despite all the experienced adjustments, this genus is still in need of some revision. Without going any further, the structure of the antheridia is not yet well understood. According to Rossi *et al.* (2019a), antheridia are of the simple type, instead of the compound type described by Tavares (1985).

Subtribe Laboulbeniinae s. str.

Genus ***Botryandromyces*** I.I.Tav. & T.Majewski
MB#631

Mycotaxon 3 (2): 195 (Tavares & Majewski 1976). – Type species: *B. ornatus* I.I.Tav.

Brief description

Monoecious. Receptacle multicelled, consisting of a lower uniseriate row of superposed cells and an upper, usually three-celled, region where the lowermost cell supports two parallel cells (Fig. 23C, *). Antheridia simple, sessile (Fig. 23C, an) or clustered on short branchlets. Perithecial outer wall consisting of unequal cells arranged in two vertical rows with three cells, and two vertical rows with four cells.

Remarks

The genus consists of two species, the type and *B. heteroceri*, which is the only species in Europe. The genus *Botryandromyces* was segregated from *Misgomyces* because (1) the different number of perithecial wall cells for each row, four cells in all of the four rows in *Misgomyces*, two rows with four cells and two rows with three cells in *Botryandromyces*; and (2) the structure of antheridia, simple in *Botryandromyces*, compound in *Misgomyces*. Nevertheless this latter character has been questioned by Rossi *et al.* (2019a) (see above under *Misgomyces*).

Botryandromyces heteroceri (Maire) I.I.Tav. & T.Majewski
MB#309837
Fig. 23C–E

Mycotaxon 3 (2): 195 (Tavares & Majewski 1976). – **Basionym**: *Misgomyces heteroceri* Maire, *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 11(8): 159 (Maire 1920) [MB#159206]. – **Type**: [Type lost?!] "Sur les pattes et les élytres d'*Heterocerus maritimus* Guérin: C. Bône, embouchure de la Seybouse, mars 1918". [Algeria] [*Laboulbenia heteroceri* is mentioned as basionym in MB, but *L. heteroceri* was never described or mentioned in the literature; probably this is a confusion with *L. heteroceratis* Thaxt., the basionym of *Botryandromyces heteroceratis* (Thaxt.) I.I.Tav. & T.Majewski, a name which was later changed to *B. ornatus* I.I.Tav.]

Diagnostic features

Lower receptacle consisting of a series of 2–8(33) cells. Upper receptacle three-celled, with the lowermost cell subtending two parallel cells (Fig. 23C, *), which support many small and irregularly shaped cells, some of them giving rise to simple antheridia (Fig. 23C, an). Perithecium with a narrow and clearly distinguished neck. [Detailed descriptions: Majewski 1994b; Weir 1994; Santamaria 2003; De Kesel 2009]

Distribution and hosts

Described as *Misgomyces heteroceri* on *Heterocerus* Fabricius, 1792 (Col. Heteroceridae) from Algeria. Also grows on the related genera *Augyles* Schioedte, 1866 and *Littorimus* Gozis, 1885. Widespread in **Europe**: Spain, France, United Kingdom, Germany, Italy, Poland, Lithuania, Greece (Majewski 2008), Hungary (Bánhegyi *et al.* 1985), Belgium (De Kesel 2009), the Netherlands (Haelewaters *et al.* 2014), Sweden (Huggert 2010), Bulgaria (Rossi *et al.* 2019a), and Austria (Rossi & Christian 2020); and **Asia**: Thailand (Santamaria & Rossi 1999), China (Zhang *et al.* 2001), and Turkey (Rossi 2016).

Collections examined from Denmark

On *Augyles hispidulus* (Kiesenwetter, 1843) (Col. Heteroceridae)
DENMARK – **Nordvestsjælland (NWZ)** • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 181*; JP det.; ZMUC C-F-122660.

On *Heterocerus fenestratus* (Thunberg, 1784) (Col. Heteroceridae)
DENMARK – **Nordøstsjælland (NEZ)** • Gundsømagle Holme; 55°44.733′ N, 12°10.933′ E; UB28; 20 Aug. 2016; *JP 117*; JP det.; ZMUC C-F-122594.

On *Heterocerus flexuosus* Stephens, 1828 (Col. Heteroceridae)
DENMARK – **Sydjylland (SJ)** • Rejsby Sluse vest for Rejsby; 55°13.931′ N, 8°40.488′ E; MG72; 8 Mar. 2020; *JP 1651*; JP det.; ZMUC C-F-124373.

On *Heterocerus fusculus* Kiesenwetter, 1843 (Col. Heteroceridae)
DENMARK – **Sydjylland (SJ)** • Rejsby Sluse vest for Rejsby; 55°13.931′ N, 8°40.488′ E; MG72; 8 Mar. 2020; *JP 1652*; JP det.; ZMUC C-F-124374.

On *Heterocerus obsoletus* Curtis, 1828 (Col. Heteroceridae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°3.218′ N, 12°15.801′ E; UB20; 10 Jun. 2017; *JP 428*; JP det.; ZMUC C-F-122913.

Remarks

First record from Denmark. The size of thalli differs considerably in relation to the growth location on the host. Longer thalli occur on elytra and pronotum (Fig. 23C), while the shorter ones are found on tarsi (Fig. 23E) as usual in most species of Laboulbeniales. Very often we find elongated, filiform thalli, with the lower receptacle consisting of up to 33 superposed cells, without mature perithecia, but showing a normal upper receptacle; some of the cells in the lower receptacle separate corner cells which form the base for short branchlets bearing clusters of flask-shaped antheridia (Fig. 23D). These differ from the typical antheridia found on the upper receptacle because of their longer efferent necks. We do not understand the meaning of this dimorphism or the presence of these extremely elongated thalli, bearing only antheridia and lacking any trace of female elements.

Genus ***Ecteinomyces*** Thaxt.
MB#1741

Proceedings of the American Academy of Arts and Sciences 38: 26 (Thaxter 1902). – Type species: *E. trichopterophilus* Thaxt.

Brief description

Monoecious. Receptacle multicelled, consisting of a uniseriate row of superposed cells, forming an axis which continues into the appendage. Antheridia sessile as corner cells on the lower part of the axis (Fig. 24A, F, an) or on slender branches above. Perithecium with a long, narrow neck; outer wall consisting of unequal cells, arranged in two vertical rows with four cells, and two vertical rows with five cells.

Remarks

The genus consists of two species, the type *E. trichopterophilus* and *E. bonariensis* Speg., the latter remaining provisionally in the genus. Only the type species is known in Europe.

Ecteinomyces trichopterophilus Thaxt.
MB#180542
Fig. 24

Proceedings of the American Academy of Arts and Sciences 38: 26 (Thaxter 1902). – *Misgomyces trichopterophilus* (Thaxt.) Thaxt. (Thaxter 1931: 304) [MB#280610]. – **Type**: “On the elytra and abdomen of *Trichopteryx Haldemani* Lec., Intervale, N.H., August, 1901”; FH. [USA]

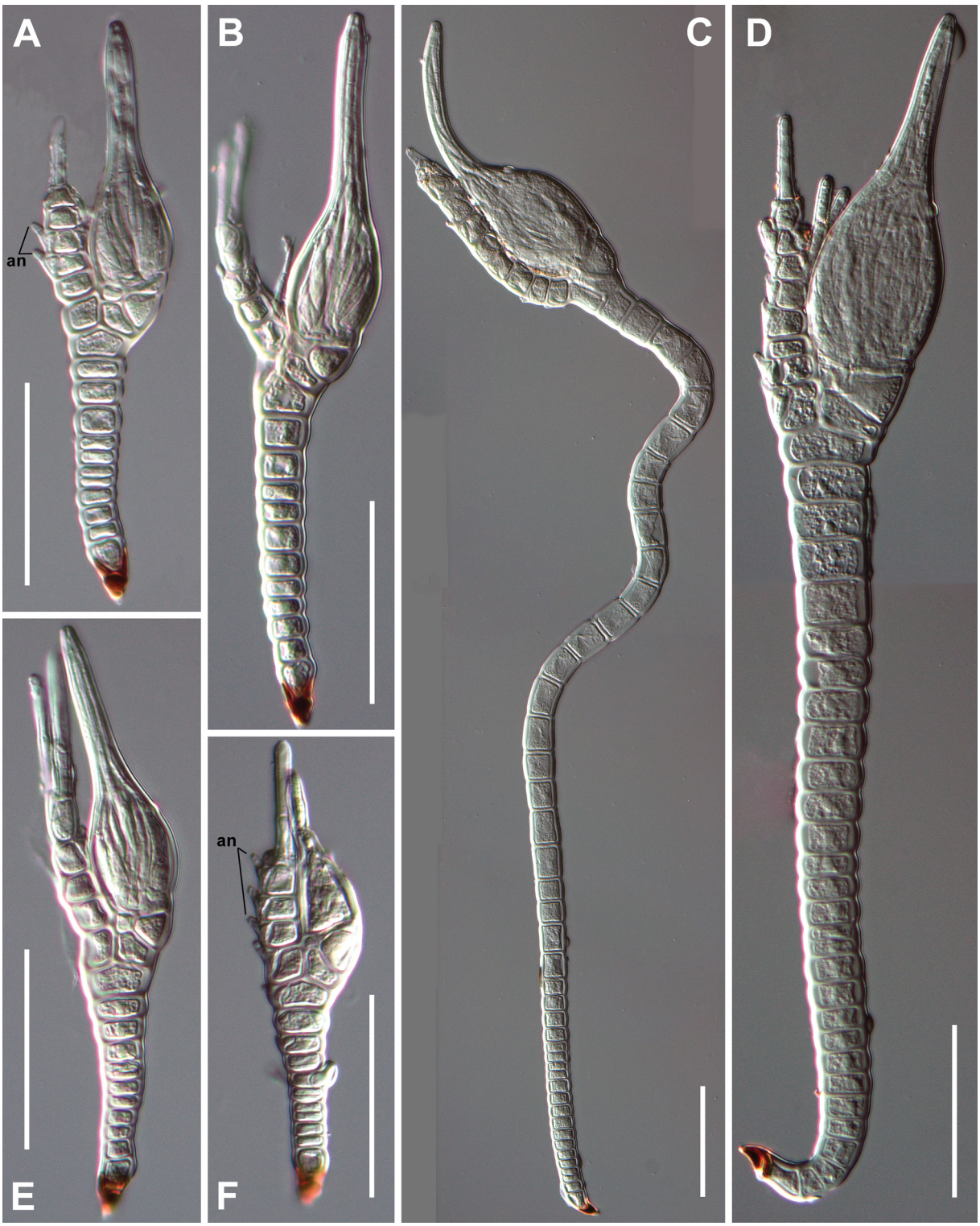

Fig. 24. *Ecteinomyces trichopterophilus* Thaxt. **A**–**E**. Mature thalli. In C, a very slender and flexuous thallus with up to 43 receptacular cells, and in D a gigantic thallus, both from *Acrotrichis intermedia*. **F**. Immature thallus. Antheridia (an) are labelled in A and F. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122497 (A–B, E–F), ZMUC C-F-122653 (C–D).

Diagnostic features

Receptacle uniseriate, consisting of a row of 3–28(–43) cells. Most of the appendage cells give rise to 1–2 corner cells that function as simple antheridia in young thalli. Perithecium with a broad, ovoidal venter and an abruptly distinguished, straight and slender neck. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Weir 1994; Santamaria 2003; De Kesel 2010]

Distribution and hosts

Found on species of *Acrotrichis* and *Baeocrara* Thomson, 1859 (this host genus only in Poland) (Col. Ptiliidae) from **America**: USA, Chile, Argentina (Majewski 2008), and Costa Rica (Goldmann & Weir 2018); **Europe**: Italy, Germany, Spain, United Kingdom, Poland (Majewski 2008), Finland (Huldén 1983), Hungary (Bánhegyi *et al.* 1985), Belgium (De Kesel & Rammeloo 1992), Denmark (Høier 2009), Sweden (Huggert 2010), the Netherlands (Haelewaters *et al.* 2014), Bulgaria (Rossi *et al.* 2019a), and Austria (Rossi & Christian 2020).

Collections examined from Denmark

On *Acrotrichis atomaria* (Degeer, 1774) (Col. Ptiliidae)

DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 23*; JP det.; ZMUC C-F-122496. – **Nordvestjylland (NWJ)** • Gammelgård på Fur; 56°50.314′ N, 8°58.971′ E; MH99; 22 Nov. 2013; *JP 417*; JP det.; ZMUC C-F-122901 • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 223*; JP det.; ZMUC C-F-122704. – **Nordvestsjælland (NWZ)** • Garbølle; 55°34.107′ N, 11°34.293′ E; PG66; 21 Apr. 2018; *JP 1063*; JP det.; ZMUC C-F-123580. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1267*; JP det.; ZMUC C-F-123795.

On *Acrotrichis brevipennis* (Erichson, 1845) (Col. Ptiliidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 646*; JP det.; ZMUC C-F-123134. – **Nordøstsjælland (NEZ)** • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 869*; JP det.; ZMUC C-F-123365. – **Sydsjælland (SZ)** • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; 17 Feb. 2019; *JP 1391*; JP det.; ZMUC C-F-123934.

On *Acrotrichis cognata* (Matthews, 1877) (Col. Ptiliidae)

DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 22*; JP det.; ZMUC C-F-122495.

On *Acrotrichis danica* Sundt, 1958 (Col. Ptiliidae)

DENMARK – **Nordøstjylland (NEJ)** • Syd for Krogsagergård; 56°37.534′ N, 9°45.551′ E; NH47; 24 Nov. 2019; *JP 1552*; JP det.; ZMUC C-F-124313.

On *Acrotrichis fascicularis* (Herbst, 1793) (Col. Ptiliidae)

DENMARK – **Østjylland (EJ)** • Almose i Fjeld Skov; 56°24.698′ N, 10°27.948′ E; NH95; 23 Nov. 2019; *JP 1549*; JP det.; ZMUC C-F-124310 • Stidsmølle i Mattrup Skov; 55°55.455′ N, 9°33.811′ E; NG39; 19 Nov. 2017; *JP 813*; JP det.; ZMUC C-F-123307.

On *Acrotrichis grandicollis* (Mannerheim, 1844) (Col. Ptiliidae)

DENMARK – **Nordøstsjælland (NEZ)** • Bispebjerg; 55°43.063′ N, 12°31.288′ E; UB47; 3 Nov. 2019; *JP 1539*; JP det.; ZMUC C-F-124299 • Skærød; 56°0.673′ N, 12°9.646′ E; UC21; 14 Jan. 2018; *JP 959*; JP det.; ZMUC C-F-123465. – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 721*; JP det.; ZMUC C-F-123213.

On *Acrotrichis intermedia* (Gillmeister, 1845) (Col. Ptiliidae)
DENMARK – **Østjylland (EJ)** • Hampen Plantage; 56°1.561′ N, 9°22.546′ E; NH20; 6 Oct. 2019; *JP 1526*; JP det.; ZMUC C-F-124281 • Vingsted; 55°40.512′ N, 9°23.500′ E; NG27; 6 Oct. 2019; *JP 1531*; JP det.; ZMUC C-F-124290. – **Sydsjælland (SZ)** • Højstrup ved Rødvig; 55°14.319′ N, 12°20.234′ E; UB32; 15 Jan. 2017; *JP 174*; JP det.; ZMUC C-F-122653.

On *Acrotrichis montandonii* (Allibert, 1844) (Col. Ptiliidae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 823*; JP det.; ZMUC C-F-123317. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 462*; JP det.; ZMUC C-F-122947 • **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1089*; JP det.; ZMUC C-F-123607.

On *Acrotrichis sitkaensis* (Motschulsky, 1845) (Col. Ptiliidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 463*; JP det.; ZMUC C-F-122948 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1342*; JP det.; ZMUC C-F-123881. – **Sydsjælland (SZ)** • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1432*; JP det.; ZMUC C-F-123979. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1249*; JP det.; ZMUC C-F-123777 • ibid.; *JP 1268*; JP det.; ZMUC C-F-123796.

On *Acrotrichis* spp. (Col. Ptiliidae)
DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14°45.096′ E; VB80; 25 Apr. 2014; *JP 502*; JP det.; ZMUC C-F-122986. – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 753*; JP det.; ZMUC C-F-123247 • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 792*; JP det.; ZMUC C-F-123287 • Høgdal; 56°6.449′ N, 9°36.941′ E; NH31; 11 Mar. 2017; *JP 352*; JP det.; ZMUC C-F-122834 • Kjellerup; 56°17.282′ N, 9°26.197′ E; NH23; 7 Jul. 2013; *JP 53*; JP det.; ZMUC C-F-122528 • ibid.; 23 Mar. 2014; *JP 122*; JP det.; ZMUC C-F-122599 • ibid.; 56°17.589′ N, 9°26.117′ E; NH23; 21 Oct. 2017; *JP 583*; JP det.; ZMUC C-F-123069 • ibid.; 56°17.614′ N, 9°26.106′ E; NH23; 18 Nov. 2017; *JP 814*; JP det.; ZMUC C-F-123308 • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 16 May 2014; *JP 310*; JP det.; ZMUC C-F-122789 • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015; *JP & H. Liljehult 510*; JP det.; ZMUC C-F-122993 • Nørreris Skov; 56°13.608′ N, 10°2.289′ E; NH63; 6 Oct. 2012; *JP 36*; JP det.; ZMUC C-F-122511 • Serup Skov; 56°14.504′ N, 9°28.051′ E; NH23; 26 Mar. 2017; JP 243; JP det.; ZMUC C-F-122723 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 981*; JP det.; ZMUC C-F-123488 • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 529*; JP det.; ZMUC C-F-123013. – **Fyn (F)** • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1064*; JP det.; ZMUC C-F-123581. – **Lolland, Falster, Møn (LFM)** • Bøtø Plantage; 54°37.629′ N, 11°57.661′ E; PF95; 17 May 2017; *JP 413*; JP det.; ZMUC C-F-122897 • Busene Have syd for Busene; 54°56.738′ N, 12°31.666′ E; UA49; 8 Oct. 2017; *JP 578*; JP det.; ZMUC C-F-123064 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 645*; JP det.; ZMUC C-F-123133 • ibid.; 4 Jun. 2018; *JP 1136*; JP det.; ZMUC C-F-123660 • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 551*; JP det.; ZMUC C-F-123037 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 839*; JP det.; ZMUC C-F-123334 • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 19 Sep. 2012; *JP 78*; JP det.; ZMUC C-F-122553 • Ulvshale; 55°2.305′ N, 12°17.042′ E; UB20; 2 May 2018; *JP 1104*; JP det.; ZMUC C-F-123622. – **Nordøstsjælland (NEZ)** • Brønshøj; 55°42.234′ N, 12°30.135′ E; UB47; 2 Jul. 2012; *JP 37*; JP det.; ZMUC C-F-122512 • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 733*; JP det.; ZMUC C-F-123226 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 590*; JP det.; ZMUC C-F-123079 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 24*; JP det.; ZMUC C-F-122497 • ibid.; 19 Mar. 2017; *JP 681*; JP det.; ZMUC C-F-123169 • Ledøje; 55°42.601′ N, 12°17.977′ E; UB37; 18 Apr. 2018; *JP 1045*; JP det.;

ZMUC C-F-123561 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 868*; JP det.; ZMUC C-F-123364 • Mølleå ved Farum Lillevang; 55°49.093′ N, 12°18.496′ E; UB38; 24 Feb. 2018; *JP 992*; JP det.; ZMUC C-F-123499 • Ryegård Dyrehave; 55°40.500′ N, 11°50.851′ E; PG77; 2 Dec. 2014; *JP 344*; JP det.; ZMUC C-F-122826 • Smørum; 55°43.749′ N, 12°18.587′ E; UB37; 16 May 2017; *JP 425*; JP det.; ZMUC C-F-122910 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 789*; JP det.; ZMUC C-F-123284. – **Nordvestsjælland (NWZ)** • Bildsø Strand; 55°27.388′ N, 11°12.219′ E; PG34; 29 Sep. 2013; *JP 123*; JP det.; ZMUC C-F-122600 • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 600*; JP det.; ZMUC C-F-123089 • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 720*; JP det.; ZMUC C-F-123212 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 853*; JP det.; ZMUC C-F-123348 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 755*; JP det.; ZMUC C-F-123249 • Nordbredden af Tissø ved Halleby Å's udløb; 55°35.602′ N, 11°18.532′ E; PG46; 18 Feb. 2017; *JP 384*; JP det.; ZMUC C-F-122867 • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 1 Apr. 2017; *JP 247*; JP det.; ZMUC C-F-122727 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 632*; JP det.; ZMUC C-F-123121. – **Sydjylland (SJ)** • Brænøre Mose; 55°23.906′ N, 9°25.714′ E; NG23; 5 Aug. 2018; *JP 1167*; JP det.; ZMUC C-F-123692 • Sølsted Mose; 55°1.829′ N, 8°50.351′ E; MF89; 2 Jun. 2013; *JP 483*; JP det.; ZMUC C-F-122967. – **Sydsjælland (SZ)** • Bimose i Broby Overdrev; 55°23.921′ N, 11°35.499′ E; PG64; 28 Jun. 2013; *JP 325*; JP det.; ZMUC C-F-122803 • Bregnemade Skov; 55°18.914′ N, 12°0.326′ E; UB13; 1 Jan. 2017; *JP 173*; JP det.; ZMUC C-F-122652 • Enemærket ved Næsbyholm; 55°22.429′ N, 11°36.776′ E; PG63; 17 Nov. 2019; *JP 1563*; JP det.; ZMUC C-F-124323 • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1355*; JP det.; ZMUC C-F-123893 • Flommen ved Sorø; 55°25.957′ N, 11°34.477′ E; PG64; 25 Jul. 2009; *JP 84*; JP det.; ZMUC C-F-122559 • Gammel Dyrehave ved Edelesminde; 55°16.930′ N, 11°58.348′ E; PG83; 27 Nov. 2016; *JP 169*; JP det.; ZMUC C-F-122648 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1009*; JP det.; ZMUC C-F-123516 • ibid.; 27 Apr. 2018; *JP 1088*; JP det.; ZMUC C-F-123606 • Haslev; 55°19.669′ N, 11°58.206′ E; PG83; 19 Jun. 2016; *JP 323*; JP det.; ZMUC C-F-122801 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 28 Feb. 2015; *JP 448*; JP det.; ZMUC C-F-122933 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 1–15 Aug. 2013; *JP 523*; JP det.; ZMUC C-F-123007 • ibid.; 15 Aug. 2013; *JP 397*; JP det.; ZMUC C-F-122880 • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; 17 Feb. 2019; *JP 1390*; JP det.; ZMUC C-F-123933 • Villa Gallina i Hesede Skov; 55°16.335′ N, 11°56.850′ E; PG82; 8 Mar. 2015; *JP 482*; JP det.; ZMUC C-F-122966.

On *Acrotrichis thoracica* (Waltl, 1838) (Col. Ptiliidae)

DENMARK – **Østjylland (EJ)** • Horsens; 55°51.580′ N, 9°50.646′ E; NG59; 13 Apr. 1947; *Høeg Dry0036*; Høeg det.; ZMUC C-F-124102.

Remarks

As a curiosity, Majewski (2008) mentioned that this species is exceptionally common in Poland and that it is fair to expect it to be common in other countries. In Denmark, *E. trichopterophilus* is also extremely common and is rare not to find it in a collection with specimens of *Acrotrichis*. Thalli are very variable in receptacle length and perithecial neck. In Fig. 24D a gigantic thallus is photographed, and in Fig. 24 C we show a very slender and flexuous thallus with up to 43 cells in the receptacle. Majewski (1994b) described up to three morphological types, without any taxonomical rank. We are not capable of distinguishing these groups among the Danish specimens.

Genus ***Laboulbenia*** Mont. & C.P.Robin
MB#2606

Histoire naturelle des végétaux parasites qui croissent sur l'homme et sur les animaux vivants. J.B.Baillière, Paris: 622 (Robin 1853). – Type species: *L. rougetii* Mont. & C.P.Robin

Thaxteria Giard, *Comptes-Rendus Hebdomadaires des Séances et Mémoires de la Société de Biologie et de ses filiales, Paris*: 156 (Giard 1892) [MB#5406]
Ceraiomyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 36: 410 (Thaxter 1901a) [MB#878]
Eumisgomyces Speg., *Anales del Museo Nacional de Historia Natural de Buenos Aires* 23: 176 (Spegazzini 1912) [MB#1927]
Laboulbeniella Speg., *Anales del Museo Nacional de Historia Natural de Buenos Aires* 23: 188 (Spegazzini 1912) [MB#2608]
Schizolaboulbenia Middelh., *Fungus* 27 (1–4): 73 (Middelhoek 1957) [MB#4896]
Scalenomyces I.I.Tav., *Mycologia Memoirs* 9: 313 (Tavares 1985) [MB#25698]

Brief description

Mostly monoecious. Receptacle typically five-celled. The two-celled pedicel (primary or lower receptacle) consists of superposed cells I and II. Cell II supports on one side the perithecial stalk cell (VI) and the perithecium with associated cells, and on the opposite side the secondary or upper receptacle with appendages. The secondary receptacle is typically three-celled, including cell III underlying ± parallel cells IV and V, separated from each other by a septum joining or not the insertion cell with cell III. The appendages (i.e., the primary appendage) are subtended by a flattened and usually darkened insertion cell. Appendages are typically arranged in two sets: the inner appendage including simple antheridia, and the outer appendage. The solitary perithecium, above the basal cells (m, n, n' and VII), has an outer wall with 4 unequal cells for each vertical row, with an ostiole surrounded by two ± prominent lips and two preostiolar blackened spots.

Remarks

Of all the genera included in the Laboulbeniales, this is the richest in number of taxa, with more than 650 species, in addition to countless infraspecific taxa of highly variable value. We have gathered 653 species in our database catalogue. Song *et al.* (2019) mentioned 633 species where 40 have been described after 2010, Haelewaters *et al.* (2019b) reported 650 accepted species and many varieties, and according to the same authors, Index Fungorum (2019) includes 897 names of taxa. More than one hundred species are known in Europe (we count 109 species), 47 have been found in Denmark. The most recently described species are *L. chionophila*, *L. halophila* (Santamaria *et al.* 2020a), *L. quarantenae* (Haelewaters & De Kesel 2020), *L. angkorensis*, *L. fusca*, *L. polyandra*, *L. scabra*, and *L. trilobata* (Kong *et al.* 2020), and *L. amblystomi* (Haelewaters *et al.* 2021).

Although species of *Laboulbenia* mostly occurs on ground beetles (Carabidae), some may also be found on other families like Staphylinidae, Gyrinidae, Chrysomelidae, Elateridae, and Corylophidae, even on other orders of Insecta like Diptera, Blattodea, Hemiptera, Hymenoptera, Orthoptera, and unrelated arthropods like mites (Acarina).

A subdivision of the genus into subgenera would be desirable, although the difficulty of managing so many taxa, data and intraspecific variability makes it a titanic task. Some attempts were carried out by Spegazzini (1917), who described several unnatural sections, which were not widely followed by subsequent authors. Unfortunately, his contemporary Roland Thaxter passed away before his sixth monograph dealing with this genus could see the light. This fact led to many new species left out but

also a probable reorganization of the genus. Many years after, Tavares (1985) distinguished 20 structural groups of species based on morphology but subgenera were not formally described.

Some characteristics are key to distinguish and group species: (1) if the septum IV–V is connected with the septum III–IV, as in *L. pedicellata*, or not as in *L. flagellata*; (2) if the insertion cell is flattened and dark, clearly distinguished from surrounding cells, as in *L. ophoni*, or pale, colourless, not distinctly contrasting from the surrounding cells, as in *L. fasciculata*; (3) whether basal cells of the outer appendage show some septa distinctly darkened and/or constricted, as in *L. clivinalis*; (4) if the outer appendage is unbranched, as in *L. notiophili*, or ± ramified, as in *L. elaphri*; (5) if cell V is totally or partially free from the perithecium, as in *L. pseudomasei*, or connected along its whole length to the perithecium, as in *L. vulgaris*. Other important features, such as the cells III, IV and V totally or partially undivided, are not found in the Danish species of *Laboulbenia*.

Key to the Danish species (partially following Majewski 1994b, and Santamaria 1998)

The included key for identification of Danish species in the genus *Laboulbenia* is broadly based on the mentioned key characteristics. Although it appears to be obvious, it should be noted that some features may be very variable, and because of this we should rely on collections with specimens in good condition and reasonably abundant. Otherwise, if we have to take into account all variations, many of them product of malformations by injury, the key would become useless and unwieldy.

1. Perithecium bearing some kind of apical outgrowths..... 2
– Perithecium without apical outgrowths 4

2. Two apical outgrowths on the perithecium; the anterior short, arcuate, the posterior longer, straight but hooked on the top. On *Gyrinus* Geoffroy, 1762 and allied genera (Col. Gyrinidae)..... ..... ***L. gyrinicola*** Speg.
– Only one solitary outgrowth. On other hosts..... 3

3. Outgrowth subapical, horn-like, darkened (may be very short!). Insertion cell not evident, reduced to a groove. Septum IV–V connected with septum III–IV. On the distal part of elytra of *Bembidion* subgenus *Notaphus* Dejean, 1821 (Col. Carabidae) ..... ***L. cornuta*** Thaxt.
– Outgrowth apical, horn-like, pale. Insertion cell flattened, darkened, and clearly distinguished from surrounding cells. Septum IV–V not connected with septum III–IV. Grows hidden near the pygidium in *Dromius* (Col. Carabidae)..... ***L. hyalopoda*** De Kesel

4. Insertion cell colourless, not darkened, or not distinctly contrasting with surrounding cells, or absent, sometimes reduced to a groove..... 5
– Insertion cell flattened, darkened, clearly distinguished from surrounding cells 12

5. Receptacle four-celled, because cells III and IV are not separated. On *Sphaerius acaroides* (Col. Sphaeriusidae). ..... ***L. sphaerii*** Santam.
– Receptacle five-celled as usual. On other hosts. 6

6. Cell V divided, proliferating into up to eight cells gradually decreasing in size, each giving rise to secondary appendages. On *Chlaenius* Bonelli, 1810 and allied genera (Col. Carabidae).... ***L. fasciculata*** Peyr.
– Cell V not divided..... 7

7. Septum IV–V not connected with septum III–IV. Cell V shorter than cell IV. Receptacle distinctly constricted between cells II and III/IV. On *Bembidion* Latreille, 1802 (Col. Carabidae)..... ***L. murmanica*** Huldén
– Septum IV–V connected with septum III–IV. Cell V as long as cell IV 8

8. Primary appendage compact, without distinction between outer and inner appendages. On *Cafius* Stephens, 1829 and allied genera (Col. Staphylinidae Staphylininae) ..... ***L. cafii*** Thaxt.
– Primary appendage separated into the two characteristic sets, i.e., the inner and outer appendages, each with respective basal cells (sometimes young thalli need to be studied; overmature or old thalli may have deteriorated appendages where this feature is difficult to see)..... 9

9. Perithecium free, measuring more than the half of the total length of the thallus. Primary septum or insertion cell located below the lowermost perithecial outer wall cells (w_1). On legs, typically on tarsi of *Bembidion* (Col. Carabidae) ..... ***L. curtipes*** Thaxt.
– Perithecium not free, shorter. Primary septum above w_1 cells 10

10. Cell IV longer than cell III. On *Bembidion* (Col. Carabidae)..... ***L. luxurians*** Peyr.
– Cell III longer than cell IV..... 11

11. Perithecial apex rounded, symmetric, with undistinguished lips. Preostiolar spots undefined but replaced with a subapical dark suffusion. On *Cillenus lateralis* (Col. Carabidae).....
..... ***L. lichtensteinii*** F.Picard
– Perithecial apex acute, asymmetric, with distinct lips. Preostiolar spots absent. On *Bledius* (Col. Staphylinidae Oxytelinae) ..... ***L. parriaudii*** Balazuc

12. Septum IV–V connected with septum III–IV 13
– Septum IV–V not connected with septum III–IV 22

13. Outer appendage unbranched, exceeding in length the perithecial apex..... 14
– Outer appendage branched or, if unusually simple, then short, not exceeding the perithecial apex, or hardly discernible from inner appendage 15

14. Appendages bent towards perithecium. Dorsal margin of perithecium straight, ventral margin curved. Cell V very narrow. On the prothorax margin of *Pterostichus* subgenus *Argutor* Dejean, 1821 (Col. Carabidae)..... ***L. kajanensis*** Huldén
– Outer appendage straight to flexuous, never bent towards perithecium. Outer and inner margins of perithecium curved. Cell V as broad as cell IV. On *Olisthopus* Dejean, 1828 (Col. Carabidae)..... ***L. olisthopi*** Speg.

15. Appendages with the 2–3 lower cells inflated and separated by thick and dark septa. Cell I showing a blackish lateral swelling above the foot. On *Philonthus* and allied genera (Col. Staphylinidae Staphylininae)..... ***L. philonthi*** Thaxt.
– Otherwise..... 16

16. Some dorsal septa above the basal cell of outer appendage distinctly blackened and constricted.....
..... 17
– Not such septa above the basal cell of outer appendage. Thalli very pale, yellowish brown, with the two preostiolar spots of the perithecium merged into a contrasting black ring. On *Ophonus* Dejean, 1821 and allied genera (Col. Carabidae) ..... ***L. ophoni*** Thaxt.

17. Insertion cell free, separated from perithecial wall. On *Clivina* Latreille, 1802 (Col. Carabidae)..... ***L. clivinalis*** Thaxt.
– Insertion cell or cell V connected along its whole length to the perithecium..... 18

18. Outer appendage consisting of 2–3 straight, long branches, arising from the suprabasal cell which bears an additional dark reddish-brown branch. On *Paederus* Fabricius, 1775 and relatives (Col. Staphylinidae Paederinae) ..... ***L. cristata*** Thaxt.
– Different 19

19. Perithecium showing 1–3 swellings or protuberances on its lower third or broadest part (septa between w_1 and w_2). On Col. Carabidae Tachyina like *Tachys* Dejean, 1821 and allied genera ..... ***L. egens*** Speg.
– Perithecium without such protuberances 20

20. Cell II with parallel margins, somewhat constricted towards the upper part. Thallus olive brown, with darker to almost hyaline areas. Outer appendage having the septa between the basal and suprabasal cells and between this and next outer cell thickened, black and constricted. On *Bembidion* and *Dyschirius* (Col. Carabidae) ..... ***L. pedicellata*** Thaxt.
– Cell II with divergent margins, not constricted upwards. Thallus almost uniform yellowish-amber. Outer appendage only with the septum between the basal cell and the posterior branch thickened, black and constricted. On other hosts 21

21. Outer appendage basal cell bulging outwards, as long or longer than cell IV. Receptacle bent outwards. On *Cafius* (Col. Staphylinidae Staphylininae) ..... ***L. littoralis*** De Kesel & Haelew.
– Outer appendage basal cell slightly inflated outwards, shorter than cell IV. Dorsal side of receptacle straight to slightly concave. On *Pogonus* Dejean, 1821 (Col. Carabidae) ..... ***L. slackensis*** Cépède & F.Picard

22. Outer appendage unbranched (rarely branched from 3rd cell or above if injured) 23
– Outer appendage branched (usually from basal or suprabasal cells of appendage) 41

23. Dioecious. A seven-celled male thallus is paired to a female thallus, attached by the blackened feet. The terminal cell functions as an antheridium. The three distal septa darkened and constricted. Typically on *Acupalpus* (Col. Carabidae) ..... ***L. inflata*** Thaxt.
– Monoecious. If some reduced thalli paired to females are present, characteristics are different (see *L. lecoareri*) 24

24. Cell V totally or partially free from perithecium, or insertion cell separated from perithecial wall 25
– Cell V and insertion cell attached to perithecial wall 27

25. Inner appendage absent. On *Trechoblemus micros* (Col. Carabidae) ..... ***L. lecoareri*** (Balazuc) Huldén
– Inner appendage present 26

26. Inner appendage consisting of a small basal cell supporting two unbranched or once ramified branches bearing pairs or clusters of antheridia; sometimes with elongated sterile branches. On *Amara* Bonelli, 1810 (Col. Carabidae) ..... ***L. aubryi*** Balazuc
– Inner appendage consisting of a small basal cell supporting two once ramified branches (rarely a 3rd branch may be present), in total four branches (or six if 3rd branch is present). Each branch gives rise to a simple three-celled appendage where the terminal cell is an antheridium bearing a long and asymmetric neck. On or near the pygidium of *Syntomus* (Col. Carabidae) ..... ***L. pygidicola*** Santam. sp. nov.

27. Inner appendage with long branches supporting lateral paired or solitary brownish antheridia near the base. On *Leistus* Frölich, 1799 (Col. Carabidae) ..... ***L. leisti*** J.Siemaszko & Siemaszko
– Inner appendage with short branches not exceeding the perithecial apex 28

28. Thallus small, total length from foot to perithecial apex less than 100 µm. On *Corylophus cassidoides* (Col. Corylophidae) ..... ***L. corylophi*** Scheloske
– Thallus longer, more than 100 µm from foot to perithecial apex (not considering growth forms found on tarsi or antennae of hosts) 29

29. Appendages bent towards perithecium. Dorsal margin of perithecium straight, ventral margin curved. Cell V very narrow. On the prothorax margin of *Pterostichus* subgenus *Argutor* (Col. Carabidae) ..... ***L. kajanensis*** Huldén
– Otherwise 30

30. Inner appendage unbranched, consisting of a basal cell, a suprabasal cell and a solitary terminal large antheridium. On *Asaphidion* Des Gozis, 1886 (Col. Carabidae) ..... ***L. thaxteri*** Cépède & F.Picard
– Inner appendage different, bearing more antheridia 31

31. Stalk cell of the perithecium (cell VI) broader than long, flattened (see also *L. stilicicola* and *L. vulgaris*) 32
– Stalk cell of the perithecium (cell VI) longer than broad, or isodiametric 34

32. Basal and suprabasal cells of the outer appendage (rarely also the 3rd cell) elongated, hyaline, narrow, contrasting with darker and broader cells above. Inner appendage consisting of 2(–3) cells bearing 2–3 antheridia. On *Acupalpus* (Col. Carabidae) ..... ***L. inexpectata*** Santam. sp. nov.
– Other characteristics 33

33. Perithecium broad (more than 45 µm in width), half free, with the tip pointing towards the ventral margin. On *Badister* (Col. Carabidae) ..... ***L. benjaminii*** Balazuc ex Santam.
– Perithecium narrow (less than 45 µm in width), about ¾ or more free, with straight tip. On Col. Carabidae of the genera *Notiophilus* Duméril, 1806, *Cymindis* Latreille, 1806, *Demetrias* Bonelli, 1810, *Dromius*, *Philorhizus* Hope, 1838, *Metadromius* Bedel, 1907, etc. ..... ***L. notiophili*** Cépède & Picard

34. Outer appendage with the basal cell forming a distinctive blunt outgrowth on its outer side. Cell II and upper part of cell I tuberculate. On *Perigona nigriceps* (Col. Carabidae) ..... ***L. manubriolata*** Thaxt.
– Otherwise 35

35. Cell II with delicately undulate and punctate margins. Inner appendage consisting of two short branches above the basal cell, each bearing a solitary lateral antheridium. On *Porotachys* Netolitzky, 1914 (Col. Carabidae) ..... ***L. picardii*** Maire
– With other characters 36

36. Inner appendage embracing the perithecium; consisting of two branches directly arising from the basal cell; each branch with 5–6 superposed cells, each giving rise to unilaterally, simple two or three-celled branches terminated by long and narrow antheridia. Cell VII protruding below the perithecium. On *Syntomus* (Col. Carabidae) ..... ***L. metableti*** Scheloske
– Inner appendage and cell VII not as above 37

37. Receptacle distinctly constricted between cells II and III–VI. Cell II inflated and broader halfway up. Outer appendage not exceeding the perithecial apex, with the basal cell separated from cells above by a fairly darkened septum. On *Bembidion* (Col. Carabidae)..... ***L. murmanica*** Huldén
– Not all the previous features showing at the same time 38

38. Cell I only a little shorter than cell II, which usually broadens distally. On Col. Carabidae..... 39
– Cell I much shorter than cell II, which is cylindrical, with parallel margins. On *Rugilus* Leach, 1819 (Col. Staphylinidae Paederinae) ..... ***L. stilicicola*** Speg.

39. Anterior margin of perithecium with a protrusion at middle height (at the level of the septum separating w_1 an w_2 tiers of perithecial outer wall cells). Perithecial apex strongly asymmetric, truncated, with flattened anterior lips. On *Bradycellus* Erichson, 1837 and *Trichocellus* Ganglbauer, 1892 (Col. Carabidae)..... ***L. eubradycelli*** Huldén
– Otherwise..... 40

40. On *Pterostichus* and allied genera (Col. Carabidae)..... ***L. argutoris*** Cépède & F.Picard
– On *Calathus* Bonelli, 1810 (Col. Carabidae)..... ***L. calathi*** T.Majewski
– On *Bembidion* and *Trechus* (Col. Carabidae) ..... ***L. vulgaris*** Peyr.

41. Insertion cell free from perithecium 42
– Insertion cell attached to perithecium..... 43

42. Cell V dividing and proliferating into a branch of variable length, which may support antheridia. Typically on *Pterostichus* subgenus *Melanius* Bonelli, 1809 (Col. Carabidae) .... ***L. pseudomasei*** Thaxt.
– Cell V undivided and not proliferating. Typically on *Diachromus* Erichson, 1837 (Col. Carabidae)..... ***L. melanaria*** Thaxt.

43. Outer appendage ramified directly above the basal cell; consisting of several slender branches, dark brown towards the basal dorsal side. Inner appendage similar to the outer. Solitary antheridia on the lower parts of inner appendage branches. Perithecial preostiolar spots black and contrasting with the pale amber-brown remainder thallus. On *Dicheirotrichus* Jacquelin du Val, 1857 (Col. Carabidae)..... ***L. giardii*** Cépède & F.Picard
– Outer appendage once ramified above the suprabasal cell; if ramified from the basal cell, then remaining characteristics different from above 44

44. Outer appendage short, slender, not exceeding perithecial apex. On *Bembidion* (Col. Carabidae)..... ***L. murmanica*** Huldén
– Outer appendage thick and long, exceeding perithecial apex..... 45

45. Perithecium with a ventral prominence formed by the intersection of outer wall cell tiers w_1 and w_2. Mostly on *Acupalpus* in a broad sense (including *Stenolophus* Dejean, 1821) (Col. Carabidae) .... ***L. stenolophi*** Speg.
– Perithecium without such prominence. On other hosts. 46

46. Insertion cell attached above the middle height of the posterior margin of the perithecial wall. Typically on *Paranchus* Lindroth, 1974, but also on others Col. Carabidae Pterostichinae .... ***L. collae*** T.Majewski
– Insertion cell attached below the middle height of the perithecial wall 47

47. Perithecium with a nearly straight anterior margin, a cylindrical and prominent apex, and the preostiolar spots blackish and confluent into a ring-like area. Antheridia solitary, sessile, lateral to branches of the inner appendage. On Col. Carabidae Harpalinae like *Harpalus* Latreille, 1802, *Ophonus* and *Anisodactylus* Dejean, 1829..... ***L. coneglianensis*** Speg.
– With other characteristics 48

48. Inner appendage forming short branchlets terminating in antheridia. Sterile branchlets, if any, not exceeding the perithecial apex. Thalli very pale yellowish brown, with the perithecial blackened preostiolar spots and insertion cell strongly contrasting. Typically on *Ophonus* and *Harpalus*, but also on other ground beetles ..... ***L. ophoni*** Thaxt.
– Inner appendage with some long sterile branches exceeding perithecial apex. Thalli differently coloured 49

49. Outer appendage dividing above the suprabasal cell into two subequal, strongly divergent branches. Perithecium asymmetric, with the ventral side distinctly more convex than the dorsal side. Perithecial tip large, with an almost flattened apex. On *Elaphrus* Fabricius, 1775 (Col. Carabidae) .... ***L. elaphri*** Speg.
– Otherwise..... 50

50. Perithecium almost entirely free. On *Oodes* Bonelli, 1810 (Col. Carabidae) .... ***L. oodiphila*** Huldén
– Perithecium not free. On other hosts 51

51. Thallus reddish coloured. Typically on *Brachinus* Weber, 1801 (Col. Carabidae) .... ***L. rougetii*** Mont. & C.P.Robin
– Thallus not reddish coloured. On Col. Carabidae Pterostichinae..... ***L. flagellata*** Peyr.

Laboulbenia argutoris Cépède & F.Picard

MB#167376

Fig. 25A–B

Bulletin Scientifique de la France et de la Belgique 42: 260 (Cépède & Picard 1908). – **Type**: [Type lost!] "Sur *Pterostichus* (*Argutor*) *interstinctus* Strm. bords de la Slack, Ambleteuse (Pas-de-Calais)". [France]

Diagnostic features

Cell V much shorter than cell IV, not connected with cell III. Septum IV–V oblique, curved. Outer appendage unbranched, typically darkened, up to 400 µm long. Inner appendage consisting of a small basal cell typically giving rise to 2–3 superposed cells supporting paired terminal antheridia, although varying greatly with age, sometimes including additional antheridia and sterile branches of very variable length. [Detailed descriptions: Majewski 1994b; Santamaria 1998]

Distribution and hosts

Known on *Pterostichus* (Col. Carabidae) in a broad sense (i.e., including subgenera like *Argutor*, *Melanius*, etc.) and other genera of the tribes Pterostichini (like *Stomis* Clairville, 1806 and *Lagarus* Chaudoir, 1838) and Patrobini (*Patrobus*). Reported from **Europe**: Austria, Finland, France, Germany, Ireland, Italy, Norway, Poland, Romania, Sweden, Switzerland, Russia (Santamaria *et al.* 1991), the Netherlands (Meijer 1975), Hungary (Bánhegyi *et al.* 1985), Belgium (De Kesel & Rammeloo 1992), United Kingdom (Weir & Beakes 1993), Spain (Santamaria 1995b), Portugal (Santamaria 1998), Lithuania (Markovskaja 2000), Latvia (De Kesel & Krastina De Kesel 2006), Czech Republic (Rossi & Máca 2006), Denmark (Høier 2009), and Bulgaria (Rossi *et al.* 2019a). Also in Japan (Santamaria *et al.* 1991).

Collections examined from Denmark

On *Pterostichus diligens* (Sturm, 1824) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14 45.260′ E; VB81; 23 Jun. 2018; *JP 1159*; JP det.; ZMUC C-F-123685. – **Østjylland (EJ)** • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP 434*; JP det.; ZMUC C-F-122919 • Høgdal; 56°6.449′ N, 9°36.941′ E; NH31; 11 Mar. 2017; *JP 354*; JP det.; ZMUC C-F-122836 • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015; *JP & H. Liljehult 515*; JP det.; ZMUC C-F-122998. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 702*; JP det.; ZMUC C-F-123191 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1077*; JP det.; ZMUC C-F-123595. – **Lolland, Falster, Møn (LFM)** • Bøtø Plantage; 54°37.629′ N, 11°57.661′ E; PF95; 17 May 2017; *JP 415*; JP det.; ZMUC C-F-122899 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1125*; JP det.; ZMUC C-F-123647 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 826*; JP det.; ZMUC C-F-123320 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1111*; JP det.; ZMUC C-F-123630 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1328*; JP det.; ZMUC C-F-123867. – **Nordøstsjælland (NEZ)** • Dragør Sydstrand; 55°35.177′ N, 12°39.996′ E; UB56; 18 Nov. 2018; *L. Kjær-Thomsen & L. Thomas 1246*; JP det.; ZMUC C-F-123774 • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 739*; JP det.; ZMUC C-F-123233 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 592*; JP det.; ZMUC C-F-123081 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 264*; JP det.; ZMUC C-F-122743 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 662*; JP det.; ZMUC C-F-123151 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 861*; JP det.; ZMUC C-F-123356 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 1 Dec. 2019; *JP 1568*; JP det.; ZMUC C-F-124328 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 625*; JP det.; ZMUC C-F-123114 • Tokkekøb Hegn; 55°52.334′ N, 12°22.229′ E; UB39; 12 Apr. 2018; *JP 1027*; JP det.; ZMUC C-F-123537 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1053*; JP det.; ZMUC C-F-123569. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 564*; JP det.; ZMUC C-F-123050 • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 216*; JP det.; ZMUC C-F-122696 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; JP 772; JP det.; ZMUC C-F-123267. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 876*; JP det.; ZMUC C-F-123373 • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 613*; JP det.; ZMUC C-F-123101 • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 719*; JP det.; ZMUC C-F-123211 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; JP 859; JP det.; ZMUC C-F-123354 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 759*; JP det.; ZMUC C-F-123253 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 639*; JP det.; ZMUC C-F-123128. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *JP 293*; JP det.; ZMUC C-F-122772 • Sølsted Mose; 55°1.829′ N, 8°50.351′ E; MF89; 2 Jun. 2013; *JP 487*; JP det.; ZMUC C-F-122971 • Sønderstrand på Rømø; 55°6.373′ N, 8°29.380′ E; MG60; 25 Oct. 2017; *H. Liljehult 616*; JP det.; ZMUC C-F-123104. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1367*; JP det.; ZMUC C-F-123907 • Flommen ved Sorø; 55°25.957′ N, 11°34.477′ E; PG64; 25 Jul. 2009; *JP 65*; JP det.; ZMUC C-F-122542 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1002*; JP det.; ZMUC C-F-123509 • ibid.; 25 Apr. 2019; *JP 1446*; JP det.; ZMUC C-F-123994 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 540*; JP det.; ZMUC C-F-123024 • ibid.; 54°59.331′ N, 12°6.357′ E; UA19; 27 Mar. 2018; *JP 1021*; JP det.; ZMUC C-F-123528 • ibid.; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1292*; JP det.; ZMUC C-F-123824 • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1436*; JP det.; ZMUC C-F-123983. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1253*; JP det.; ZMUC C-F-123781.

On *Pterostichus strenuus* (Panzer, 1797) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14°45.096′ E; VB80; 25 Apr. 2014; *H. Liljehult 233*; JP det.; ZMUC C-F-122713 • ibid.; *JP 506*; JP det.; ZMUC C-F-122989. – **Østjylland (EJ)** • Funder Ådal; 56°7.650′ N, 9°29.806′ E; NH32; 25 Jun. 2010; *Naturhistorisk Museum 35*; JP det.; ZMUC C-F-122510 • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 825*; JP det.; ZMUC C-F-123319 • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 16 May 2014; JP 311; JP det.; ZMUC C-F-122790 • Nørreris Skov; 56°13.608′ N, 10°2.289′ E; NH63; 6 Oct. 2012; *JP 42*; JP det.; ZMUC C-F-122517 • Stidsmølle i Mattrup Skov; 55°55.455′ N, 9°33.811′ E; NG39; 19 Nov. 2017; JP 811; JP det.; ZMUC C-F-123305 • Vingsted; 55°40.512′ N, 9°23.500′ E; NG27; 6 Oct. 2019; *JP 1533*; JP det.; ZMUC C-F-124292. – **Fyn (F)** • Brændholt Bjerg; 55°20.928′ N, 10°8.712′ E; NG73; 18 May 2016; *JP 90*; JP det.; ZMUC C-F-122565 • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 701*; JP det.; ZMUC C-F-123190 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1076*; JP det.; ZMUC C-F-123594. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 12 May 1993; *S. Langemark & O.E. Meyer 903*; JP det.; ZMUC C-F-123401 • ibid.; 7 Jun. 1993; *S. Langemark & O.E. Meyer 898*; JP det.; ZMUC C-F-123396 • ibid.; 16 Jun. 1993; *S. Langemark & O.E. Meyer 917*; JP det.; ZMUC C-F-123415 • ibid.; 8 Jul. 1993; *S. Langemark & O.E. Meyer 904*; JP det.; ZMUC C-F-123402 • ibid.; 19 Jul. 1993; *S. Langemark & O.E. Meyer 923*; JP det.; ZMUC C-F-123421 • ibid.; 29 Nov. 2014; *JP 456*; JP det.; ZMUC C-F-122941 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 657*; JP det.; ZMUC C-F-123146 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1327*; JP det.; ZMUC C-F-123866. – **Nordøstjylland (NEJ)** • Vandplasken ved Kærsgård Strand; 57°31.199′ N, 9°53.070′ E; NJ57; 21 Nov. 2017; *JP 804*; JP det.; ZMUC C-F-123299. – **Nordøstsjælland (NEZ)** • Bispebjerg; 55°43.063′ N, 12°31.288′ E; UB47; 3 Nov. 2019; *JP 1538*; JP det.; ZMUC C-F-124298 • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 738*; JP det.; ZMUC C-F-123232 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 593*; JP det.; ZMUC C-F-123082 • Gundsømagle; 55°43.398′ N, 12°10.842′ E; UB27; 6 Apr. 2019; *L. Kjær-Thomsen & L. Thomas 1400*; JP det.; ZMUC C-F-123946 • Gurre Slot; 56°1.171′ N, 12°30.313′ E; UC41; 24 Feb. 2019; *L. Kjær-Thomsen & L. Thomas 1394*; JP det.; ZMUC C-F-123937 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 17*; JP det.; ZMUC C-F-122490 • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB47; 19 Sep. 2013; *H. Liljehult 298*; JP det.; ZMUC C-F-122777 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 2 Dec. 2011; *JP 475*; JP det.; ZMUC C-F-122959 • ibid.; 29 Apr. 2017; *JP 403*; JP det.; ZMUC C-F-122886 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 624*; JP det.; ZMUC C-F-123113 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1237*; JP det.; ZMUC C-F-123764 • Smørum; 55°43.749′ N, 12°18.587′ E; UB37; 16 May 2017; *JP 424*; JP det.; ZMUC C-F-122909 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 23 Mar. 2017; *JP 471*; JP det.; ZMUC C-F-122955 • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 137*; JP det.; ZMUC C-F-122613 • ibid.; 30 Mar. 2019; *JP 1406*; JP det.; ZMUC C-F-123952. – **Nordvestjylland (NWJ)** • Gammelgård på Fur; 56°50.314′ N, 8°58.971′ E; MH99; 22 Nov. 2013; *JP 418*; JP det.; ZMUC C-F-122902 • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 565*; JP det.; ZMUC C-F-123051 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 771*; JP det.; ZMUC C-F-123266. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; JP 875; JP det.; ZMUC C-F-123371 • Klintebjerg ved Klint; 55°57.351′ N, 11°34.463′ E; PH60; 1 May 2016; *JP 55*; JP det.; ZMUC C-F-122530 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 858*; JP det.; ZMUC C-F-123353 • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 1 Apr. 2017; *JP 250*; JP det.; ZMUC C-F-12273. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1366*; JP det.; ZMUC C-F-123906 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1003*; JP det.; ZMUC C-F-123510 • ibid.; 27 Apr. 2018; *JP 1078*; JP det.; ZMUC C-F-123596 • ibid., 25 Apr. 2019; *JP 1445*; JP det.; ZMUC C-F-123993 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1374*; JP det.; ZMUC C-F-123915 • Østerskov ved

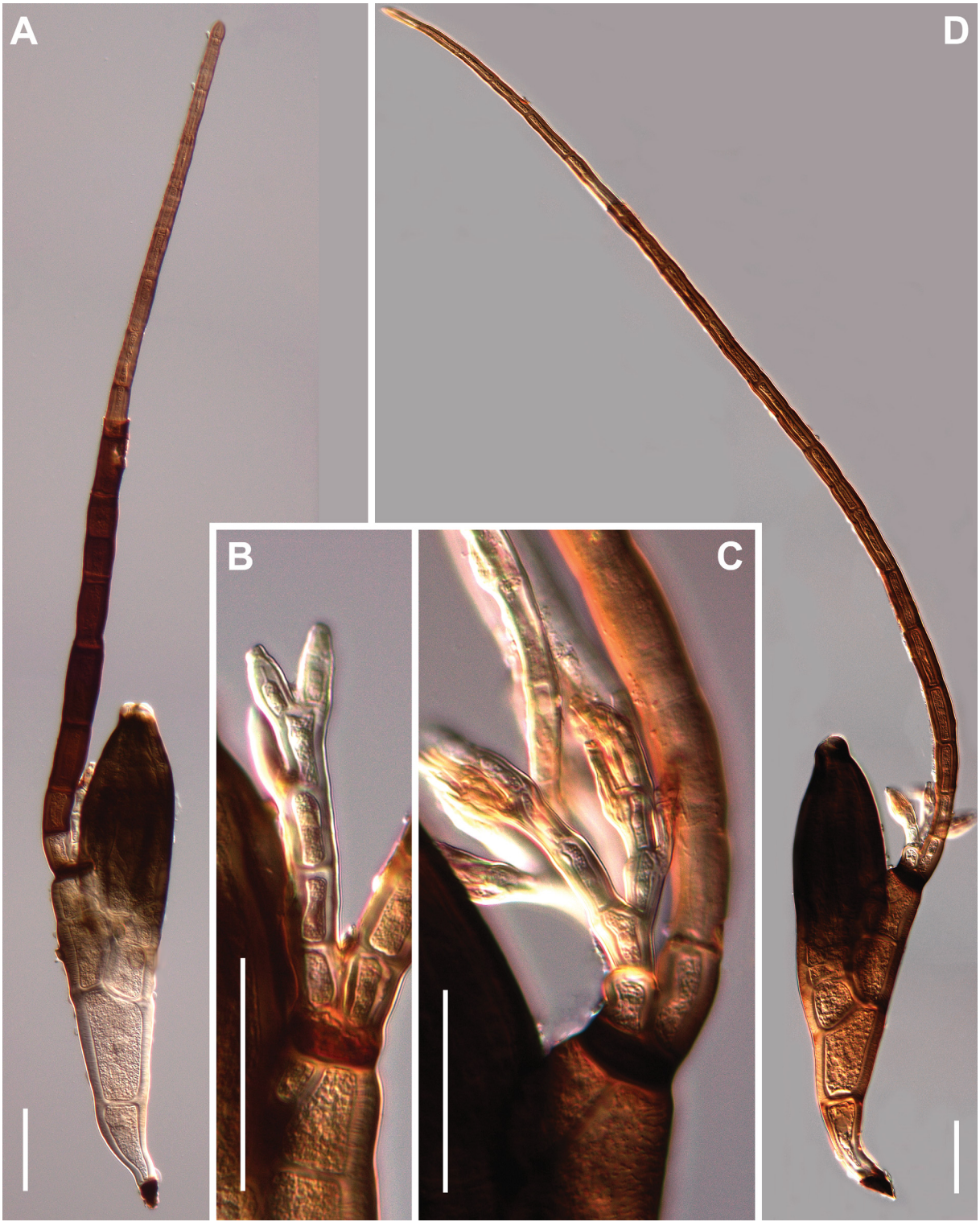

Fig. 25. *Laboulbenia* spp. **A**–**B**. *L. argutoris* Cépède & F.Picard. **A**. Mature thallus. **B**. Inner appendage in detail. – **C**–**D**. *L. aubryi* Balazuc. **C**. Inner appendage and area around insertion cell in detail. **D**. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122696 (A), ZMUC C-F-123050 (B), ZMUC C-F-122592 (C–D).

Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1291*; JP det.; ZMUC C-F-123823 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 22 Jul. 2013; *H. Enghoff 306*; JP det.; ZMUC C-F-122785 • Villa Gallina i Hesede Skov; 55°16.335′ N, 11°56.850′ E; PG82; 8 Mar. 2015; *JP 477*; JP det.; ZMUC C-F-122961. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1247*; JP det.; ZMUC C-F-123775 • ibid.; *JP 1252*; JP det.; ZMUC C-F-123780.

Remarks

This is a species difficult to recognize without knowing the identity of the hosts. It lacks striking characteristics and can be confused with other species showing unbranched outer appendage like *L. rigida* Thaxt. and *L. polyphaga* Thaxt. The inner appendage changes with age, and a large series of thalli in good condition is needed to obtain some undamaged thalli showing this portion of the thallus as originally described. According to De Kesel *et al.* (2020) proliferation of inner appendage occurs more frequently in thalli from *P. diligens* than in those from *P. strenuus*.

Laboulbenia aubryi Balazuc
MB#316110
Figs 25C–D, 103B

Revue de Mycologie 43 (4): 393 (Balazuc 1979). – **Type**: "Sur *Cyrtonotus* (*Leironotus*) *rotundicollis* (Schauf.) (Col. Carabidae Pterostichinae Amarini), de la Sierra de la Demanda, province de Logroño, Espagne (J. Aubry leg., X–1976) [No. 37.78, type, according to Santamaria 1998: 41]"; PC. [Spain]

Diagnostic features

Cell V oval, about half the length of cell IV, not connected with cell III; its inner margin separated from perithecium at least in its distal portion. Insertion cell separated from perithecium. Outer appendage unbranched, up to 650 µm long. Inner appendage consisting of a small basal cell supporting two simple or once ramified branches bearing pairs or clusters of antheridia; sometimes including variable and rather elongated sterile branches. [Detailed descriptions: Santamaria 1998; Majewski 1999]

Distribution and hosts

On ground beetles of the genus *Amara* (= *Leironotus* Ganglbauer, 1891). Described from Spain and reported from India and Nepal (Santamaria *et al.* 1991), as well as from Poland (Majewski 1999) and Belgium (Haelewaters & De Kesel 2020) from *Amara*. The record on *Agonum* from United Kingdom (Weir 1996) lacks iconography and requires confirmation.

Collections examined from Denmark

On *Amara municipalis* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Nordøst for Bispebjerg Station; 55°42.508′ N, 12°32.786′ E; UB47; 18 Aug. 2016; *JP 115*; JP det.; ZMUC C-F-122592.

Remarks

First record from Denmark. The finding of this species in Denmark on *Amara* is not surprising because it also was found in neighbouring Poland on the same host.

Laboulbenia benjaminii Balazuc ex Santam.
MB#446186
Fig. 26A

Flora Mycologica Iberica 4: 45 (Santamaria 1998). – **Type**: "Sur *Baudia anomala* (Perris), subsp. *pseudopeltata* M. Dew. (Col. Carab. Licinidae, subfam. Badistrinae) à l'étang de La Capelle (Gard) [France] [No. 47.57]"; PC.

Laboulbenia benjamini Balazuc (Balazuc 1971a: 114) (nom. inval.) [MB#316112]
Laboulbenia benjaminii Balazuc (Balazuc 1974a: 15) (nom. inval.) [MB#535214]

Diagnostic features

Cell V oval, about half of the length of cell IV, not connected with cell III. Outer appendage unbranched, up to 500 µm long. Inner appendage consisting of a small basal cell supporting two to a few branches, simple or scarcely divided into pairs or small clusters of terminal antheridia; sometimes bearing long sterile branches. [Detailed descriptions: Majewski 1994b; Santamaria 1998]

Distribution and hosts

On *Badister* in a broad sense (Col. Carabidae) from France (type), Poland, Spain, Belgium, Korea (Majewski 2008). Also in Denmark (Høier 2009) and Czech Republic (Rossi *et al.* 2010). The type was described on the genus *Baudia* which now is a subgenus of *Badister*.

Collections examined from Denmark

On *Badister bullatus* (Schrank, 1798) (Col. Carabidae)
DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 699*; JP det.; ZMUC C-F-123188. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 14*; JP det.; ZMUC C-F-122487.

On *Badister dilatatus* Chaudoir, 1837 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 654*; JP det.; ZMUC C-F-123143.

On *Badister dorsiger* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 655*; JP det.; ZMUC C-F-123144.

On *Badister lacertosus* Sturm, 1815 (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Nørreskoven; 55°47.865′ N, 12°23.054′ E; UB38; 1–12 May 2006; *J. Høier 1570*; P. Jørum det.; ZMUC C-F-124331 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 781*; JP det.; ZMUC C-F-123276. – **Sydsjælland (SZ)** • Gammel Dyrehave ved Edelesminde; 55°16.930′ N, 11°58.348′ E; PG83; 27 Nov. 2016; *JP 172*; JP det.; ZMUC C-F-122651.

On *Badister peltatus* (Panzer, 1797) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 744*; JP det.; ZMUC C-F-123238.

On *Badister sodalis* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 747*; JP det.; ZMUC C-F-123241. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N,

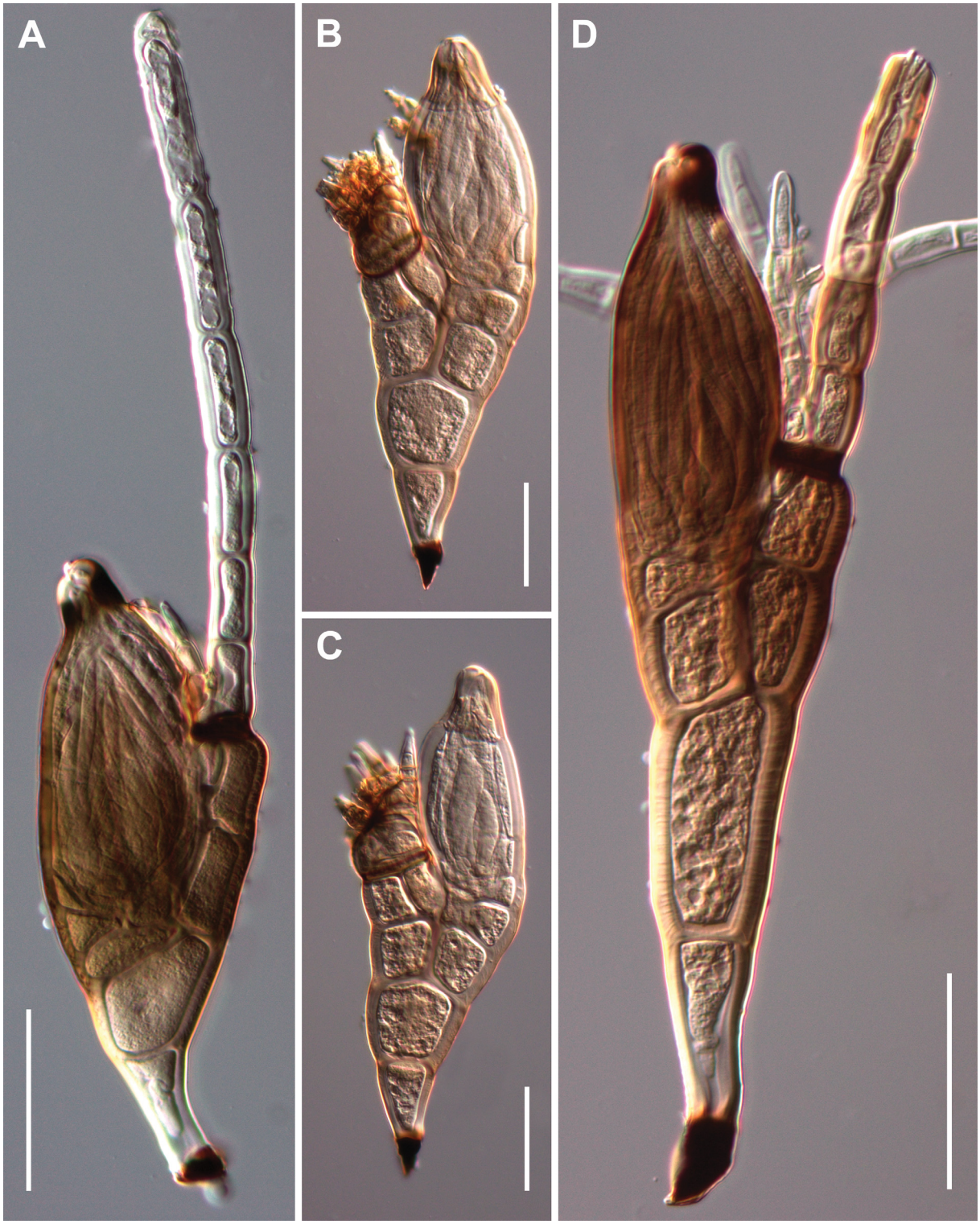

Fig. 26. *Laboulbenia* spp. **A**. *L. benjaminii* Balazuc ex Santam. Mature thallus. – **B**–**C**. *L. cafii* Thaxt. **B**. Mature thallus. **C**. Submature thallus. – **D**. *L. calathi*. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122487 (A), ZMUC C-F-124213 (B–C), ZMUC C-F-122526 (D).

10°7.211′ E; NG75; 2 Apr. 2014; *JP 698*; JP det.; ZMUC C-F-123187 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1073*; JP det.; ZMUC C-F-123591. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 25 May 1993; *S. Langemark & O.E. Meyer 911*; JP det.; ZMUC C-F-123409 • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 547*; JP det.; ZMUC C-F-123033 • Ny Kirstineberg Storskov; 54°48.376′ N, 11°49.365′ E; PF87; 17 May 2017; *H. Liljehult 442*; JP det.; ZMUC C-F-122927 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1325*; JP det.; ZMUC C-F-123864. – **Nordøstsjælland (NEZ)** • Bognæs Storskov; 55°41.242′ N, 12°1.678′ E; UB17; 1 Aug. 2013; *JP 363*; JP det.; ZMUC C-F-122846 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 266*; JP det.; ZMUC C-F-122745 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 15*; JP det.; ZMUC C-F-122488 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 782*; JP det.; ZMUC C-F-123277 • ibid.; 23 Mar. 2017; *JP 470*; JP det.; ZMUC C-F-122954. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 609*; JP det.; ZMUC C-F-123097 • Garbølle; 55°34.107′ N, 11°34.293′ E; PG66; 21 Apr. 2018; *JP 1062*; JP det.; ZMUC C-F-123579 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 856*; JP det.; ZMUC C-F-123351 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 641*; JP det.; ZMUC C-F-123129. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Jun. 2019; *JP 1475*; JP det.; ZMUC C-F-124055 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1417*; JP det.; ZMUC C-F-123963 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 15 Aug. 2013; *JP 396*; JP det.; ZMUC C-F-122879.

Remarks

Balazuc (1971a) described pale, nearly hyaline thalli, depicting one thallus having a perithecium with a very inflated venter and a strongly constricted neck; the unbranched outer appendage consisting of eight cells with noticeably constricted septa. This description was very restrictive and differs from additional new records of *L. benjaminii* in literature. Majewski (1994b) reported the species for the first time after the original description, broadening the description to embrace thalli with unbranched, yellowish-brown outer appendage, length up to 500 µm, bearing an inner appendage with paired antheridia borne on short dichotomous branches; these thalli were bigger than those of Balazuc's type. Subsequent records fit and follow Majewski's description and concept of *L. benjaminii*. Rossi *et al.* (2019a) found thalli on *Badister bullatus* (Schrank) from Bulgaria with atypical bifurcate outer appendage.

Laboulbenia cafii Thaxt.
MB#147111
Fig. 26B–C

Proceedings of the American Academy of Arts and Sciences 35: 162 (Thaxter 1899). – **Type**: [Not designated] [Ind. loc.] "On *Cafius seminitens* Horn, and *C. canescens* Mann, U.S. National Museum, Los Angeles, California. On *C. sericeus* Holme, Brit. Mus. No. 437, Great Britain. On *Cafius* sp., Brit. Mus. No. 425, "Europe", No. 395, Hong Kong; *C. bisulcatus* Sol., Chili. On elytra and legs"; FH.

Diagnostic features

Cell V oval, as long and nearly as broad as cell IV, connected with cell III at the inner corner. Insertion cell very flattened, almost reduced to a blackened groove. Primary appendage compact, not separated into the two classical sets. Basal cell of appendage large and flattened, supporting several small, irregularly shaped cells which bear a variable number of short and simple branches, each consisting of 3–4 superposed, short, inflated cells which are separated from each other by constricted, dark septa. [Detailed descriptions: Thaxter 1908; Sugiyama 1973; Santamaria 1998]

Distribution and hosts

On Col. Staphylinidae of the genera *Cafius*, *Remus* Holme, 1837 and *Phucobius* Sharp, 1874 (the latter according to Sugiyama 1973) from **Europe**: France, Spain, United Kingdom, former Yugoslavia; **America**: Chile, USA; **Asia**: Hong Kong, India, Japan; and **Oceania**: Australia (Santamaria *et al.* 1991). Also in Italy (Colla 1934), Canary Islands (Arndt & Santamaria 2004), China (Shen & Ye 2006), Sweden (Huggert 2010), and Singapore (Haelewaters & Yaakop 2014). The old record from Belgium by De Kesel (1998) belongs to *L. littoralis* (De Kesel & Haelewaters 2014a).

Collections examined from Denmark

On *Remus sericeus* Holme, 1837 (Col. Staphylinidae Staphylininae)

DENMARK – **Fyn (F)** • Knudshoved; 55°18.212′ N, 10°49.828′ E; PG13; 11 Nov. 2018; *JP 1226*; JP det.; ZMUC C-F-123753. – **Nordøstjylland (NEJ)** • Deget Island ved Fredrikshavn; 57°27.066′ N, 10°34.785′ E; NJ96; 10 Jul. 1893; *J.P. Johansen Dry0145*; J.P. Johansen det.; ZMUC C-F-124213.

Remarks

First record from Denmark. This species is cosmopolitan, so its presence in Denmark was expectable.

Laboulbenia calathi T.Majewski
MB#363729
Fig. 26D, 104A

Polish Botanical Studies 7: 89 (Majewski 1994b). – **Type**: "On *Calathus melanocephalus* (Linnaeus), Ws. Pomiechówek, 28.8.1974 (TM. 1474 – holotype); KRAM. [Poland]

Diagnostic features

Cell V oval, half or a third of the length of cell IV, not connected with cell III, distinctively paler than its surroundings. Outer appendage unbranched. Inner appendage consisting of a small basal cell supporting short branches terminated by few antheridia in young thalli, but proliferating into some variably elongated sterile branches when ageing. [Detailed description: Santamaria 1998]

Distribution and hosts

This species is characteristic on *Calathus* (Col. Carabidae). In addition to the type from Poland, it is known from **Europe**: Spain (Santamaria 1996a), Belgium (De Kesel 1998), Lithuania (Markovskaja 2000), Latvia (De Kesel & Krastina De Kesel 2006), Switzerland (Hoess & Senn-Irlet 2009), Czech Republic (Rossi *et al.* 2010), the Netherlands (Haelewaters & De Kesel 2010), and Bulgaria (Rossi *et al.* 2019a). Most of the records of *L. polyphaga* var. *calathicola* Speg. may also be here included, viz. Italy (Spegazzini 1914), France (Colla 1926), and Romania (Bánhegyi 1949); but records on *Bradycellus* from Algeria (Maire 1920) and Morocco (Maire & Werner 1937) probably belong to *L. eubradycelli*.

Collections examined from Denmark

On *Calathus cinctus* Motschulsky, 1850 (Col. Carabidae)

DENMARK – **Fyn (F)** • Knudshoved Marina; 55°17.781′ N, 10°50.542′ E; PG12; 18 Oct. 2017; *JP 585*; JP det.; ZMUC C-F-123071. – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 7 May 2017; *JP 399*; JP det.; ZMUC C-F-122882. – **Nordøstsjælland (NEZ)** • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1055*; JP det.; ZMUC C-F-123572 • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 134*; JP det.; ZMUC C-F-122610.

On *Calathus fuscipes* (Goeze, 1777) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 3 Aug. 2019; *JP 1488*; JP det.; ZMUC C-F-124074.

On *Calathus melanocephalus* (Linnaeus, 1758) (Col. Carabidae)
DENMARK – **Fyn (F)** • Bagenkop; 54°45.201′ N, 10°40.616′ E; PF06; 5 Oct. 2016; *JP 148*; JP det.; ZMUC C-F-122627. – **Lolland, Falster, Møn (LFM)** • Nykøbing; 54°46.279′ N, 11°52.845′ E; PF87; 17 May 2017; *JP 411*; JP det.; ZMUC C-F-122895 • Ulvshale; 55°2.301′ N, 12°16.244′ E; UB20; 25 Sep. 2016; *JP 145*; JP det.; ZMUC C-F-122624. – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 135*; JP det.; ZMUC C-F-122611 • ibid., 21 Jun. 2017; JP 440; JP det.; ZMUC C-F-122925. – **Nordvestsjælland (NWZ)** • Eriksminde syd for Korshage; 55°57.744′ N, 11°46.504′ E; PH70; 27 Oct. 2019; *JP 1535*; JP det.; ZMUC C-F-124294 • Kongstrup Klint på Røsnæs; 55°43.730′ N, 10°58.299′ E; PG27; 20–26 Sep. 2014; *JP 235*; JP det.; ZMUC C-F-122715 • Maglesø Plantage; 55°38.136′ N, 11°41.186′ E; PG66; 18 Feb. 2017; *JP 284*; JP det.; ZMUC C-F-122763. – **Sydsjælland (SZ)** • Køge Nordhavn; 55°27.698′ N, 12°11.386′ E; UB24; 19 Oct. 2019; *JP 1517*; JP det.; ZMUC C-F-124272.

On *Calathus micropterus* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Gribskov, Fændriksvang; 56°1.005′ N, 12°21.245′ E; UC30; 1–30 Aug. 2014; *J. Heilmann-Clausen et al. 51*; P. Jørum det.; ZMUC C-F-122526.

Remarks

First record from Denmark. This is a very common species, and its presence in Denmark is not surprising.

Laboulbenia clivinalis Thaxt.
MB#140929
Fig. 27A–B

Proceedings of the American Academy of Arts and Sciences 35: 165 (Thaxter 1899). – **Type**: "On *Clivina collaris* Herbst, Brit. Mus. No. 456, … England"; FH. [type, according to Thaxter 1908: 408]

Laboulbenia henricii S.Colla (Colla1926: 185) [Not registered in MycoBank]

Diagnostic features

Cell V wedge-shaped, as long or longer and as broad as cell IV, connected with cell III. Outer appendage branched once or more times above a variably darkened suprabasal cell; septum separating basal and suprabasal cells oblique and blackened (Fig. 27B, arrows). Inner appendage consisting of a basal cell which is half as long as the outer basal cell, in young thalli bearing 2–3 simple and short branches with solitary terminal antheridium (Fig. 27B), later proliferating into a variable number of sterile branches in mature thalli (Fig. 27A). [Detailed descriptions: Thaxter 1908; Cépède & Picard 1908; Majewski 1994b; Santamaria 1998]

Distribution and hosts

On species of the genus *Clivina* (Col. Carabidae) in many countries in **Europe**: Bulgaria, Finland, France, Germany, Hungary, Italy, Norway, Poland, Romania, Russia, Spain, Sweden, Switzerland, United Kingdom (Santamaria *et al.* 1991), Belgium (De Kesel 1995), Lithuania (Markovskaja 2000), Czech Republic (Rossi & Máca 2006), Latvia (De Kesel & Krastina De Kesel 2006), the Netherlands (Haelewaters *et al.* 2012), and Austria (Rossi & Christian 2020). Also in **Africa**: Algeria, Cameroon; **Asia**: Burma, Indonesia, Philippines, Thailand, Vietnam (Santamaria *et al.* 1991), China and Cambodia

(Kong *et al.* 2020); and recently reported from **America**: Canada and USA (Haelewaters *et al.* 2019b). The record from China by Shen & Ye (2006) is wrong according to Kong *et al.* (2020).

Collections examined from Denmark

On *Clivina fossor* (Linnaeus, 1758) (Col. Carabidae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 697*; JP det.; ZMUC C-F-123186. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 5 May 1993; *S. Langemark & O.E. Meyer 99*; JP det.; ZMUC C-F-122574. – **Nordøstsjælland (NEZ)** • Espergærde; 56°0.591′ N, 12°33.074′ E; UC40; 24 May 2016; *M.H. Post 358*; JP det.; ZMUC C-F-122840 • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB47; 12 Mar. 2015; *H. Liljehult 97*; JP det.; ZMUC C-F-122572 • ibid.; 26 May 2015; *H. Liljehult 28*; JP det.; ZMUC C-F-122501. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 567*; JP det.; ZMUC C-F-123053 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 770*; JP det.; ZMUC C-F-123265. – **Nordvestsjælland (NWZ)** • Garbølle; 55°34.107′ N, 11°34.293′ E; PG66; 21 Apr. 2018; *JP 1061*; JP det.; ZMUC C-F-123578. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1440*; JP det.; ZMUC C-F-123987 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1276*; JP det.; ZMUC C-F-123806 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 961*; JP det.; ZMUC C-F-123467.

Remarks

First record from Denmark where its presence was expected given the wide distribution of this species.

Laboulbenia collae T.Majewski
MB#363730
Fig. 27C

Polish Botanical Studies 7: 104 (Majewski 1994b). – **Type**: "On *Agonum* (*Anchomenus*) *albipes* (Fabricius). Ks. Berezki, 15.9.1972 (TM. 1123 – holotype)"; KRAM. [Poland]

Laboulbenia filifera var. *pseudostolonicola* S.Colla (Colla 1925: 262) [Not registered in MycoBank]

Diagnostic features

Cell V oval, a third of the length of cell IV, not connected with cell III. Outer appendage hyaline to uniformly pale brown coloured, consisting of two similar branches arising from the suprabasal cell. Inner appendage consisting of a basal cell smaller than basal cell of outer appendage, supporting 1–2 once divided branches bearing solitary or paired terminal antheridia, sterile appendages infrequent. [Detailed description: Santamaria 1998]

Distribution and hosts

Other than the type, this species infects *Cardiomera genei* Bassi, 1834 from Italy (Colla 1925) and Spain (Santamaria 1986), both as *L. filifera* var. *pseudostolonicola*. Later reported on *Paranchus* and *Agonum* from Belgium (De Kesel 1998) and on *Paranchus* from the Netherlands (Haelewaters *et al.* 2012). Also from Switzerland on *Anisodactylus* (Hoess & Senn-Irlet 2009). The host *Agonum albipes* (Fabricius, 1796) is also known as *Paranchus albipes* (Fabricius, 1796) and *Anchus ruficornis* (Goeze, 1777) in old literature. Hosts are Col. Carabidae.

Fig. 27. *Laboulbenia* spp. **A**–**B**. *L. clivinalis* Thaxt. **A**. Mature thallus. **B**. Three immature thalli showing the oblique and blackened septum separating basal and suprabasal cells of outer appendage (arrows), a diagnostic character. – **C**. *L. collae* T.Majewski. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122501 (A–B), ZMUC C-F-123503 (C).

Collections examined from Denmark

On *Paranchus albipes* (Fabricius, 1796) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14 45.260′ E; VB81; 23 Jun. 2018; *JP 1158*; JP det.; ZMUC C-F-123683, C-F-123684. – **Nordøstsjælland (NEZ)** • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB48; 21 Jan. 2018; *J. Søgaard Hansen 996*; J. Søgaard Hansen; ZMUC C-F-123503 • Næsset, Rudersdal; 55°48.469′ N, 12°25.759′ E; UB38; 18 Apr. 2018; *M. Kofoed-Hansen 1105*; M. Kofoed-Hansen; ZMUC C-F-123623.

Remarks

First record from Denmark. *Laboulbenia collae* may be distinguished from similar species like *L. filifera* by its bigger size, above 300 µm from foot to perithecial apex; and from *L. flagellata* by longer cells II, III and VI, and by the uniformly coloured basal and suprabasal cells of outer appendage whereas appear ± dorsally obscured in *L. flagellata*. The distinctiveness of *Laboulbenia collae* from *L. flagellata* has been recently supported with molecular analysis (Haelewaters *et al.* 2019b).

Laboulbenia coneglianensis Speg.
MB#222726
Fig. 28A

Redia 10: 47 (Spegazzini 1914, as *coneglanensis*). – **Type**: [Not designated] [Ind. loc.] "In LPS. Sulle elitre dell'*Ophonus pubescens* a Edolo, Valcamonica (Coll. Mus. Zool. Firenze, n. 110) e comune e abbondante a Varese, a Vittorio, a Fregona ed a Conegliano, estate ed autunno 1912". [Italy]

Laboulbenia ophoni var. *dilatata* Maire (Maire 1920: 149) [MB#139658]

Diagnostic features

Thalli typically bent. Outer appendage pale brown coloured, consisting of two similar, very elongated, diverging branches arising from the suprabasal cell. Antheridia solitary, sessile, lateral to branches of the inner appendage. Perithecium showing a nearly straight ventral margin, a cylindrical and prominent apex, and preostiolar spots blackened and confluent into a ring-like area. [Detailed descriptions: Terada 1998b; Santamaria 1998]

Distribution and hosts

Known on Col. Carabidae Harpalini belonging to the genera *Harpalus*, *Ophonus*, *Pseudophonus* Motschulsky, 1844 and *Anisodactylus* in **Europe**: Belgium, Germany, Greece, Italy, Poland, Romania, Spain, former Yugoslavia (Santamaria *et al.* 1991), Switzerland (Baumgartner 1923, as *L. ophoni* var. *dilatata*), Russia (Siemaszko & Siemaszko 1928, as *L. ophoni* var. *dilatata*), Hungary (Bánhegyi 1940), France (Balazuc 1990), Lithuania (Markovskaja 2000), Sweden (Huggert 2010), Bulgaria (Rossi *et al.* 2019a). Also in Japan (Terada 1998b) and Algeria (Maire 1920, as *L. ophoni* var. *dilatata*). Records from other genera of carabids than the four mentioned above require verification (like *Platynus* Bonelli, 1810, *Chlaenius*, *Anchomenus* Bonelli, 1810, *Agonum*, *Pterostichus*).

Collections examined from Denmark

On *Anisodactylus binotatus* (Fabricius, 1787) (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Lersøparken i København Ø.; 55°42.493′ N, 12°32.612′ E; UB47; 6 May 2018; *H. Liljehult 1107*; H. Liljehult det.; ZMUC C-F-123625. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1081*; JP det.; ZMUC C-F-

123599 • ibid.; 25 Apr. 2019; *JP 1438*; JP det.; ZMUC C-F-123985 • ibid.; 3 Aug. 2019; JP 1492; JP det.; ZMUC C-F-124078.

On *Harpalus affinis* (Schrank, 1781) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Valbyparken; 55°38.568′ N, 12°31.183′ E; UB47; 8 Aug. 2009; *L.H. Hansen 72*; JP det.; ZMUC C-F-122547.

On *Harpalus griseus* (Panzer, 1797) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.806′ N, 12°32.340′ E; UA49; 3-20 Jul. 2013; *O. Karsholt 183*; JP det.; ZMUC C-F-122662.

On *Harpalus latus* (Linnaeus, 1758) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 832*; JP det.; ZMUC C-F-123326. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1283*; JP det.; ZMUC C-F-123815. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1257*; JP det.; ZMUC C-F-123785.

Remarks

First record from Denmark. *Laboulbenia coneglianensis* has been considered a synonym of *L. flagellata* by some authors (Balazuc 1974b; Majewski 1994b). Both species are closely related but may be separated according to Terada (1998b), who analyzed in detail the morphological traits of the two species, by the full black ring area below the perithecial ostiole of *L. coneglianensis* whereas in *L. flagellata* both preostiolar spots are separated, by the perithecial apex which is distinctively prominent and cylindrical in *L. coneglianensis*, by the solitary antheridia, not paired as in *L. flagellata*, as well as other characteristics previously detailed by Santamaria (1998). Molecular studies have supported the distinctiveness as species of *L. coneglianensis* (Haelewaters *et al.* 2019b). According to De Kesel *et al.* (2020), *L. coneglianensis* could be a species complex in need of study with an integrative taxonomical approach.

Laboulbenia anisodactyli was described by Spegazzini (1914) on *Anisodactylus binotatus* from Italy and later reported from Romania (Bánhegyi 1949), ex-Yugoslavia (Bánhegyi 1960) and Hungary (Bánhegyi *et al.* 1985). Its distinctiveness as a separate species has not even been debated because of Spegazzini's poor description and photographs. Considered a synonym of *L. coneglianensis* or *L. flagellata*, its status should be reviewed, especially if it is indeed a synonym of *L. coneglianensis*, since then its name has priority.

Spegazzini (1914) described two infraspecific taxa (without a defined rank) for *L. coneglianensis* with epithets *psittacea* and *grisea* lacking any taxonomical value.

Laboulbenia cornuta Thaxt.
MB#146244
Fig. 28B

Proceedings of the American Academy of Arts and Sciences 30: 476 (Thaxter 1895). – **Type**: "On *Bembidium complanatum* Mann., Washington (Miss Parker)"; FH. [USA]

Diagnostic features

As *L. luxurians* but with an oblique flat cell III, a larger cell V and with a ± conspicuous protuberance near the perithecial apex (Fig. 28B, *). [Detailed descriptions: Thaxter 1896; Majewski 2006]

Distribution and hosts

On the distal portion of elytra of species of *Bembidion* in the subgenus *Notaphus* (Col. Carabidae). Described from USA, also reported from Cuba, Hungary, Spain and Poland (Majewski 2008).

Collections examined from Denmark

On *Bembidion varium* (Olivier, 1795) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 457*; JP det.; ZMUC C-F-122942 • Ulvshale; 55°2.270′ N, 12°15.392′ E; UB20; 6 Jun. 2018; *JP 1121*; JP det.; ZMUC C-F-123643.

Fig. 28. *Laboulbenia* spp. **A**. *L. coneglianensis* Speg. Three mature thalli. – **B**. *L. cornuta* Thaxt. Mature thallus with labelled perithecial protuberance (*). – **C**. *L. corylophi* Scheloske. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123599 (A), ZMUC C-F-123643 (B), ZMUC C-F-122476 (C).

Remarks

First record from Denmark. Although the host is very common and widespread in Denmark, this is an uncommon species, and scarce when found, with only one or two thalli on each host.

Laboulbenia corylophi Scheloske
MB#332774
Fig. 28C, 106A

Parasitologische Schriftenreihe 19: 117 (Scheloske 1969). – **Type**: "Auf Halsschild und Elytren von *Corylophus cassidoides* (Col., Orthoperidae). Bruchwald bei Tennenlohe/Erlangen. Deutschland. Holotypus Abb. 23". [Germany]

Diagnostic features

Cell V obtriangular, slightly shorter than cell IV, not connected with cell III. Septum II–VI strongly oblique. Outer appendage unbranched, with a darkened, broadened basal cell. Inner appendage consisting of a basal cell which is shorter than the outer basal cell, bearing 1–2 short branches which, in young thalli, support solitary terminal antheridia. Thallus not exceeding the 100 µm in length; dark brown except for the hyaline cell I, cell V, and apices of appendages and perithecium. [Detailed description: Majewski 1994b]

Distribution and hosts

Described from Germany on *Corylophus cassidoides* (Col. Corylophidae) and found on the same host in Poland (Majewski 1986a), Slovakia, and Czech Republic (Rossi *et al.* 2019b).

Collections examined from Denmark

On *Corylophus cassidoides* (Marsham, 1802) (Col. Corylophidae)

DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14 45.260′ E; VB81; 23 Jun. 2018; *JP 1154*; JP det.; ZMUC C-F-123678. – **Østjylland (EJ)** • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015; *JP & H. Liljehult 511*; JP det.; ZMUC C-F-122994 • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; 10 Nov. 2018; *JP 1233*; JP det.; ZMUC C-F-123760. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 683*; JP det.; ZMUC C-F-123171. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1137*; JP det.; ZMUC C-F-123661 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 838*; JP det.; ZMUC C-F-123333. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 665*; JP det.; ZMUC C-F-123154 • ibid.; 12 Apr. 2017; *JP 5*; JP det.; ZMUC C-F-122476 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 871*; JP det.; ZMUC C-F-12336 • Nærum; 55°48.616′ N, 12°32.706′ E; UB48; 13 Nov. 2016; *JP 128*; JP det.; ZMUC C-F-122605. – **Nordvestjylland (NWJ)** • Fiskbæk Å ved Fiskbæk; 56°30.762′ N, 9°18.258′ E; NH16; 24 Nov. 2019; *JP 1548*; JP det.; ZMUC C-F-124309. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 599*; JP det.; ZMUC C-F-123088 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 852*; JP det.; ZMUC C-F-123347 • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 1 Apr. 2017; *JP 248*; JP det.; ZMUC C-F-122728. – **Sydsjælland (SZ)** • Enemærket ved Næsbyholm; 55°22.429′ N, 11°36.776′ E; PG63; 17 Nov. 2019; *JP 1557*; JP det.; ZMUC C-F-124318 • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1353*; JP det.; ZMUC C-F-123892 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1590*; JP det.; ZMUC C-F-124351.

Remarks

First record from Denmark. Because of the minute size of the host insects, around one mm long, this species may be easily overlooked, perhaps being more common than records in the literature seem to indicate.

Laboulbenia cristata Thaxt.
MB#236717
Fig. 29A

Proceedings of the American Academy of Arts and Sciences 28: 174 (Thaxter 1893). – **Type**: [Not designated] [Ind. loc.] "On elytra, abdomen, and legs of *Paederus littorarius* Grav. and *P. obliteratus* Lec., Maine; *Paederus* sp.? Mexico and Nicaragua; *Paederus ruficollis* Fabr., Austria"; FH.

Diagnostic features

Cell V rectangular in optical section, as long as cell IV. Septum IV–V vertical, connected with septum III–IV. Outer appendage consisting of 2–3 rather straight, apparently rigid, elongate branches arising above the suprabasal cell which bears a dorsal additional branch, often reduced to a rimmed darkened expansion (Fig. 29A, arrow). Inner appendage consisting of a basal cell which is half as long as the outer basal cell, giving rise to 1–2 simple or once ramified branches bearing 1–2 apical antheridia each. [Detailed descriptions: Thaxter 1896; Sugiyama 1973; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Very common on *Paederus* (Col. Staphylinidae Paederinae) and some closely related genera (*Megapaederus*? – this genus does not exist, it probably refers to *Megalopaederus* Scheerpeltz, 1957 –, *Uncopaederus* Korge, 1969, *Madecapaederus* Fagel, 1958) from the five continents (Santamaria *et al.* 1991; Majewski 2008). Recently recorded from Thailand (Rossi & Bernardi 2018), Cambodia, Romania (Kong *et al.* 2020), and Slovenia (Rossi & Christian 2020).

Collections examined from Denmark

On *Paederus riparius* (Linnaeus, 1758) (Col. Staphylinidae Paederinae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 686*; JP det.; ZMUC C-F-123174 • Kratholm ved Bellinge; 55°19.710′ N, 10°19.335′ E; NG83; 18 May 2016; *JP 88*; JP det.; ZMUC C-F-122563. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 647*; JP det.; ZMUC C-F-123135 • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; *JP 1520*; JP det.; ZMUC C-F-124275 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1335*; JP det.; ZMUC C-F-123874. – **Nordøstjylland (NEJ)** • Syd for Krogsagergård; 56°37.534′ N, 9°45.551′ E; NH47; 24 Nov. 2019; *JP 1553*; JP det.; ZMUC C-F-124314. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 727*; JP det.; ZMUC C-F-123220 • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1216*; JP det.; ZMUC C-F-123743 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 1*; JP det.; ZMUC C-F-122471 • ibid.; 19 Mar. 2017; *JP 668*; JP det.; ZMUC C-F-123157 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 865*; JP det.; ZMUC C-F-123361 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 405*; JP det.; ZMUC C-F-122888 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 621*; JP det.; ZMUC C-F-123109 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1048*; JP det.; ZMUC C-F-123564. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 888*; JP det.; ZMUC C-F-123386 • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 603*; JP det.; ZMUC C-F-123092 • Nordbredden

af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 845*; JP det.; ZMUC C-F-123340 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 633*; JP det.; ZMUC C-F-123122. – **Sydjylland (SJ)** • Brænøre Mose; 55°23.906′ N, 9°25.714′ E; NG23; 5 Aug. 2018; *JP 1163*; JP det.; ZMUC C-F-123688. – **Sydsjælland (SZ)** • Avnø; 55°5.206′ N, 11°45.142′ E; PG70; 14 Dec. 2014; *M. A. Krag 159*; JP det.; ZMUC C-F-122638 • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Apr. 2019; *JP 1423*; JP det.; ZMUC C-F-123969 • ibid.; 9 Jun. 2019; *JP 1473*; JP det.; ZMUC C-F-124053 • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1360*; JP det.; ZMUC C-F-123898 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1407*; JP det.; ZMUC C-F-123953 • Østerskov ved Langebæk; 54°59.331′ N, 12°6.357′ E; UA19; 27 Mar. 2018; *JP 1018*; JP det.; ZMUC C-F-123525 • ibid.; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; JP det.; ZMUC C-F-

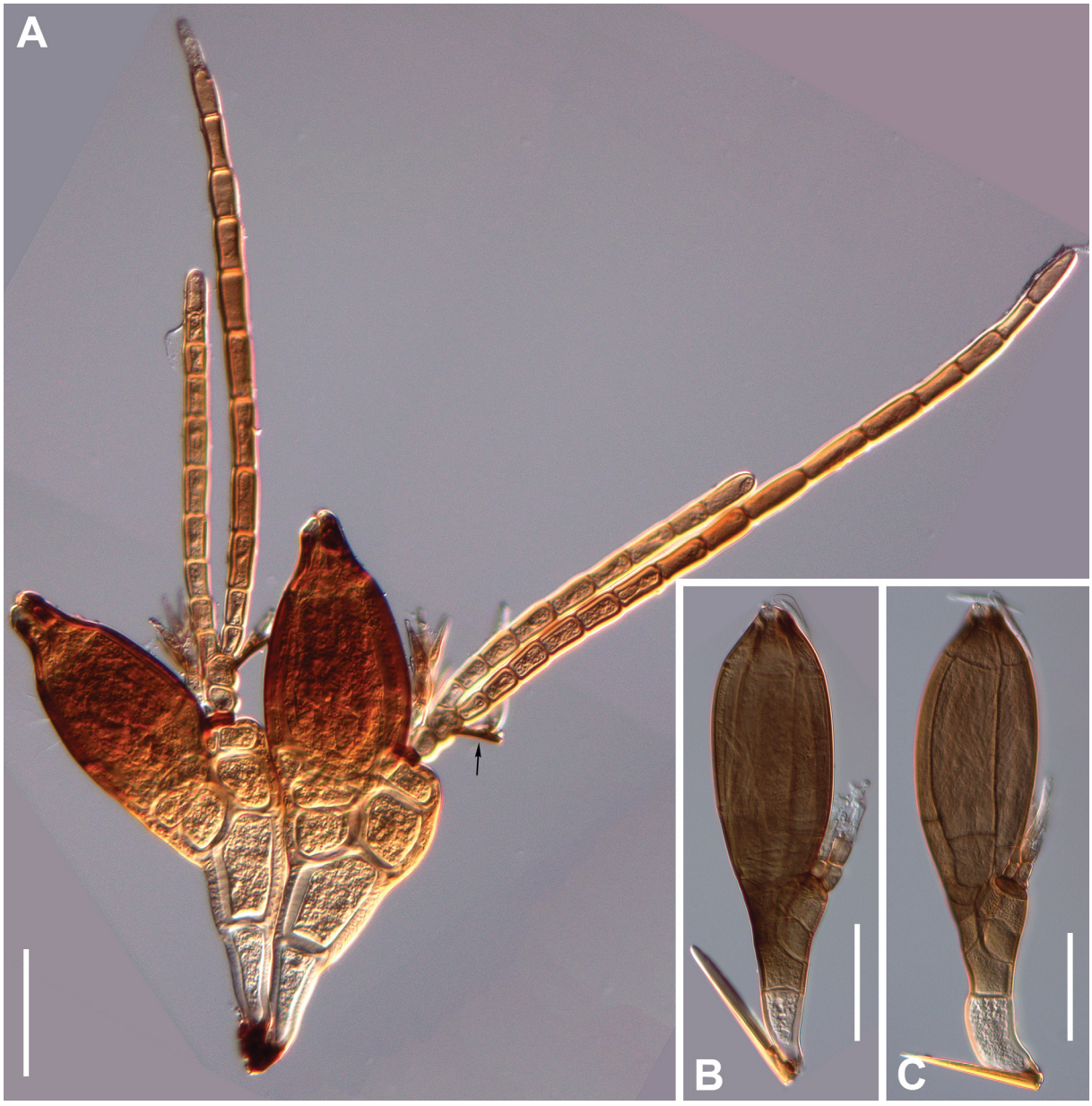

Fig. 29. *Laboulbenia* spp. **A**. *L. cristata* Thaxt. Two mature thalli. – **B**–**C**. *L. curtipes* Thaxt. Mature thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122471 (A), ZMUC C-F-123641 (B–C).

1298; JP det.; ZMUC C-F-123831 • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1433*; JP det.; ZMUC C-F-123980.

Remarks

First record from Denmark. It is probably one of the most common species of the genus *Laboulbenia*. Unmistakable species that does not seems to be related to any other. It does not present variations that deserve to be mentioned.

Laboulbenia curtipes Thaxt.
MB#250016
Fig. 29B–C

Proceedings of the American Academy of Arts and Sciences 29: 107 (Thaxter 1894). – **Type**: "On *Bembidium bimaculatum*, Washington (Miss Parker)"; FH. [USA]

Diagnostic features

Cell V oval, as long or longer than cell IV, connected with cell III. Insertion cell not contrasting because it is dark brown like the surrounding cells. Outer appendage unbranched, with similar basal and suprabasal cells, separated with a blackened and constricted septum; upper part of the appendage deteriorating easily with ageing. Inner appendage consisting of a basal cell slightly shorter than basal cell of outer appendage, bearing 1–2 caducous antheridia directly or above its respective supporting cells. Perithecium conspicuously inflated, free, measuring more than the half of the total length of the thallus. [Detailed descriptions: Thaxter 1896; Majewski 1994b; Santamaria 1998]

Distribution and hosts

This species can be found on the legs, especially the tarsi, of *Bembidion* in a broad sense (Col. Carabidae) from USA (type) and a few countries in **Europe** (Spain, Poland, Finland, Sweden, Russia) (Majewski 2008). Recently recorded from Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Bembidion assimile* Gyllenhal, 1810 (Col. Carabidae)
DENMARK – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1368*; JP det.; ZMUC C-F-123909 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1448*; JP det.; ZMUC C-F-123998.

On *Bembidion mannerheimii* Sahlberg, 1827 (Col. Carabidae)
DENMARK – **Fyn (F)** • Kohaveskov ved Landkildegård; 55°22.750′ N, 10°27.979′ E; NG93; 24 Aug. 2001; *H. Liljehult 1398*; JP det.; ZMUC C-F-123943.

On *Bembidion obliquum* Sturm, 1825 (Col. Carabidae)
DENMARK – **Sydjylland (SJ)** • Rejsby Sluse vest for Rejsby; 55°13.931′ N, 8°40.488′ E; MG72; 8 Mar. 2020; *JP 1650*; JP det.; ZMUC C-F-124372.

On *Bembidion varium* (Olivier, 1795) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.270′ N, 12°15.392′ E; UB20; 6 Jun. 2018; *JP 1121*; JP det.; ZMUC C-F-123641. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1008*; JP det.; ZMUC C-F-123515.°

Remarks

First record from Denmark. Although considered a growth form of *L. pedicellata* and *L. luxurians* occurring on tarsi by some authors (Scheloske 1969), this conception is questioned because thalli of these two species may be found interspersed with those of *L. curtipes*; in such cases all thalli maintain their specific characteristics.

Laboulbenia egens Speg.
MB#560228
Fig. 30A

Anales de la Sociedad Científica Argentina 85 (3): 323 (Spegazzini 1918). – **Type**: "Sobre las patas de pequeños *Tachys*? indeterminados cazados debajo de macetas de flores en mi casa, Roma. Sept. 1913"; LPS. [Italy]

Laboulbenia paupercula Speg. (Spegazzini 1915b: 59) [MB#219455] (nomen praeoccupum), nec *L. paupercula* Thaxt. (Thaxter 1891: 269) [MB#219368]

Diagnostic features

Cell I with a brownish shaded distal area, contrasting with the homogenously hyaline cell II. Septum IV–V vertical, ± straight, connected with septum III–IV. Cells IV and V similar in shape and size. Outer appendage not exceeding the perithecial apex, chiefly consisting of a crista-like structure formed by a few short branchlets arising from an isodiametric, trapezoidal, suprabasal cell (best seen in immature thalli). Basal cell of outer appendage protruding dorsally, showing a dark distal septum. Perithecium with a very convex ventral margin, with 1–3 swellings in its lower third. [Detailed descriptions: Majewski 1994b; Santamaria 1998]

Distribution and hosts

Reported on Col. Carabidae Tachyina of the genera *Elaphropus* Motschulsky, 1839, *Eotachys* Jeannel, 1941, *Paratachys* Casey, 1918, *Tachys*, *Tachyphanes* Jeannel, 1946, *Tachyta* Kirby, 1837 and *Tachyura* Motschulsky, 1862, usually named *Tachys* in a broad sense. Exceptionally on *Bembidion* (Majewski 1994b; Haelewaters *et al.* 2019b). In **Europe**: Czech Republic, France, Hungary, Italy, Poland, Romania, Spain (Santamaria *et al.* 1991), Belgium (De Kesel & Rammeloo 1992), United Kingdom (Weir 1996), Switzerland (Hoess & Senn-Irlet 2009); **Africa**: Algeria, Cameroon, Canary Islands, Egypt, Madagascar (Santamaria *et al.* 1991), Sierra Leone (Rossi & Leonardi 2018); **America**: Guadalupe (Santamaria *et al.* 1991), USA (Haelewaters *et al.* 2019b); and **Asia**: Bali Island, Israel, Japan, Korea, Taiwan, Thailand (Santamaria *et al.* 1991), Turkey (Rossi 2016), and Cambodia (Try *et al.* 2017).

Collections examined from Denmark

On *Elaphropus parvulus* (Dejean, 1831) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 7 May 2017; *JP 400*; JP det.; ZMUC C-F-122883.

Remarks

First record from Denmark. The host species is rare in Denmark and only found at a few scattered localities. Out of the ca 100 examined individuals of the host only one infected specimen was found. The fungus should therefore be considered as very rare in Denmark. *Laboulbenia egens* is a well-distinguished species, although it has sometimes been confused by several authors with *Laboulbenia tachyis* Thaxt. in East Asian records (Sugiyama 1973, 1978a; Lee *et al.* 1982; Lee & Sugiyama 1984; Sugiyama &

Phanichapol 1984; Sugiyama & Majewski 1985b). *Laboulbenia tachyis* may be quickly distinguished from *L. egens* by the oblique septum IV–V which is not connected with septum III–IV (Santamaria 1998). Majewski (1994b) mentioned the similarity of this species with *L. pedicellata* and even the existence of intermediate forms. Nevertheless, *Laboulbenia egens* is well-characterized by several features: (1) absence of preapical blackened spots on the perithecium, (2) conspicuous bulging protuberances in the lower third of the ventral side in perithecium, (3) cell II with parallel margins, (4) cell II distinctively hyaline relate to shaded cell I below, (5) diagonal blackened septum separating the basal and suprabasal cells of outer appendage; as well as other characters that separate it from *L. pedicellata* if we compare them with the analogous: (1) preapical blackened spots of perithecium present, (2) no protuberances or if any, they are much less evident and located at the middle height of perithecium, (3) cell II ± constricted, (4) cell II variably tinged with brown, (5) blackened septum above the basal cell of outer appendage which is horizontal or almost so.

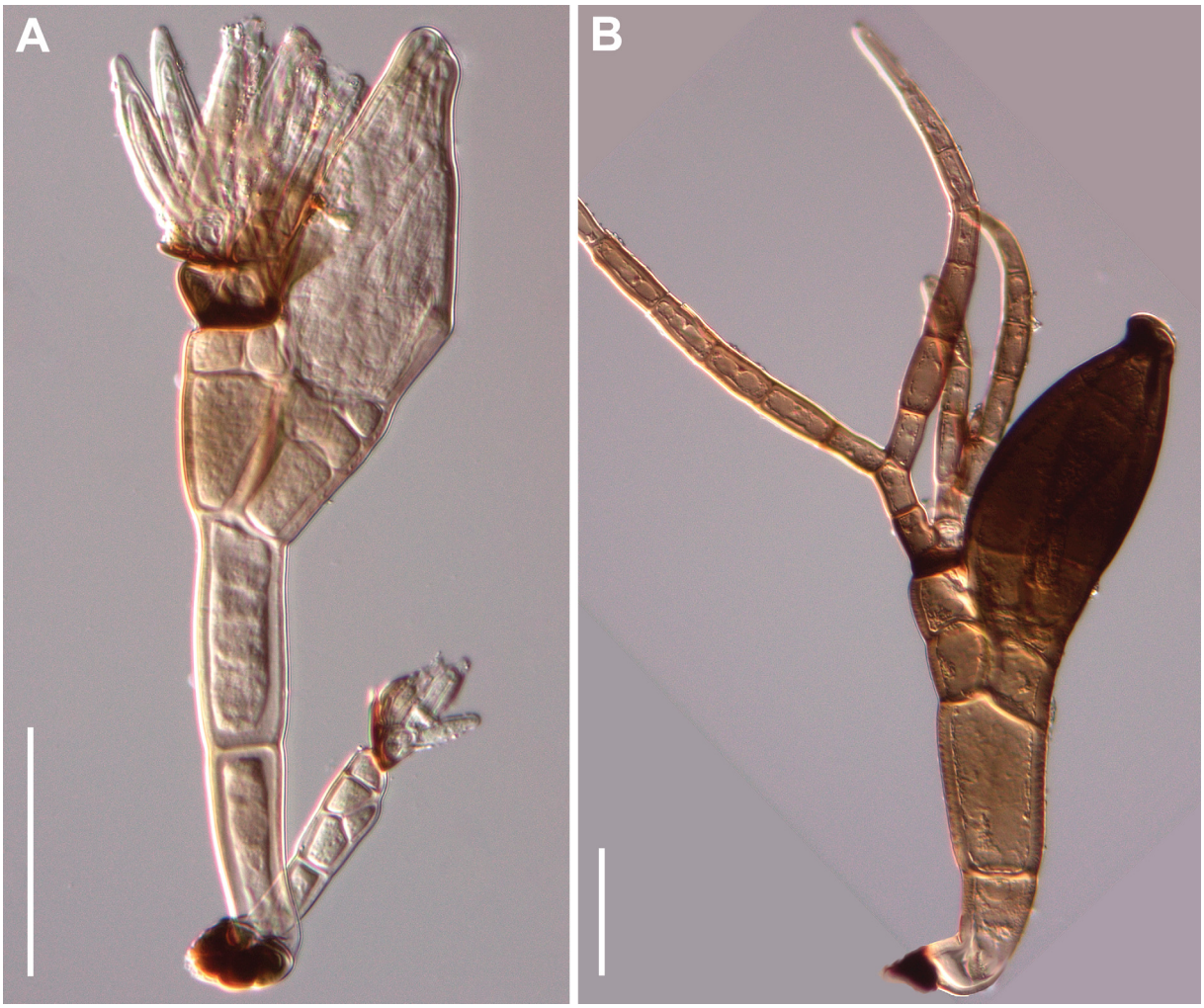

Fig. 30. *Laboulbenia* spp. **A**. *L. egens* Speg. Paired thalli, one mature at left and one immature at right. – **B**. *L. elaphri* Speg. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122883 (A), ZMUC C-F-123141 (B).

Laboulbenia elaphri Speg.
MB#180484
Fig. 30B

Anales del Museo Nacional de Historia Natural de Buenos Aires 26: 464 (Spegazzini 1915a). – **Type**: "Sulle elitre del *Elaphrus cupreus* originario del Belgio (Coll. Mus. Civ. Genova, n.21)"; LPS. [Belgium]

Laboulbenia buehlmannii Poelt (Poelt 1952: 116) [MB#299200]

Laboulbenia bänningeri Baumgartner (Baumgartner 1951: 32r) (nom. inval., as *L. Bännigeri*) [Not registered in MycoBank]

Diagnostic features

Outer appendage once ramified into two subequal branches above the second cell. Perithecium asymmetric with the ventral side distinctly more convex than the dorsal side; perithecial tip large with an almost flattened apex. [Detailed description: Majewski 1994b]

Distribution and hosts

Known on *Elaphrus* (Col. Carabidae) from **Europe**: Belgium (type), Finland, France, Germany, Hungary, Poland, Sweden, Russia (Santamaria *et al.* 1991), Latvia (De Kesel & Krastina De Kesel 2006), Switzerland (Hoess & Senn-Irlet 2009), Czech Republic (Rossi *et al.* 2010). Also reported on *Nebria ochotica* Sahlberg from China (Lee & Lim 2000), a record that requires confirmation. Rostrup (1916) mentioned the host but not the fungus name from Denmark.

Collections examined from Denmark

On *Elaphrus cupreus* Duftschmid, 1812 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 652*; JP det.; ZMUC C-F-123141. – **Nordøstsjælland (NEZ)** • Brønshøj (Degnemosen); 55°42.043′ N, 12°30.352′ E; UB47; 26 May 2016; *JP 287*; JP det.; ZMUC C-F-122766. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 83*; JP det.; ZMUC C-F-122558.

Remarks

First record from Denmark. Rossi *et al.* (2010) characterized well this species, which is difficult to separate morphologically from *L. flagellata* except for the flattened and large perithecial apex. *Laboulbenia elaphricola* J. Siemaszko & Siemaszko (1928), sometimes included among the synonyms of *L. elaphri*, is a distinct species (De Kesel & Krastina De Kesel 2006; Rossi & Christian 2020).

Laboulbenia eubradycelli Huldén
MB#104409
Fig. 31A, 104B

Karstenia 25: 4 (Huldén 1985). – **Type**: "Slide L. Huldén 1. On *Bradycellus caucasicus*. Collecting data of the host: Finland. Ab:Lohja, 7.V.1983 Luther (holotype)"; MZH.

Laboulbenia bradycelli Balazuc ex Balazuc (Santamaria *et al.* 1991: 22) [MB#355012]

Laboulbenia bradycelli Balazuc (Balazuc 1974a: 15) (nom. inval.) [Not registered in MycoBank]

Diagnostic features

Cell V obtriangular, distinctively paler than its surroundings, half or less of the length of cell IV, not connected with cell III. Outer appendage unbranched, with some cells darker; up to 400 μm long. Inner appendage consisting of a basal cell half as long and narrower than basal cell of outer appendage, supporting 1–2 short, once divided branches each bearing 1–2 terminal antheridia. Perithecial apex strongly asymmetrical and truncated. Ventral margin of the perithecium exhibiting some elevations (Fig. 31A, arrows). [Detailed descriptions: Majewski 1994b; Santamaria 1998]

Distribution and hosts

This species has been reported on *Bradycellus* and *Trichocellus* (Col. Carabidae) from many countries in **Europe**: France (Balazuc 1974a), Poland (Majewski 1981), Russia, Finland (Huldén 1983), Spain (Balazuc *et al.* 1983), United Kingdom, Italy, Belgium, Norway, Germany, Sweden (Huldén 1985), Czech Republic (Rossi & Máca 2006), Denmark (Høier 2009), Switzerland (Hoess & Senn-Irlet 2009), Slovakia (Rossi *et al.* 2010), the Netherlands (Haelewaters *et al.* 2012), and Bulgaria (Rossi *et al.* 2019a). Also from Madeira (Huldén 1985) and Mexico (Santamaria *et al.* 1991).

Collections examined from Denmark

On *Bradycellus caucasicus* (Chaudoir, 1846) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 15 Sep. 2006; JP 76; JP det.; ZMUC C-F-122551 • ibid.; 17 May 2009; *JP 58*; JP det.; ZMUC C-F-122533. – **Sydsjælland (SZ)** • Jarsskov; 55°9.108′ N, 11°46.800′ E; PG71; 21 Dec. 2003; *P.N. Buhl 184*; JP det.; ZMUC C-F-122663. – **Vestjylland (WJ)** • Simmelmose; 55°46.255′ N, 9°3.535′ E; NG08; 1 May 2001; *H. Liljehult 195*; JP det.; ZMUC C-F-122674.

On *Bradycellus csikii* Laczó, 1912 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 31 May 2009; *JP 59*; JP det.; ZMUC C-F-122534. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 930*; JP det.; ZMUC C-F-123430 • ibid.; *I. Aggerholm 943*; JP det.; ZMUC C-F-123447 • Knarmod i Tofte Skov; 56°51.824′ N, 10°15.470′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 949*; JP det.; ZMUC C-F-123455 • Toftgården i Tofte Skov; 56°50.789′ N, 10°12.918′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 946*; JP det.; ZMUC C-F-123451. – **Nordvestsjælland (NWZ)** • Maglesø Plantage; 55°38.136′ N, 11°41.186′ E; PG66; 18 Feb. 2017; *JP 285*; JP det.; ZMUC C-F-122764. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 543*; JP det.; ZMUC C-F-123027.

On *Bradycellus harpalinus* (Audinet-Serville, 1821) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Dueodde; 54°59.442′ N, 15°4.510′ E; WA09; 2 Jul. 2007; *JP 71*; JP det.; ZMUC C-F-122546. – **Østjylland (EJ)** • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP 436*; JP det.; ZMUC C-F-122921. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 705*; JP det.; ZMUC C-F-123195. – **Lolland, Falster, Møn (LFM)** • Bøtø Plantage; 54°37.629′ N, 11°57.661′ E; PF95; 17 May 2017; *JP 414*; JP det.; ZMUC C-F-122898 • Løgnor; 54°47.069′ N, 11°48.697′ E; PF87; 5 Nov. 2006; *JP 1458*; JP det.; ZMUC C-F-124009. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 931*; JP det.; ZMUC C-F-123431 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 25 Apr. 2009; *JP 193*; JP det.; ZMUC C-F-122672. – **Nordøstsjælland (NEZ)** • Dyrehaven; 55°47.347′ N, 12°33.957′ E; UB48; 1 Jan. 2017; *H. Liljehult 283*; JP det.; ZMUC C-F-122762 • ibid.; 20 Apr. 2017; *H. Liljehult 274*; JP det.; ZMUC C-F-122753 • Gilbjerghoved; 56°7.389′ N, 12°16.478′ E; UC32; 11 Mar. 2017; *L. Kjær-Thomsen 1040*; JP det.; ZMUC C-F-123556 • Liseleje; 56°1.048′ N, 11°58.454′ E; PH81; 30 Oct. 2016; *JP 133*; JP det.; ZMUC C-F-122609 • Ryegård Dyrehave;

55°40.500′ N, 11°50.851′ E; PG77; 2 Dec. 2014; *JP 345*; JP det.; ZMUC C-F-122827 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1239*; JP det.; ZMUC C-F-123766 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 28.22017; *H. Liljehult 360*; JP det.; ZMUC C-F-122843 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1029*; JP det.; ZMUC C-F-123541 • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 30 Mar. 2019; *JP 1405*; JP det.; ZMUC C-F-123951. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 885*; JP det.; ZMUC C-F-123383. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 1 Nov. 2013; *JP 225*; JP det.; ZMUC C-F-122706 • Sønderstrand på Rømø; 55°6.373′ N, 8°29.380′ E; MG60; 25 Oct. 2017; *H. Liljehult 617*; JP det.; ZMUC C-F-123105. – **Sydsjælland (SZ)** • Åshøje Overdrev; 55°26.368′ N, 12°6.359′ E; UB14; 6 Oct. 2018; *L. Kjær-Thomsen & L. Thomas 1236*; JP det.; ZMUC C-F-123763. – **Vestjylland (WJ)** • Blåvand; 55°33.418′ N, 8°5.193′ E; MG45; 29 Aug.–13 Sep. 2014; *E. Vesterhede & F. Vilhelmsen 110*; JP det.; ZMUC C-F-122587 • Simmelmose; 55°46.255′ N, 9°3.535′ E; NG08; 1 May 2001; *H. Liljehult 194*; JP det.; ZMUC C-F-122673 • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1256*; JP det.; ZMUC C-F-123784.

On *Bradycellus ruficollis* (Stephens, 1828) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Asserbo Plantage; 56°1.794′ N, 12°1.589′ E; UC11; 15 Oct. 2017; *JP 575*; JP det.; ZMUC C-F-123061. – **Vestjylland (WJ)** • Myrtue; 55°33.859′ N, 8°17.845′ E; MG55; 21 May 2017; *JP 423*; JP det.; ZMUC C-F-122908.

On *Bradycellus verbasci* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Gedesby; 54°35.290′ N, 11°58.199′ E; UA17; 20 Aug.–5 Sep. 2013; *E. Vesterhede 186*; JP det.; ZMUC C-F-122665 • Mellemskoven; 54°47.633′ N, 12°4.370′ E; UA17; 20 Aug.–5 Sep. 2013; *E. Vesterhede 190*; JP det.; ZMUC C-F-122669 • Møns Klint, Syd; 54°56.806′ N, 12°32.340′ E; UA49; 25 Jul.–15 Aug. 2013; *O. Karsholt 187*; JP det.; ZMUC C-F-122666 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1317*; JP det.; ZMUC C-F-123853. – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°39.168′ N, 12°34.750′ E; UB47; 14 Apr. 2001; *H. Liljehult 387*; JP det.; ZMUC C-F-122870 • Botanisk Have i København; 55°41.214′ N, 12°34.289′ E; UB47; 18–25 Jul. 2013; *JP & O. Karsholt 192*; JP det.; ZMUC C-F-122671, C-F-122775 • København Ø.; 55°42.151′ N, 12°33.576′ E; UB47; 19–27 Aug. 2013; *JP & O. Karsholt 191*; JP det.; ZMUC C-F-122670 • Nordøst for Bispebjerg Station; 55°42.508′ N, 12°32.786′ E; UB47; 22 Aug. 2016; *JP 119*; JP det.; ZMUC C-F-122596. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; JP 884; JP det.; ZMUC C-F-123382 • ibid.; 27 Dec. 2016; *H. Liljehult 392*; JP det.; ZMUC C-F-122875. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1284*; JP det.; ZMUC C-F-123816. – **Vestjylland (WJ)** • Blåvand; 55°33.418′ N, 8°5.193′ E; MG45; 29 Aug.–13 Sep. 2014; *E. Vesterhede & F. Vilhelmsen 109*; JP det.; ZMUC C-F-122586 • Ho; 55°33.304′ N, 8°12.945′ E; MG55; 27 Aug.–6 Sep. 2013; *E. Vesterhede & F. Vilhelmsen 234*; JP det.; ZMUC C-F-122714 • Sønder Resen Naturpark; 56°22.404′ N, 9°4.786′ E; NH04; 23 Mar. 2019; *L. Kjær-Thomsen & L. Thomas 1402*; JP det.; ZMUC C-F-123948.

On *Trichocellus cognatus* (Gyllenhal, 1827) (Col. Carabidae)
DENMARK – **Nordvestsjælland (NWZ)** • Vesterlyng; 55°44.548′ N, 11°18.285′ E; PG47; 4 Nov. 2017; *J. Søgaard Hansen 1041*; JP det.; ZMUC C-F-123557.

On *Trichocellus placidus* (Gyllenhal, 1827) (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP 435*; JP det.; ZMUC C-F-122920 • Havnen i Randers; 56°27.687′ N, 10°3.546′ E; NH65; 19 May 2013; *JP 372*; JP det.; ZMUC C-F-122855 • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 16 May 2014; *JP 312*; JP det.; ZMUC C-F-122791 • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015;

JP & H. Liljehult 514; JP det.; ZMUC C-F-122997 • Serup Skov; 56°14.504′ N, 9°28.051′ E; NH23; 26 Mar. 2017; JP 241; JP det.; ZMUC C-F-122721 • Ørnsø ved Silkeborg; 56°9.446′ N, 9°31.488′ E; NH32; 11 Mar. 2017; *JP 276*; JP det.; ZMUC C-F-122755 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 979*; JP det.; ZMUC C-F-123486 • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 530*; JP det.; ZMUC C-F-123014. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 704*; JP det.; ZMUC C-F-123194 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1074*; JP det.; ZMUC C-F-123592 • Sydøst for Humble; 54°49.077′ N, 10°43.349′ E; PF17; 5 Oct. 2016; *JP 131*; JP det.; ZMUC C-F-122607. – **Lolland, Falster, Møn (LFM)** • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 549*; JP det.; ZMUC C-F-123035 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1112*; JP det.; ZMUC C-F-123631 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1318*; JP det.; ZMUC C-F-123854. – **Nordøstjylland (NEJ)** • Syd for Krogsagergård; 56°37.534′ N, 9°45.551′ E; NH47; 24 Nov. 2019; *JP 1554*; JP det.; ZMUC C-F-124315. – **Nordøstsjælland (NEZ)** • Engen ud for Kongelunden; 55°34.244′ N, 12°33.668′ E; UB46; 20 Jan. 2017; *H. Liljehult 280*; JP det.; ZMUC C-F-122759 • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 736*; JP det.; ZMUC C-F-123229 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 591*; JP det.; ZMUC C-F-123080 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 268*; JP det.; ZMUC C-F-122747 • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB47; 12 Mar. 2015; *H. Liljehult 189*; JP det.; ZMUC C-F-122668 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1240*; JP det.; ZMUC C-F-123767 • Utterslev Mose; 55°42.775′ N, 12°30.443′ E; UB47; 25 May 2013; *JP 185*; JP det.; ZMUC C-F-122664. – **Nordvestjylland (NWJ)** • Fiskbæk Å ved Fiskbæk; 56°30.762′ N, 9°18.258′ E; NH16; 24 Nov. 2019; *JP 1547*; JP det.; ZMUC C-F-124308 • Gammelgård på Fur; 56°50.314′ N, 8°58.971′ E; MH99; 22 Nov. 2013; *JP 421*; JP det.; ZMUC C-F-122905 • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 568*; JP det.; ZMUC C-F-123054 • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 375*; JP det.; ZMUC C-F-122858. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 883*; JP det.; ZMUC C-F-123381 • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 606*; JP det.; ZMUC C-F-123095 • Nordbredden af Tissø ved Halleby Å's udløb; 55°35.602′ N, 11°18.532′ E; PG46; 18 Feb. 2017; *JP 385*; JP det.; ZMUC C-F-122868 • Saltbæk; 55°44.625′ N, 11°6.633′ E; PG37; 19 Jan. 2019; *L. Kjær-Thomsen & L. Thomas 1343*; JP det.; ZMUC C-F-123882 • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 1 Apr. 2017; JP 251; JP det.; ZMUC C-F-122731. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *H. Liljehult 294*; JP det.; ZMUC C-F-122773 • Sølsted Mose; 55°1.829′ N, 8°50.351′ E; MF89; 2 Jun. 2013; *JP 485*; JP det.; ZMUC C-F-122969 • Store Søgård Sø; 54°56.251′ N, 9°27.063′ E; NF28; 23 Apr. 2000; *H. Liljehult 328*; JP det.; ZMUC C-F-122806. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 491*; JP det.; ZMUC C-F-122975 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1005*; JP det.; ZMUC C-F-123512 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 28 Feb. 2015; *JP 446*; JP det.; ZMUC C-F-122931 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1285*; JP det.; ZMUC C-F-123817 • ibid.; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; JP 542; JP det.; ZMUC C-F-123026 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 1–15 Aug. 2013; *JP 528*; JP det.; ZMUC C-F-123012 • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; 17 Feb. 2019; *JP 1387*; JP det.; ZMUC C-F-123930 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1586*; JP det.; ZMUC C-F-124347. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1255*; JP det.; ZMUC C-F-123783.

Remarks

Huldén (1985) described and separated this species from *L. bradycelli*, but now there is little doubt that *L. eubradycelli* and *L. bradycelli* are conspecific. Because *L. eubradycelli* was legitimately described

Fig. 31. *Laboulbenia* spp. **A**. *L. eubradycelli* Huldén. Mature thallus showing elevations on ventral margin of perithecium (arrows). – **B**–**F**. *L. fasciculata* Peyr. **B**, **E**. Mature thalli. **C**–**D**. Immature thalli with labelled insertion cell (ic). **F**. Mature thallus on *Chlaenius* from Spain. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122533 (A), ZMUC C-F-124273 (B), ZMUC C-F-123598 (C), ZMUC C-F-122639 (D–E), BCB-XE56 (F).

before *L. bradycelli* it has priority according to Code rules. This is a variable species, extremely common in Denmark, perhaps a collective species, including some undescribed taxa (De Kesel 1997).

Laboulbenia fasciculata Peyr.
MB#193860
Fig. 31B–F

Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1 68: 248 (Peyritsch 1873). – **Type**: [Type lost?!] "Auf den Flügeldecken und Extremitäten von *Chlaenius vestitus* F.". [Austria, according to Balazuc 1974b]

Laboulbenia brachiata Thaxt. (Thaxter 1890: 11) [MB#246812]

Diagnostic features

Cell V subtriangular, dividing into up to eight cells which gradually decrease in size upwards, each cell bearing a small cell which gives rise to secondary appendages. Appendages numerous; outer and inner set of appendages (the primary appendage itself) indistinct from nearby secondary appendages, all together include ± inflated basal cells separated by constricted and variably darkened septa. Insertion cell with the same colour as surrounding cells (Fig. 31C–D, ic). [Detailed descriptions: Thaxter 1896; Sugiyama 1973; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Typical hosts belong to Col. Carabidae of the genus *Chlaenius* and allied genera (*Chlaeniellus* Reitter, 1908, *Parachlaenius* Kolbe, 1894). The genus *Patrobus* was initially reported as the host for *L. brachiata*. It also occurs in many other genera of Carabidae belonging to subfamily *Cicindelinae* and tribes *Patrobini*, *Chlaenini*, *Omophronini*, *Pterostichini*, *Brachinini*, *Bembidiini* and *Nebriini* (Santamaria *et al.* 1991; Majewski 2008). Widely distributed in Europe, Africa, America and Asia (Santamaria *et al.* 1991). Not found in Oceania. Records subsequent to or omitted in Santamaria *et al.* (1991) are: Latvia (Briedis 1934), Taiwan (Juan & Chien 1996), Belgium (De Kesel 1998), Czech Republic (Rossi & Máca 2006), Denmark (Høier 2007), Cambodia (Try *et al.* 2017), Eritrea, Bulgaria (Rossi *et al.* 2019a), and the Netherlands (Haelewaters & De Kesel 2020).

Collections examined from Denmark

On *Patrobus atrorufus* (Ström, 1768) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Hjelm Kobbel; 54°54.863′ N, 12°14.918′ E; UA28; 28 Aug. 2019; *JP 1506*; JP det.; ZMUC C-F-124093 • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 12 May 1993; *S. Langemark & O.E. Meyer 901*; JP det.; ZMUC C-F-123399 • ibid.; 19 Jul. 1993; *S. Langemark & O.E. Meyer 921*; JP det.; ZMUC C-F-123419 • ibid.; 28 Jul. 1993; *S. Langemark & O.E. Meyer 919*; JP det.; ZMUC C-F-123417 • ibid.; 16–24 Aug. 1993; *S. Langemark & O.E. Meyer 914*; JP det.; ZMUC C-F-123412 • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; *JP 1518*; JP det.; ZMUC C-F-124273. – **Nordøstsjælland (NEZ)** • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB47; 19 Sep. 2013; *H. Liljehult 299*; JP det.; ZMUC C-F-122778 • Peberholm; 55°35.865′ N, 12°45.308′ E; UB56; 13 Apr. 2005; *S. Frank 73*; JP det.; ZMUC C-F-122548. – **Nordvestsjælland (NWZ)** • Garbølle; 55°34.107′ N, 11°34.293′ E; PG66; 21 Apr. 2018; *JP 1060*; JP det.; ZMUC C-F-123577. – **Sydsjælland (SZ)** • Flommen ved Sorø; 55°25.957′ N, 11°34.477′ E; PG64; 23 Aug. 2009; *JP 57*; JP det.; ZMUC C-F-122532 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1083*; JP det.; ZMUC C-F-123601 • ibid.; 25 Apr. 2019; *JP 1439*; JP det.; ZMUC C-F-123986 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 12 Jul. 2013; *H. Enghoff 160*; JP det.; ZMUC C-F-122639 • ibid.;

1–15 Aug. 2013; *JP 527*; JP det.; ZMUC C-F-123011 • ibid.; 15 Aug. 2013; *JP 394*; JP det.; ZMUC C-F-122877 • ibid.; 2 Jul. 2014; *JP 383*; JP det.; ZMUC C-F-122866.

On *Pterostichus rhaeticus* Heer, 1837 (Col. Carabidae)
DENMARK – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1080*; JP det.; ZMUC C-F-123598.

Remarks

Laboulbenia fasciculata, *L. brachiata* and *L. variabilis* form a rather compact group of hardly separable species. To begin with, synonymy of *L. fasciculata* and *L. brachiata* might be re-examined. *Laboulbenia brachiata* was described by Thaxter (1890) on *Patrobus longicornis* (Say, 1823) and on *P. tenuis* LeConte, 1850 from USA. From the beginning, Thaxter (1896) expressed some doubts about the distinctiveness of his own species, to be later included among the synonyms of *L. fasciculata* (Thaxter 1908). In order to clarify the status of these two species, we have attempted to borrow the type of *L. brachiata* from FH but it was unavailable. The same is true for the type of *L. fasciculata*, an old species which probably lacks the support of slides kept in a herbarium. Thalli from *Patrobus*, which should correspond to what was described as *L. brachiata*, show some differences with those from *Chlaenius*, particularly the much darker appendages. For comparison, we have included Fig. 31F from a Spanish thallus found on *Chlaenius*. To draw conclusions, a challenging study should be carried out with more material from different hosts and localities, supported by molecular analysis.

Laboulbenia variabilis was the last of the three species to be described (Thaxter 1892). The list of hosts reported for this taxon is remarkable and extremely wide-ranging. It consists of ground beetles belonging to *Anomoglossus* Chaudoir, 1857, *Chlaenius*, *Omophron* Latreille, 1802, *Nebria* Latreille, 1802, *Pterostichus*, *Patrobus* and *Platynus* from USA and other American countries. Thaxter (1908) added new records on *Tetracha* Hope, 1838, *Platysma* Bonelli, 1810, *Poecilus* Bonelli, 1810, *Aspidoglossa* Putzeys, 1846, *Brachygnathus* Perty, 1830 from more American countries, to consider his species as "absolutely confined to the western hemisphere". Moreover, he added a short sentence indicating that *L. fasciculata* shows "a certain resemblance to *L. variabilis* to which it may be related". Spegazzini (1912, 1915a, 1917) added new records from Argentina, Uruguay and Paraguay on new host genera like *Feroniomorpha* Chaudoir, 1876, *Metius* (as *Antarctia*), *Platysma* and *Loxandrus* LeConte, 1852. Spegazzini (1917) described three "forms" named *clivinicola*, *eumetabola*, and *pachytelica*, respectively on *Ardistomis* Putzeys, 1846 (as *Ardistomus*) from Argentina, on *Platynus*? from Uruguay, and on *Athrostictus* (as *Hypolithus*, a name belonging to an Elateridae beetle!) from Paraguay. With these, even more confusion was added to the delimitation of this species. Colla (1925, 1926, 1934) added some Italian records on *Chlaenius* which don't help too much. Lastly, Haelewaters *et al.* (2019b) restored the species and recorded it from several species of *Pterostichus*, *Patrobus*, and *Chlaenius* from USA and Canada, writing that is an "easily recognized" species and "it may be that different hosts (species or genera) carry distinct cryptic or near-cryptic phylogenetic species". We have not studied any American material of this species complex, so we cannot do anything but highlight the doubts we have about its distinctiveness.

Laboulbenia flagellata Peyr.
MB#193832
Fig. 32

Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1 68: 247 (Peyritsch 1873). – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "Der Pilz befällt die Flügeldecken von *Bembidium lunatum* Duft., … Ausserdem

habe ich ihn auf *Anchomenus albipes* F., and *A. marginatus* L. angetroffen". [Austria, according to Balazuc 1974b]

Laboulbenia anceps Peyr. (Peyritsch 1873: 247) [MB#172583]
Laboulbenia elongata Thaxt. (Thaxter 1890: 10) [MB#187192]
Laboulbenia lepida Thaxt. (Thaxter 1896: 323) [MB#222474]
Laboulbenia anisodactyli Speg. (Spegazzini 1914: 46) [MB#150969]
Laboulbenia pierantonii S.Colla. (Colla 1926: 172) [Not registered in MycoBank]
Laboulbenia rougetii var. *europhili* Siemaszko & W.Siemaszko (Siemaszko & Siemaszko 1928: 203) [MB#139517]

Diagnostic features

Cell V obtriangular, half of the length of cell IV, not connected with cell III. Outer appendage with the lower dorsal margin ± obscured; once branched above the suprabasal cell. Inner appendage consisting of a basal cell slightly shorter and narrower than basal cell of outer appendage, supporting a variable number of sterile and fertile branches bearing paired lateral antheridia. [Detailed descriptions: Sugiyama 1973; Majewski 1994b; Santamaria 1998; Villarreal *et al.* 2010; De Kesel & Gerstmans 2011]

Distribution and hosts

Laboulbenia flagellata is a very common and cosmopolitan species found on the five continents, infecting not less than 12 tribes and more than 80 genera of ground beetles (Santamaria *et al.* 1991; Majewski 2008; Haelewaters *et al.* 2019b). Early reported in Denmark by Rostrup (1916, 1935).

Collections examined from Denmark

On *Agonum emarginatum* (Gyllenhal, 1827) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1151*; JP det.; ZMUC C-F-123675.

On *Agonum fuliginosum* (Panzer, 1809) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14°45.096′ E; VB80; 25 Apr. 2014; *JP 507*; JP det.; ZMUC C-F-122990 • Svartingedalen ved Baggeå; 55°11.740′ N, 14°45.260′ E; VB81; 23 Jun. 2018; *JP 1161*; JP det.; ZMUC C-F-123687. – **Østjylland (EJ)** • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 794*; JP det.; ZMUC C-F-123289 • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP 437*; JP det.; ZMUC C-F-122922 • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 16 Feb. 2018; JP 977; JP det.; ZMUC C-F-123484 • Ørnsø ved Silkeborg; 56°9.446′ N, 9°31.488′ E; NH32; 11 Mar. 2017; *JP 277*; JP det.; ZMUC C-F-122756. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 707*; JP det.; ZMUC C-F-123197 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1071*; JP det.; ZMUC C-F-123588. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 660*; JP det.; ZMUC C-F-123149 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 830*; JP det.; ZMUC C-F-123324 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1306*; JP det.; ZMUC C-F-123841. – **Nordøstjylland (NEJ)** • Vesterskoven i Tofte Skov; 56°50.346′ N, 10°13.361′ E; NJ70; 7 Aug. 2013; *JP 316*; JP det.; ZMUC C-F-122795. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 735*; JP det.; ZMUC C-F-123228 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 594*; JP det.; ZMUC C-F-123083 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 262*; JP det.; ZMUC C-F-122741 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 664*; JP det.; ZMUC C-F-123153 • ibid.; 12 Apr. 2016; *JP 18*; JP det.; ZMUC C-F-122491 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 631*; JP det.; ZMUC C-F-

Fig. 32. A–**G**. *Laboulbenia flagellata* Peyr. Mature thalli from *Agonum fuliginosum* (A), *Agonum muelleri* (B), *Loricera pilicornis* (C), *Anisodactylus binotatus* (D), *Platynus assimilis* (E–F), and *Anchomenus dorsalis* (G). Scale bars: 50 µm. Photographs from slides ZMUC C-F-122491 (A), ZMUC C-F-122590 (B), ZMUC C-F-123321 (C), ZMUC C-F-122589 (D), ZMUC C-F-122578 (E–F), ZMUC C-F-122829 (G).

123120 • Vaserne; 55°49.129′ N, 12°26.343′ E; UB38; 21 Apr. 2018; *L. Thomas 1119*; JP det.; ZMUC C-F-123639. – **Nordvestjylland (NWJ)** • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 773*; JP det.; ZMUC C-F-123268. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 881*; JP det.; ZMUC C-F-123379 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 642*; JP det.; ZMUC C-F-123130. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *JP 291*; JP det.; ZMUC C-F-122770. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 489*; JP det.; ZMUC C-F-122973 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1443*; JP det.; ZMUC C-F-123991 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 544*; JP det.; ZMUC C-F-123028 • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1437*; JP det.; ZMUC C-F-123984. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1254*; JP det.; ZMUC C-F-123782.

On *Agonum gracile* Sturm, 1824 (Col. Carabidae)
DENMARK – **Nordøstjylland (NEJ)** • Tranesig i Tofte Skov; 56°51.597′ N, 10°13.575′ E; NJ70; 1 Oct. 2010; *JP 74*; JP det.; ZMUC C-F-122549.

On *Agonum marginatum* (Linnaeus, 1758) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Nordhavnstippen på Københavns Nordhavn; 55°43.091′ N, 12°37.088′ E; UB57; 29 Apr. 2018; *JP 1090*; JP det.; ZMUC C-F-123608 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1051*; JP det.; ZMUC C-F-123567. – **Sydjylland (SJ)** • Sønderstrand på Rømø; 55°6.373′ N, 8°29.380′ E; MG60; 25 Oct. 2017; *H. Liljehult 619*; JP det.; ZMUC C-F-123107.

On *Agonum micans* (Nicolai, 1822) (Col. Carabidae)
DENMARK – **Fyn (F)** • Kratholm ved Bellinge; 55°19.710′ N, 10°19.335′ E; NG83; 18 May 2016; *JP 87*; JP det.; ZMUC C-F-122562.

On *Agonum muelleri* (Herbst, 1784) (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 16 Feb. 2018; *JP 978*; JP det.; ZMUC C-F-123485. – **Nordøstsjælland (NEZ)** • Brønshøj; 55°42.234′ N, 12°30.135′ E; UB47; 22 Jun. 2016; *JP 113*; JP det.; ZMUC C-F-122590 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 2 Dec. 2011; *JP 474*; JP det.; ZMUC C-F-122958. – **Nordvestjylland (NWJ)** • Legind; 56°45.832′ N, 8°48.782′ E; MH89; 19 Oct. 2008; *JP 75*; JP det.; ZMUC C-F-122550. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.469′ N, 11°23.147′ E; PG47; 18 Feb. 2017; *JP 340*; JP det.; ZMUC C-F-122819.

On *Agonum piceum* (Linnaeus, 1758) (Col. Carabidae)
DENMARK – **Nordøstjylland (NEJ)** • Syd for Krogsagergård; 56°37.534′ N, 9°45.551′ E; NH47; 24 Nov. 2019; *JP 1556*; JP det.; ZMUC C-F-124317. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1248*; JP det.; ZMUC C-F-123776.

On *Agonum thoreyi* Dejean, 1828 (Col. Carabidae)
DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14°45.260′ E; VB81; 23 Jun. 2018; *JP 1160*; JP det.; ZMUC C-F-123686. – **Østjylland (EJ)** • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 531*; JP det.; ZMUC C-F-123015. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 708*; JP det.; ZMUC C-F-123198. – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 831*; JP det.; ZMUC C-F-123325. – **Nordøstsjælland (NEZ)** • Auderød Skov; 55°59.117′ N, 12°5.579′ E; UC10; 28 Jan. 2018; *J. Søgaard Hansen 997*; J. Søgaard Hansen det.; ZMUC C-F-123504 • Brønshøj (Degnemosen); 55°42.043′ N, 12°30.352′ E; UB47; 26 May 2016; *JP 289*; JP det.; ZMUC C-F-122768 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 595*; JP det.; ZMUC C-F-123084

• Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 862*; JP det.; ZMUC C-F-123357 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1052*; JP det.; ZMUC C-F-123568. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 566*; JP det.; ZMUC C-F-123052. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *JP 292*; JP det.; ZMUC C-F-122771. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1365*; JP det.; ZMUC C-F-123905 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1442*; JP det.; ZMUC C-F-123990 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 545*; JP det.; ZMUC C-F-123029 • ibid.; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1273*; JP det.; ZMUC C-F-123803.

On *Agonum versutum* Sturm, 1824 (Col. Carabidae)
DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14°45.096′ E; VB80; 25 Apr. 2014; *JP 505*; JP det.; ZMUC C-F-122988.

On *Agonum viduum* (Panzer, 1797) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 659*; JP det.; ZMUC C-F-123148.

On *Anchomenus dorsalis* (Pontoppidan, 1763) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Øst for Østerlars; 55°9.619′ N, 14°59.763′ E; VB91; 25 Apr. 2014; *JP 210*; JP det.; ZMUC C-F-122689. – **Nordøstsjælland (NEZ)** • Brøndby; 55°39.089′ N, 12°24.487′ E; UB37; 22 Apr. 2016; *JP 45*; JP det.; ZMUC C-F-122520. – **Sydsjælland (SZ)** • Holtug Kalkbrud; 55°20.470′ N, 12°26.678′ E; UB33; 21 Sep. 2013; *JP 347*; JP det.; ZMUC C-F-122829.

On *Anisodactylus binotatus* (Fabricius, 1787) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Utterslev Mose; 55°42.714′ N, 12°29.907′ E; UB47; 3 Jun. 2016; *H.S. Pedersen 112*; JP det.; ZMUC C-F-122589.

On *Harpalus affinis* (Schrank, 1781) (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.282′ N, 9°26.197′ E; NH23; 16 Oct. 2014; *JP 320*; JP det.; ZMUC C-F-122798. – **Nordøstsjælland (NEZ)** • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 2 Dec. 2011; *JP 476*; JP det.; ZMUC C-F-122960.

On *Loricera pilicornis* (Fabricius, 1775) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 827*; JP det.; ZMUC C-F-123321. – **Nordøstsjælland (NEZ)** • Brønshøj (Degnemosen); 55°42.043′ N, 12°30.352′ E; UB47; 26 May 2016; *JP 288*; JP det.; ZMUC C-F-122767 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 265*; JP det.; ZMUC C-F-122744. – **Sydsjælland (SZ)** • Flommen ved Sorø; 55°25.957′ N, 11°34.477′ E; PG64; 25 Jul. 2009; *JP 77*; JP det.; ZMUC C-F-122552 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 22 Jul. 2013; *H. Enghoff 308*; JP det.; ZMUC C-F-122787.

On *Nebria brevicollis* (Fabricius, 1792) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Esrum Lund; 56°2.938′ N, 12°22.141′ E; UC31; 1–12 May 2006; *J. Høier 1571*; P. Jørum; ZMUC C-F-124332 • Lille Hareskov ved Harrevads Bro; 55°45.966′ N, 12°22.601′ E; UB38; 1–12 May 2006; *J. Høier 1573*; P. Jørum; ZMUC C-F-124334 • Nørreskoven; 55°47.865′ N, 12°23.054′ E; UB38; 1–12 Sep. 2006; *J. Høier 1572*; P. Jørum; ZMUC C-F-124333.

On *Oxypselaphus obscurus* (Herbst, 1784) (Col. Carabidae)

DENMARK – **Østjylland (EJ)** • Hampen Sø; 56°1.082′ N, 9°23.149′ E; NH20; 21 Mar. 2014; *JP 433*; JP det.; ZMUC C-F-122918. – **Fyn (F)** • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1070*; JP det.; ZMUC C-F-123587. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 8 Jul. 1993; *S. Langemark & O.E. Meyer 907*; JP det.; ZMUC C-F-123405 • ibid.; 19 Jul. 1993; *S. Langemark & O.E. Meyer 922*; JP det.; ZMUC C-F-12342 • ibid.; 16–24 Aug. 1993; *S. Langemark & O.E. Meyer 912*; JP det.; ZMUC C-F-123410 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 653*; JP det.; ZMUC C-F-123142 • ibid.; 4 Jun. 2018; *JP 1126*; JP det.; ZMUC C-F-123648 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 829*; JP det.; ZMUC C-F-123323 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1109*; JP det.; ZMUC C-F-123627 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1309*; JP det.; ZMUC C-F-123844. – **Nordøstsjælland (NEZ)** • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *H. Enghoff 267*; JP det.; ZMUC C-F-122746 • Hættingsholm; 55°49.260′ N, 12°13.967′ E; UB38; 21 Apr. 2018; *L. Thomas 1118*; JP det.; ZMUC C-F-123638 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 407*; JP det.; ZMUC C-F-122891 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 780*; JP det.; ZMUC C-F-123275 • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 30 Mar. 2019; JP 1404; JP det.; ZMUC C-F-123950. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 880*; JP det.; ZMUC C-F-123378 • Nordbredden af Skarresø; 55°39.469′ N, 11°23.147′ E; PG47; 18 Feb. 2017; *JP 339*; JP det.; ZMUC C-F-122818. – **Sydjylland (SJ)** • Draved Skov; 55°0.964′ N, 8°58.395′ E; MF99; 1 Jun. 2013; *JP 304*; JP det.; ZMUC C-F-122783 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 539*; JP det.; ZMUC C-F-123023 • Sølsted Mose; 55°1.829′ N, 8°50.351′ E; MF89; 2 Jun. 2013; *JP 488*; JP det.; ZMUC C-F-122972. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1004*; JP det.; ZMUC C-F-123511 • ibid.; 27 Apr. 2018; *JP 1082*; JP det.; ZMUC C-F-123600 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1278*; JP det.; ZMUC C-F-123808 • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; 17 Feb. 2019; *JP 1386*; JP det.; ZMUC C-F-123929.

On *Paranchus albipes* (Fabricius, 1796) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Døndalens udløb; 55°13.656′ N, 14 53.078′ E; VB92; 24 Jun. 2018; *JP 1143*; JP det.; ZMUC C-F-123666. – **Nordøstsjælland (NEZ)** • Kongens bøge, Gribskov; 56°0.755′ N, 12°22.033′ E; UC13; 20 Apr. 2018; *L. Kjær-Thomsen 1116*; JP det.; ZMUC C-F-123636.

On *Platynus assimilis* (Paykull, 1790) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Døndal; 55°13.489′ N, 14 52.936′ E; VB92; 26 May 2017; *L.K. Thomsen & L. Thomas 426*; JP det.; ZMUC C-F-122911 • Svartingedalen ved Baggeå; 55°11.740′ N, 14°45.260′ E; VB81; 23 Jun. 2018; *JP 1157*; JP det.; ZMUC C-F-123682. – **Lolland, Falster, Møn (LFM)** • Keldskov; 54°40.114′ N, 11°33.363′ E; PF66; 15 Jun. 2012; *H. Liljehult 44*; JP det.; ZMUC C-F-122519 • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 5 May 1993; *S. Langemark & O.E. Meyer 895*; JP det.; ZMUC C-F-123393 • ibid.; 12 May 1993; *S. Langemark & O.E. Meyer 104*; JP det.; ZMUC C-F-122579 • ibid.; 25 May 1993; *S. Langemark & O.E. Meyer 909*; JP det.; ZMUC C-F-123407 • ibid.; 16 Jun. 1993; *S. Langemark & O.E. Meyer 103*; JP det.; ZMUC C-F-122578 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1108*; JP det.; ZMUC C-F-123626. – **Nordøstjylland (NEJ)** • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 935*; JP det.; ZMUC C-F-123435. – **Nordøstsjælland (NEZ)** • Herthadal, Lejre; 55°36.853′ N, 11°56.621′ E; PG86; 20 May 2018; *L. Kjær-Thsen 1117*; L. Kjær-Thomsen det.; ZMUC C-F-123637 • Lille Lyngby Mose; 55°40.831′ N, 12°29.094′ E; UC20; 28 Jan. 2018; *J. Søgaard Hansen 998*; J. Søgaard Hansen det.; ZMUC C-F-123505. – **Nordvestsjælland (NWZ)** • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 757*; JP det.; ZMUC C-F-123251 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 855*; JP det.; ZMUC C-F-123350. – **Sydsjælland (SZ)** • Åshøje Overdrev; 55°26.368′ N,

12°6.359′ E; UB14; 6 Oct. 2018; *L. Kjær-Thomsen & L. Thomas 1235*; JP det.; ZMUC C-F-123762 • Østerskov ved Langebæk; 54°59.331′ N, 12°6.357′ E; UA19; 27 Mar. 2018; *JP 1020*; JP det.; ZMUC C-F-123527 • ibid.; 3 Jan. 2019; *JP 1277*; JP det.; ZMUC C-F-123807 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 22 Jul. 2013; *H. Enghoff 307*; JP det.; ZMUC C-F-122786 • ibid.; 2 Jul. 2014; *JP 382*; JP det.; ZMUC C-F-122865.

On *Platynus livens* (Gyllenhal, 1810) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14°45.096′ E; VB80; 25 Apr. 2014; *H. Liljehult 231*; JP det.; ZMUC C-F-122712. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1418*; JP det.; ZMUC C-F-123964.

On *Pterostichus oblongopunctatus* (Fabricius, 1787) (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Jonstrup Vang ved Store Sejben Mose; 55°45.452′ N, 12°22.217′ E; UB38; 1–12 Jul. 2006; *J. Høier 1575*; P. Jørum det.; ZMUC C-F-124336 • Lille Hareskov ved Harrevads Bro; 55°45.966′ N, 12°22.601′ E; UB38; 1–12 May 2006; *J. Høier 1574*; P. Jørum det.; ZMUC C-F-124335.

On *Pterostichus vernalis* (Panzer, 1796) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Øst for Østerlars; 55°9.619′ N, 14°59.763′ E; VB91; 25 Apr. 2014; *JP 211*; JP det.; ZMUC C-F-122690. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1326*; JP det.; ZMUC C-F-123865. – **Nordøstsjælland (NEZ)** • Utterslev Mose; 55°42.714′ N, 12°29.907′ E; UB47; 28 Oct. 2012; *JP 43*; JP det.; ZMUC C-F-122518. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 877*; JP det.; ZMUC C-F-123374 • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 612*; JP det.; ZMUC C-F-123100 • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 718*; JP det.; ZMUC C-F-123210 • Nordbredden af Skarresø; 55°39.469′ N, 11°23.147′ E; PG47; 18 Feb. 2017; *JP 338*; JP det.; ZMUC C-F-122817. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1001*; JP det.; ZMUC C-F-123508 • ibid.; 27 Apr. 2018; *JP 1079*; JP det.; ZMUC C-F-123597 • ibid.; 25 Apr. 2019; *JP 1444*; JP det.; ZMUC C-F-123992 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1290*; JP det.; ZMUC C-F-123822 • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1435*; JP det.; ZMUC C-F-123982.

Remarks

Laboulbenia flagellata is a binomen associated with an awkward species, described with very loose characters, waiting for a type designation and a precise delimitation of characteristics. Translation from German Peyritsch's (1873) protologue states: "bright yellowish brown, only with a blackened perithecial apex and base as well, appendages few in number (4–7), rather similar, unbranched or divided from the base, not tinged, typically exceeding the perithecial apex". In short, characteristics shared by numerous species. Moreover, Peyritsch (1873) mentioned three hosts: *Bembidium lunatum* (sic) (a host which now typically has been mentioned yielding *Laboulbenia vulgaris* or *Laboulbenia pedicellata* or perhaps some related species but never *L. flagellata*), *Anchomenus albipes* (now *Paranchus albipes*) (which is now the typical host for *L. collae*, although mixed infections with *L. flagellata* are common according to De Kesel, pers. comm.), and lastly, *Anchomenus marginatus* (now *Agonum marginatum*). The genus *Agonum* seems to be acceptable as the only one of these three genera where we find what most authors have assumed over the years to be *L. flagellata*. Therefore, an epitypification is highly desirable, where this host or any related might be considered as the mostly appropriate.

It is generally accepted by students of Laboulbeniales that *L. flagellata* is a species complex. Over the years, laboulbeniologists have been delimiting the taxon only a little better, resulting in what we

have today. However, the amount of synonyms (from five to nine, depending on the authors′ criteria) and around ten infraspecific taxa, lacking any relevance, have meanwhile proliferated to increase the confusion. De Kesel & Van Den Neucker (2005) studied the morphological plasticity of *L. flagellata* obtained from *Agonum* spp. and *Loricera pilicornis* relative to environmental factors, concluding that there is no morphological evidence for segregation of their studied samples into different species. A very initial study with molecular techniques and morphometrics, using thalli from different species of ground beetles, demonstrated the existence of two clades (Haelewaters *et al.* 2019b). These two clades separate significantly thalli from *Limodromus assimilis* (Paykull, 1790) (= *Platynus assimilis*) from those on *Agonum micans* and *Loricera pilicornis*. Unfortunately the absence of typification for the species and the broadness of its concept reduce the impact of this study because it cannot be assured that what is sequenced is certainly a *L. flagellata* because of the absence of a fair morphological characterization including iconography in the protologue.

We have had at our disposal very abundant material from Denmark which has permitted us to perceive the enormous morphological variation of thalli within the concept of *L. flagellata*. Without being able to attain significant conclusions, we present some images which eloquently exemplify the status of the "species complex". In Fig. 32 photographs of fungi from *Agonum fuliginosum* (Fig. 32A), *A. muelleri* (Fig. 32B), *Anchomenus dorsalis* (Fig. 32G), *Anisodactylus binotatus* (Fig. 32D), *Loricera pilicornis* (Fig. 32C) and *Platynus assimilis* (Fig. 32E–F) have been included. Thalli from *Agonum* spp. fit what may be broadly accepted as a "typical" *L. flagellata*; in the middle we have the thalli from *Anisodactylus* and *Loricera* Latreille, 1802 showing some interesting differences; and finally we have thalli from *Platynus* and *Anchomenus* that may represent future new species.

Laboulbenia gigantea Istvánffi, which has been considered a synonym of *L. flagellata* for a very long time, was reinstated in a recent study by Rossi & Christian (2020)

Laboulbenia giardii Cépède & F.Picard
MB#183129
Fig. 33A–B

Bulletin Scientifique de la France et de la Belgique 42: 258 (Cépède & Picard 1908, as *L. giardi*). – **Type**: [Type lost!] "Sur les tarses de *Bradycellus* (*Dichirotrichus*) *pubescens* Payk., Carolles (Manche), recueilli par l'abbé Pasquet". [France]

Diagnostic features

Cell V obtriangular, not connected with cell III. Outer appendage consisting of several slender branches, once divided from the basal cell, up to 500 µm long, dark brown towards the lower outer margin (Fig. 33A–B, arrows). Inner appendage similar to the outer, with a basal cell slightly shorter and narrower than the basal cell of outer appendage, often partially suffused with dark brown following the outer appendage darkening. Solitary antheridia on the lower parts of the inner appendage branches. Perithecial preostiolar spots black and contrasting with the pale amber-brown remainder thallus. [Detailed description: Santamaria 1998]

Distribution and hosts

Specific on *Dicheirotrichus* (Col. Carabidae); but also reported on *Agonum* (Colla 1925; Huggert 2010) and *Platynus* (Bánhegyi 1940), records that require confirmation. Only known from **Europe**: Finland, France, Germany, Greece, the Netherlands, Hungary, Italy, Spain, Sweden, Switzerland, United Kingdom, Russia (Santamaria *et al.* 1991), Belgium (De Kesel & Rammeloo 1992), and Slovakia (Rossi *et al.* 2010).

Collections examined from Denmark

On *Dicheirotrichus gustavii* Crotch, 1871 (Col. Carabidae)

DENMARK – **Fyn (F)** • Sprogø; 55°20.012′ N, 10°58.263′ E; PG23; 7 Sep. 2013; *JP 212*; JP det.; ZMUC C-F-122691. – **Sydjylland (SJ)** • Rejsby Sluse vest for Rejsby; 55°13.931′ N, 8°40.488′ E; MG72; 8 Mar. 2020; *JP 1648*; JP det.; ZMUC C-F-124371 • Rømødæmningen; 55°8.811′ N, 8°36.691′ E; MG71; 20 Apr. 2000; *H. Liljehult 86*; JP det.; ZMUC C-F-122561. – **Vestjylland (WJ)** • Myrtue; 55°33.859′ N, 8°17.845′ E; MG55; 31 Mar. 1988; *JP Dry0048*; JP det.; ZMUC C-F-124114.

Remarks

First record from Denmark. Its presence in Denmark is not surprising because this species is known from some neighbouring countries.

Laboulbenia gyrinicola Speg.
MB#190613
Fig. 33C–D

Redia 10: 34 (Spegazzini 1914). – **Type**: [Not designated] [Ind. loc.] "Comune specialmente sul margine delle elitre di *Gyrinus natator*, a Sturla presso Genova, Dodero (Coll. Mus. Civ. Genova, n. 95) e nei fossati dei dintorni di Conegliano, Veneto, sett., ott. e nov. 1912-13"; LPS. [Italy]

Diagnostic features

Thallus almost entirely darkened, nearly opaque, except for the somewhat hyaline appendages, lower receptacle and perithecial apex. Cell V obtriangular, large, more than half of the length of cell IV, not connected with cell III. Insertion cell absent, replaced by several rounded small cells giving rise to many crowded branchlets consisting of small, inflated cells, separated by dark and constricted septa. Perithecial apex bearing two horn-like outgrowths, one of them erect and hooked, the other with an arcuate and blunt apex (Fig. 33D). [Detailed descriptions: Balazuc 1971b; Majewski 1994b; Santamaria 1998; De Kesel & Werbrouck 2008]

Distribution and hosts

Occurs on Col. Gyrinidae of the genus *Gyrinus* and, less often, on *Aulonogyrus* Motschulsky, 1853 (Balazuc 1990) and *Orectochilus* Dejean, 1833 (Majewski 1994b). Reported from **Europe**: Belgium, Czech Republic, Finland, France, Hungary, Italy, Poland, Romania, Spain, Sweden, Switzerland, United Kingdom, Russia, former Yugoslavia (Santamaria *et al.* 1991), Greece (Castaldo *et al.* 2004), the Netherlands (Haelewaters *et al.* 2012), Bulgaria (Rossi *et al.* 2019a), and Austria (Rossi & Christian 2020); from Northern **Africa** (Algeria, Morocco; Maire 1916a); and from **Asia** (Yemen; Rossi *et al.* 2019a). The record from Japan (Ishikawa 1952) needs confirmation. Records from USA and Argentina included by Majewski (2008) give the impression of a misidentification of *L. gyrinidarum* Thaxt.

Collections examined from Denmark

On *Gyrinus caspius* Ménétriés, 1832 (Col. Gyrinidae)

DENMARK – **Vestjylland (WJ)** • Esbjerg; 55°29.375′ N, 8°26.363′ E; MG64; 26 May 1919; *V. Hansen Dry0154*; V. Hansen det.; ZMUC C-F-124220 • Tipperne; 55°52.452′ N, 8°14.261′ E; MG59; 3 Oct. 1974; *E. Rald Dry0155*; E. Rald det.; ZMUC C-F-124221

On *Gyrinus distinctus* Aubé, 1838 (Col. Gyrinidae)

DENMARK – **Østjylland (EJ)** • Borresø; 56°7.587′ N, 9°36.759′ E; NH32; 6 Sep. 1935; *V. Hansen Dry0156*; V. Hansen det.; ZMUC C-F-124222. – **Nordøstjylland (NEJ)** • Boelstrøm, Læsø;

57°17.480′ N, 11°4.936′ E; PJ25; 27 Jul. 1967; *Jacobsen Dry0157*; M. Holmen det.; ZMUC C-F-124223. – **Nordøstsjælland (NEZ)** • Ellemosen ved Tisvilde; 56°1.538′ N, 12°6.225′ E; UC11; 1 Sep. 1968; *O. Lomholt Dry0158*; O. Lomholt det.; ZMUC C-F-124224. – **Vestjylland (WJ)** • Nymindegab; 55°48.831′ N, 8°11.439′ E; MG48; 14 Jun. 1977; *V. Mahler Dry0159*; V. Mahler det.; ZMUC C-F-124225.

On *Gyrinus marinus* Gyllenhal, 1808 (Col. Gyrinidae)

DENMARK – **Bornholm (B)** • Gråmyr ved Gudhjem; 55°12.613′ N, 14°57.843′ E; VB91; 24 Jun. 2018; *JP 1142*; JP det.; ZMUC C-F-123665. – **Østjylland (EJ)** • Hald Sø; 56°22.778′ N, 9°21.101′ E; NH24; 16 May 1942; *P. Johnsen Dry0161*; P. Johnsen det.; ZMUC C-F-124227. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 31 May 2013; *JP 106*; JP det.; ZMUC C-F-122581, C-F-122582. – **Vestjylland (WJ)** • Birkild; 56°26.196′ N, 8°29.010′ E; MH65; 4 May 2014; *O. Mehl Dry0160*; O. Mehl det.; ZMUC C-F-124226.

On *Gyrinus paykulli* Ochs, 1927 (Col. Gyrinidae)

DENMARK – **Nordøstsjælland (NEZ)** • Ellemosen ved Tisvilde; 56°1.538′ N, 12°6.225′ E; UC11; 1 Sep. 1968; *O. Lomholt Dry0164*; O. Lomholt det.; ZMUC C-F-124230 • Jystrup, Hvidsø; 55°31.338′ N, 11°51.834′ E; PG85; 31 May 2018; *M. Holmen 1393*; M. Holmen det.; ZMUC C-F-123936 • Nordhavnstippen på Københavns Nordhavn; 55°43.091′ N, 12°37.088′ E; UB57; 29 Apr. 2018; *JP 1095*; JP det.; ZMUC C-F-123612. – **Sydsjælland (SZ)** • Herlufsholm; 55°14.687′ N, 11°45.015′ E; PG72; 2 Aug. 1932; *V. Hansen Dry0162*; V. Hansen det.; ZMUC C-F-124228. – **Vestjylland (WJ)** • Nymindegab; 55°48.831′ N, 8°11.439′ E; MG48; 14 Jun. 1977; *V. Mahler Dry0163*; V. Mahler det.; ZMUC C-F-124229.

On *Gyrinus substriatus* Stephens, 1828 (Col. Gyrinidae)

DENMARK – **Nordøstjylland (NEJ)** • Sæby Å; 57°20.379′ N, 10°29.867′ E; NJ95; Sep. 1883; *J.P. Johansen Dry0165*; J.P. Johansen det.; ZMUC C-F-124231. – **Nordøstsjælland (NEZ)** • Esrum Å; 56°3.317′ N, 12°22.381′ E; UC31; 2 Aug. 2018; *M. Holmen 1174*; M. Holmen det.; ZMUC C-F-123698 • Stasevang; 55°53.993′ N, 12°27.441′ E; UB49; 10 Aug. 1956; *Johs. Petersen Dry0166*; Johs. Petersen det.; ZMUC C-F-124232.

On *Gyrinus suffriani* Scriba, 1855 (Col. Gyrinidae)

DENMARK – **Østjylland (EJ)** • Skærså ved Ry; 56°4.566′ N, 9°46.273′ E; NH41; 15 May 1947; *K.O. Leth Dry0167*; K.O. Leth; ZMUC C-F-124233.

Remarks

First record from Denmark. *Laboulbenia gyrinicola* should be carefully compared with *Laboulbenia gyrinidarum* Thaxt., an American species, and especially with *Laboulbenia fennica* Huldén, the other European species which occurs on Gyrinidae, and with which it sometimes coexists. *Laboulbenia gyrinicola* and *L. fennica* may be well-distinguished only because the latter has short and rudimentary perithecial projections. Other characteristics mentioned in the literature for *L. fennica* are: cell III is longer than IV, and septa III–IV and VI–VII are located almost at the same level. All these characters appear to be very variable, as well as the shape of perithecial projections. Further studies using integrative taxonomy are needed to warrant the distinctiveness of *L. fennica*. In relation to this it is worth to mention that *L. fennica* has not been found in Denmark despite the significant quantity of samples reviewed.

On Col. Gyrinidae we know 34 species of *Laboulbenia*, viz.: *L. afrogyri* Balazuc (Balazuc 1975b, on *Aulonogyrus* from Africa), *L. anomala* Thaxt. (Thaxter 1899, on *Orectogyrus* Régimbart, 1884 from Africa), *L. aquatica* Thaxt. (Thaxter 1899, on *Gyretes*? Brullé, 1835 from South America), *L. bicornis* Thaxt. (Thaxter 1899, on *Dineutes* Macleay, 1825 from Africa and near east Asia), *L. birmanica* Speg. (Spegazzini 1915a, on *Orectochilus* from Burma), *L. borealis* Speg. (Spegazzini 1915a, and its synonym *L. chaetophora* Thaxt. – Thaxter 1905 –, on *Gyrinus* and *Dineutes* from Asia, North America

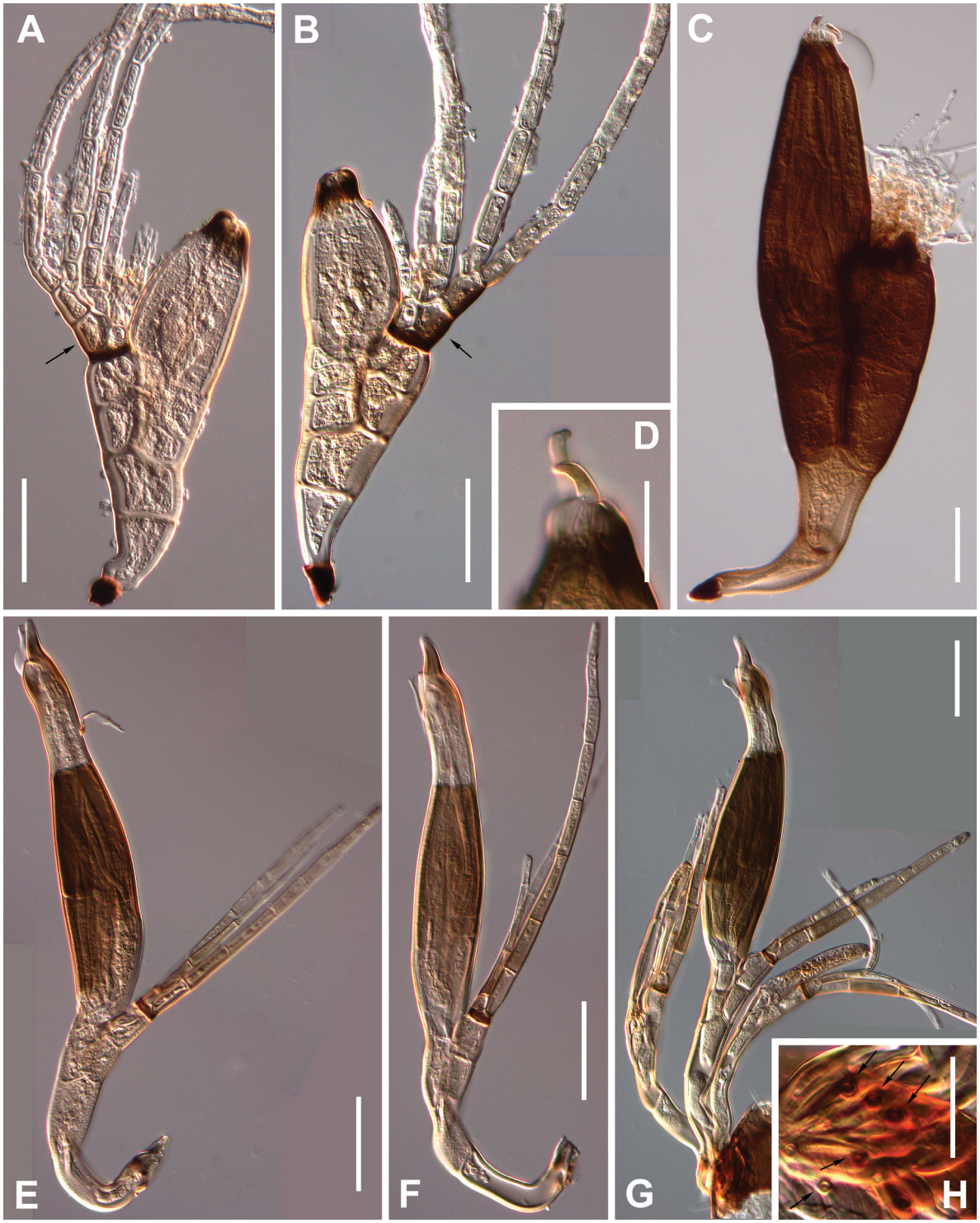

Fig. 33. *Laboulbenia* spp. **A**–**B**. *L. giardii* Cépède & F.Picard. Mature thalli showing dark lower margin of outer appendage (arrows), a diagnostic character. – **C**–**D**. *L. gyrinicola* Speg. **C**. Mature thallus. **D**. Perithecial apex with outgrowths in detail. – **E**–**H**. *L. hyalopoda* De Kesel. **E**–**F**. Mature thalli. **G**. Mature thallus accompanied by two young thalli. **H**. Dark rings (arrows) belonging to the feet of several thalli. Scale bars: A–C, E–G = 50 µm; D, H = 25 µm. Photographs from slides ZMUC C-F-122561 (A–B), ZMUC C-F-123665 (C), ZMUC C-F-123698 (D), ZMUC C-F-122889 (E–F, H), ZMUC C-F-122629 (G).

and Madagascar), *L. coarctata* Thaxt. (Thaxter 1899, on *Orectochilus* from India), *L. constricta* Thaxt. (Thaxter 1899, on *Orectogyrus* from Africa), *L. crassipes* Speg. (Spegazzini 1915a, on *Orectochilus* from Burma and India), *L. cubensis* Thaxt. (Thaxter 1899, on *Dineutes* from USA, Mexico and Cuba), *L. dactylophora* Thaxt. (Thaxter 1899, on *Orectogyrus* from Africa), *L. denticulata* Thaxt. (Thaxter 1899, on *Dineutes* from Australia), *L. desgodii* Speg. (Spegazzini 1915a, on *Orectogyrus* from Africa), *L. dineutis* Thaxt. (Thaxter 1899, on *Dineutes* from Asia, Papua New Guinea and Africa), *L. drepanalis* Thaxt. (Thaxter 1899, on *Gyretes* from Panama and USA), *L. fallax* Thaxt. (Thaxter 1899, on *Gyretes* from America), *L. fennica* Huldén (Huldén 1983, on *Gyrinus* from Europe), *L. franciscoloi* W.Rossi (Rossi 1986, on *Dineutus* from Sierra Leone), *L. funeralis* Thaxt. (Thaxter 1912a, on several genera of Gyrinidae from America), *L. guerinii* C.P.Robin (Robin 1853, on *Gyretes* from America), *L. gyrinicola*, *L. gyrinidarum* Thaxt. (Thaxter 1892, on *Gyrinus* from America), *L. heterocheila* Thaxt. (Thaxter 1899, on *Dineutes* and *Macrogyrus* Straneo, 1939 from Indonesia), *L. leathsi* Speg. (Spegazzini 1912, on *Gyrinus* from Chile), *L. leptopus* Speg. (Spegazzini 1917, on Gyrinidae from South America), *L. oberthuri* Thaxt. (Thaxter 1895, on *Orectogyrus* from Madagascar), *L. orechtochili* Thaxt. (Thaxter 1899, on *Orechtochilus* from Asia), *L. orechtochilicola* Speg. (Spegazzini 1915a, on *Orechtochilus* from Burma), *L. pachystoma* Speg. (Spegazzini 1917, on *Gyretes* from South America), *L. rotundata* Thaxt. (Thaxter 1905, on *Dineutes* from Indonesia), *L. satanas* Balazuc (Balazuc 1973c, on *Orechtochilus* from Philippines), *L. songhaiensis* W.Rossi (Rossi 1986, on *Aulonogyrus* from Sierra Leone), *L. strangulata* Thaxt. (Thaxter 1899, on *Orechtochilus* from Asia), and *L. valida* Speg. (Spegazzini 1915a, on *Orechtochilus* from Celebes).

Laboulbenia hyalopoda De Kesel
MB#446744
Fig. 33E–H

Sterbeeckia 18: 17 (De Kesel 1998). – **Type**: "HOLOTYPUS: De Kesel 991 (BR), die 28.VIII.1987, in locis Heide Kalmthout (Antverpia, Belgia), ad sternitum abdominalis Dromii linearii (Olivier) (Coleoptera, Carabidae) lectus; BR. [Belgium]

Diagnostic features

Cell V oval, slightly shorter than cell IV, not connected with cell III; its inner margin separated from perithecium at least in its distal portion. Insertion cell separated from perithecium. Outer appendage unbranched, brown. Inner appendage once divided above the basal cell, consisting of two simple, hyaline branches, both terminated by solitary, poorly distinguished antheridia. Basal cell of inner appendage much smaller than basal cell of outer appendage. Perithecium bearing a long ligula-like lip.

Distribution and hosts

This species grows hidden near or on the pygidium of *Paradromius* Dejean, 1826 (often as *Dromius*) (Col. Carabidae) from Belgium (type), Latvia (De Kesel & Krastina De Kesel 2006), United Kingdom (Lazenby 2017), Sweden and Canary Islands (Huggert 2010).

Collections examined from Denmark

On *Paradromius linearis* (Olivier, 1795) (Col. Carabidae)

DENMARK – **Fyn (F)** • Bagenkop; 54°45.201′ N, 10°40.616′ E; PF06; 5 Oct. 2016; *JP 149*; JP det.; ZMUC C-F-122629 • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 694*; JP det.; ZMUC C-F-123182. – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 3 Aug. 2019; *JP 1487*; JP det.; ZMUC C-F-124073 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1110*; JP det.; ZMUC C-F-123629. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 737*; JP det.; ZMUC C-F-123231 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 406*; JP

det.; ZMUC C-F-122889 • Syd for Veddelev; 55°40.346′ N, 12°4.915′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 335*; JP det.; ZMUC C-F-122813. – **Nordvestsjælland (NWZ)** • Halleby Å ved Bjerge Sydstrand; 55°33.194′ N, 11°10.079′ E; PG35; 24 Oct. 2018; *JP 1209*; JP det.; ZMUC C-F-123736 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1279*; JP det.; ZMUC C-F-123809.

Remarks

First record from Denmark. A photo of this species is given here for the first time. *Laboulbenia hyalopoda* often coexists with *L. notiophili* on the same host and could be suspected as a growth-form, although no morphological variation has been observed in the latter species when growing on less suitable places. We consider *L. hyalopoda* a good species with striking morphological characteristics. Molecular analysis has been suggested to confirm its distinctiveness by De Kesel *et al.* (2020). *Laboulbenia hyalopoda* grows on a very specific position of host, near the copulatory apparatus, and its transmission between hosts seems evidently correlated with mating behaviour. The foot is pale, appearing to have a lateral attachment demonstrated by the presence of dark rings (Fig. 33H, arrows).

Laboulbenia inexpectata Santam. sp. nov.
MB#840602
Fig. 34

Diagnosis

Similar to *L. argutoris* Cépède & F.Picard, but differing by the base of outer appendage which consists of 2(–3) hyaline to pale cells contrasting with darkened cells above, and by the inner appendage structure.

Etymology

The species epithet means “unexpected”, because this species was unexpectedly found among many samples of beetles of the genus *Acupalpus* where other common species may be collected (e.g., *L. inflata* and *L. stenolophi*).

Type material

Holotype
DENMARK – **Sydjylland (SJ)** • Kongens Mose; 55°0.745′ N, 8°56.557′ E; MF99; On *Acupalpus exiguus* Dejean, 1829 (Col. Carabidae); 16 Apr. 2000; *H. Liljehult 29*; JP det.; ZMUC C-F-122502.

Paratypes
DENMARK • same data as for holotype; ZMUC C-F-122503, C-F-122504, C-F-122505.

Description

Thallus brown, much darker or even blackened at preostiolar spots and foot; much paler, almost hyaline, at basal areas of appendage, ostiole, cell V and lower area of cell I. Basal cell of receptacle (I) obconical, 2–3 times as long as broad, slightly constricted at middle height, geniculate at base, almost hyaline except for the upper quarter which is variably brown as the remaining receptacle above. Suprabasal cell of receptacle (II) slightly longer than broad, gradually broadening from below upwards. Septum II–VI oblique. Cell III trapezoidal to rhomboidal, almost isodiametric. Cell V small, paler than its surroundings, situated at the upper-inner corner of cell IV and separated from it by an oblique, curved septum that does not reach septum III–IV. Insertion cell thick, deep dark brown.

Outer appendage unbranched, very long, three or more times as long as thallus length from foot to perithecial apex, consisting of 15 or more cells which are 2–4 times as long as broad each; apparently rigid (noticeable by needle manipulation when detaching the fungus from host cuticle), uniformly dark

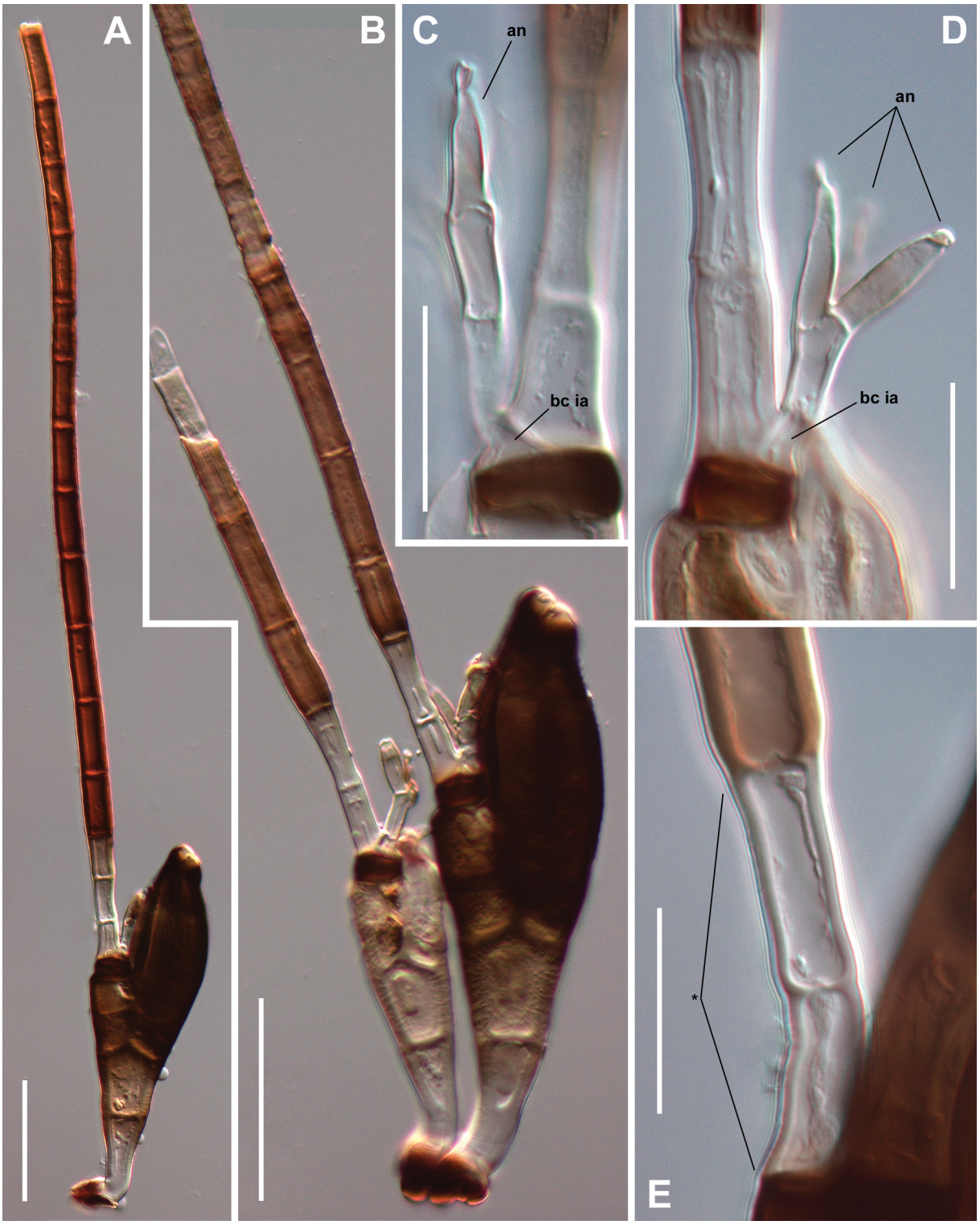

Fig. 34. *Laboulbenia inexpectata* Santam. sp. nov. **A**. Mature thallus. **B**. Paired mature and immature thalli. **C**–**D**. Inner appendage and lower part of outer appendage in detail, with labelled antheridia (an) and basal cell of inner appendage (bc ia). **E**. Lower cells of outer appendage in detail (*). Scale bars: A–B = 50 µm; C–E = 20 µm. Photographs from slides ZMUC C-F-122502 (holotype) (A–B), ZMUC C-F-122504 (C, E), ZMUC C-F-122503 (D).

brown above second, or less common, third cell, the 2(–3) lower cells (i.e., basal and suprabasal cells) hyaline or pale brown, narrower than dark cells above (Fig. 34E, *). Inner appendage short, hyaline to pale brown, consisting of a minute basal cell (about a quarter in length and half as broad than basal cell of outer appendage) (Fig. 34C–D, bc ia) supporting 1(–2) elongated cells (about 2–3 times as long as broad), bearing three elongate, slightly brownish, flask-shaped antheridia (Fig. 34C, an) forming a tripod-like structure (Fig. 34D, an). Some additional cells under the antheridia were observed in a damaged or altered inner appendage. No sterile branches have been observed.

Perithecial stalk cell (VI) flattened, as broad but shorter than adjacent cell IV. Perithecium ovoidal, with convex margins, showing confluent black preostiolar spots which form a ring below the pale ostiole, that points outwards through a truncated tip.

Length from foot to apex of perithecium 151–161 µm. Perithecium (including basal cells) 74–82 × 28–35 µm. Length from foot to tip of outer appendage (when undamaged) 348–498 µm.

Thalli were found mostly on elytra and pronotum of the hosts. Four infected beetles were found in a sun-exposed heath bog.

Remarks

This probably rare species may be compared with several other species of the genus *Laboulbenia* showing an unbranched outer appendage, a reduced inner appendage (without sterile branches), and a mostly darkened receptacle including perithecium. All these features are shared by *L. argutoris* and perhaps *L. benjaminii*, from which the new species can be separated by the structure of the appendages, especially the outer appendage, with the two hyaline basal cells, contrasting to the rest of the dark appendage.

Laboulbenia inflata Thaxt.
MB#220293
Fig. 35A

Proceedings of the American Academy of Arts and Sciences 27: 41 (Thaxter 1892). – **Type**: "On *Bradycellus rupestris* Say, South Dakota (Aldrich)"; FH. [USA]

Diagnostic features

Dioecious. Male thallus consisting of seven superposed cells, with the three distal septa brown and constricted, and the apical cell functioning as an antheridium (Fig. 35A, arrow). Female thallus with a small, oval cell V, not connected with cell III, half as long or shorter as cell IV. Outer appendage unbranched, including an inflated basal cell supporting about four cells separated by black and constricted septa. Inner appendage consisting of 2–3 branches with lower cells similar to those of the outer appendage. [Detailed descriptions: Thaxter 1896; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Infects Col. Carabidae of the genus *Acupalpus* in a broad sense (including *Stenolophus*) and *Bradycellus*. Known from **Europe**: Germany, France, Italy, Poland, Spain, United Kingdom, Greece (Majewski 2008), Belgium (De Kesel 1998), Switzerland (Hoess & Senn-Irlet 2009), Denmark (Høier 2009), Sweden (Huggert 2010), the Netherlands (Haelewaters *et al.* 2014), Bulgaria (Rossi *et al.* 2019a), and Hungary (Rossi & Christian 2020); **America**: USA (Thaxter 1892), Brazil (Balazuc 1974c), and the Galapagos Archipelago (Arndt & Desender 2002). The record of *L. acupalpi* (now *L. stenolophi*) from South Korea should belong here (Majewski 2008).

Collections examined from Denmark

On *Acupalpus dubius* Schilsky, 1888 (Col. Carabidae)

DENMARK – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 715*; JP det.; ZMUC C-F-123207. – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG61; 21 May 2017; *JP 422*; JP det.; ZMUC C-F-122907.

On *Acupalpus exiguus* Dejean, 1829 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 833*; JP det.; ZMUC C-F-123327 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1313*; JP det.; ZMUC C-F-123848. – **Nordøstsjælland (NEZ)** • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 864*; JP det.; ZMUC C-F-123360 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 630*; JP det.; ZMUC C-F-123119 • Ryegård Dyrehave; 55°40.500′ N, 11°50.851′ E; PG77; 2 Dec. 2014; *JP 346*; JP det.; ZMUC C-F-122828 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 28 Feb. 2017; *H. Liljehult 359*; JP det.; ZMUC C-F-122842. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 569*; JP det.; ZMUC C-F-123055 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 775*; JP det.; ZMUC C-F-123270. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 882*; JP det.; ZMUC C-F-123380 • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 716*; JP det.; ZMUC C-F-123208 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 637*; JP det.; ZMUC C-F-123126. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 492*; JP det.; ZMUC C-F-122976 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1281*; JP det.; ZMUC C-F-123812 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 963*; JP det.; ZMUC C-F-123470.

On *Acupalpus flavicollis* (Sturm, 1825) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 834*; JP det.; ZMUC C-F-123328 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1315*; JP det.; ZMUC C-F-123851. – **Nordøstsjælland (NEZ)** • Asserbo Plantage; 56°1.984′ N, 12°0.817′ E; UC11; 28 Apr. 2019; *JP 1457*; JP det.; ZMUC C-F-124008 • Gentofte; 55°44.005′ N, 12°33.020′ E; UB47; 28 May 2018; *A.A. Illum 1115*; JP det.; ZMUC C-F-123635 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 863*; JP det.; ZMUC C-F-123359 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1028*; JP det.; ZMUC C-F-123539. – **Nordvestsjælland (NWZ)** • Eriksminde syd for Korshage; 55°57.744′ N, 11°46.504′ E; PH70; 27 Oct. 2019; *JP 1536*; JP det.; ZMUC C-F-124295. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 28 Feb. 2015; *JP 447*; JP det.; ZMUC C-F-122932 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 964*; JP det.; ZMUC C-F-123471.

Remarks

Santamaria (1996b) studied this species and suggested its dioecious nature arguing that diminutive thalli attached at the foot with thalli bearing perithecia were males, with the uppermost cell functioning as a simple, solitary, flask-shaped phialide. The presence of diminutive thalli paired to thalli bearing a perithecium but lacking antheridia was reported in other species of *Laboulbenia*, a few of which are found in Europe (Rossi & Santamaria 2008). Haelewaters *et al.* (2019b) cast doubts on this statement but De Kesel *et al.* (2020) accept the dioecy since their drawings highlight it.

Fig. 35. *Laboulbenia* spp. **A**. *L. inflata* Thaxt. Female thallus paired with a diminutive male (arrow). – **B**–**C**. *L. kajanensis* Huldén. Mature thalli. – **D**–**E**. *L. lecoareri* (Balazuc) Huldén. **D**. Paired mature and young thalli. **E**. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122828 (A), ZMUC C-F-122697 (B), ZMUC C-F-123372 (C), ZMUC C-F-123475 (D–E).

Laboulbenia kajanensis Huldén
MB#108113
Fig. 35B–C

Karstenia 23: 56 (Huldén 1983). – **Type**: "Holotype. Slide L. Huldén 3, Collecting data of the host: Finland. Ok: Paltamo, 23.V.1949, leg. Hellman. Host. *Pterostichus diligens* (Sturm) (Coleoptera, Carabidae). The parasite was found on the left side of the prothorax"; MZH.

Diagnostic features

Cell V very narrow, shorter than cell IV, not connected with cell III. Outer appendage unbranched. Inner appendage slender and shorter than the outer, consisting of a small basal cell giving rise to 3–4 branchlets terminated with antheridia or to a single sterile branch in old thalli. Usually, the appendages appear bent in relation to the perithecial axis. Perithecium with dorsal margin straight in contrast to curved ventral margin. [Detailed description: Majewski 1994b]

Distribution and hosts

Only known from Finland, Poland (Majewski 1994b), and Belgium (De Kesel *et al.* 2020) on *Pterostichus* (*Argutor*) *diligens* and *P.* (*A.*) *strenuus* (Panzer) (Col. Carabidae). Thalli grow on the ventral side of the left margin of prothorax.

Collections examined from Denmark

On *Pterostichus diligens* (Sturm, 1824) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Tokkekøb Hegn; 55°52.334′ N, 12°22.229′ E; UB39; 6 May 2013; *JP 329*; JP det.; ZMUC C-F-122807. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 216*; JP det.; ZMUC C-F-122697. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 876*; JP det.; ZMUC C-F-123372. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1421*; JP det.; ZMUC C-F-123967.

Remarks

First record from Denmark. A photo of this species is given here for the first time. This species seems to be restricted to grow on the left prosternum of its hosts. In this regard as well as in the peculiar positioning of appendages, this species resembles *L. contorta* Thaxt. (Santamaria 1998) and *L. chionophila* Santam. (Santamaria *et al.* 2020a).

Laboulbenia lecoareri (Balazuc) Huldén
MB#104411
Fig. 35D–E

Karstenia 25: 6 (Huldén 1985). – **Basionym**: *Laboulbenia subterranea* subsp. *lecoareri* Balazuc, *Bulletin Mensuel de la Société Linnéenne de Lyon* 43(8): 306 (Balazuc 1974e) [MB#352876]. – **Type**: "Hôte: *Trechoblemus micros* (Herbst) (Col. Carab. *Trechidae*),… Une centaine d'exemplaires … proviennent d'une ancienne carrière souterraine de gypse voisine du carrefour du Tremble en fôret de l'Isle-Adam (Val-d'Oise, commune de Nerville)"; PC. [France]

Diagnostic features

Cell V obtriangular, half or less of the length of cell IV, not connected with cell III. Outer appendage unbranched, very elongated, up to 500 µm long, consisting of many variably long cells, where the basal

and suprabasal cells are distinctively narrow and paler than the ones above. Inner appendage absent. Insertion cell thick and separated from the perithecial wall. [Detailed description: Majewski 1994b]

Distribution and hosts

Typically infesting *Trechoblemus micros* (Col. Carabidae) (often as *Trechus*) but also mentioned on *Thalassophilus longicornis* (Sturm, 1825) (Balazuc 1990) from France, Germany, Hungary, Norway, Poland, United Kingdom (Santamaria *et al.* 1991), Belgium (De Kesel 1998), Ukraine (Majewski 2008) and Switzerland (Hoess & Senn-Irlet 2009).

Collections examined from Denmark

On *Trechoblemus micros* (Herbst, 1784) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Gedser Strand; 54°33.588′ N, 11°58.187′ E; PF95; 27 Jun. 1903; *Chr. Engelhart Dry0054*; Chr. Engelhart det.; ZMUC C-F-124120. – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 968*; JP det.; ZMUC C-F-123475.

Remarks

First record from Denmark. A photo of this species is given here for the first time. This species could be suspected of being dioecious because of the presence of diminutive, likely male thalli paired with normal ones (Fig. 35D) and the absence of an inner appendage. Nevertheless, Balazuc's drawings (1974e: fig. 51d–e) display a very minute basal cell of inner appendage, sometimes giving rise to a very thin branch weirdly divided into squarish cells; he also illustrated an accompanying diminutive thallus. Majewski (1994b) described an inner appendage but did not support it with figures. De Kesel *et al.* (2020) drew this inner appendage in one of their figures. Perhaps the inner appendage is caducous and disappears with maturation of thalli.

Laboulbenia leisti J.Siemaszko & Siemaszko
MB#269178
Fig. 36A–B

Polskie Pismo Entomologiczne 6: 203 (Siemaszko & Siemaszko 1928). – **Type**: [Type destroyed!] "In elytris *Leisti rufescentis* F. Poloniae, Pulawy. I.P.". [Poland]

Diagnostic features

Cell V obtriangular, half or less of the length of cell IV, not connected with cell III. Outer appendage unbranched, up to 700 µm long, the 2–3 lower cells contrasting by their darker or paler colour from the cells above. Inner appendage consisting of a small number of variably elongated branches, ramified from the base, supporting paired or solitary dark antheridia (Fig. 36B, an). Basal cell of inner appendage slightly shorter than the outer. [Detailed descriptions: Majewski 1994b; Weir 1994; Santamaria 1998]

Distribution and hosts

On Col. Carabidae of the genus *Leistus*. This is a species only known from **Europe**: Poland, Spain, France, Belgium, United Kingdom, Germany, Hungary, Romania, Finland (Majewski 2008), Denmark (Høier 2009), Switzerland (Hoess & Senn-Irlet 2009), Sweden (Huggert 2010), Czech Republic, Slovakia (Rossi *et al.* 2010), and the Netherlands (Haelewaters *et al.* 2012). De Kesel *et al.* (2020) reported *L. leisti* on *Agonum muelleri* from Belgium, a host record which requires confirmation.

Collections examined from Denmark

On *Leistus ferrugineus* (Linnaeus, 1758) (Col. Carabidae)

DENMARK – **Fyn (F)** • Fyns Hoved; 55°36.736′ N, 10°35.706′ E; PG06; 4 Jan. 2015; *K.B. Nielsen 281*; JP det.; ZMUC C-F-122760. – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 136*; JP det.; ZMUC C-F-122612. – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 254*; JP det.; ZMUC C-F-122734. – **Sydsjælland (SZ)** • Holtug Kalkbrud; 55°20.470′ N, 12°26.678′ E; UB33; 21 Sep. 2013; *JP 348*; JP det.; ZMUC C-F-122830 • Stevns Fyr nord for Vindehuse; 55°17.420′ N, 12°27.183′ E; UB33; 19 Nov. 2014; *JP 156*; JP det.; ZMUC C-F-122635.

Remarks

Thalli of *Laboulbenia leisti* collected in Denmark are well-distinguished by the appendage structure which agrees with that described by Majewski (1994b).

Laboulbenia lichtensteinii F.Picard
MB#222216
Fig. 36C–D

Bulletin Scientifique de la France et de la Belgique 50: 449 (Picard 1917; as *L. lichtensteini*). – **Type**: [Type lost!] "Sur le thorax, les élytres et les pattes de *Cillenus lateralis* Curt., … trouvés en juin 1915 à Roscof (Finistère) par M. Jean Lichtenstein". [France]

Diagnostic features

Cell V obtriangular, similar in size and shape to cell IV. Septum IV–V vertical, connected with septum III–IV. Insertion cell forming a black horizontal furrow. Appendages get damaged early, can only be seen to be well-organised in young thalli (Fig. 36D). Outer appendage consisting of 3–4 simple, short branches, arising from an irregular and almost flattened basal cell; basal and dorsal margins darkened. Inner appendage consisting of 1–2 simple branches, each bearing one solitary antheridium; basal cell minute. Perithecium ovoidal, with a broadly obtuse apex filled with joining irregular black spots [Detailed description: Santamaria 1998]

Distribution and hosts

Exclusive on the Col. Carabidae *Cillenus lateralis* (sometimes as *Bembidion* in old literature), a bizarre carabid stenotopic for sheltered, usually estuarine, mudflats with fine sand or gravel on the upper middle and upper shores. Typically found under stones or deposits of *Ulva* and *Enteromorpha* on or near the strandline, but can withstand considerable periods of immersion in saltwater. It feeds largely on talitrids. It is a suboceanic southern-temperate species found on coasts from southern Denmark and the British Isles south to the Iberian Peninsula and North Africa but not in the Eastern Mediterranean (Anderson & McFerran 2001). The fungus has been reported in France (type), Spain (Santamaria 1993b), United Kingdom (Weir 1996), and the Netherlands (Haelewaters *et al.* 2012). The record from Belgium by De Kesel (1998) is erroneous because the host was truly collected in the Netherlands according to De Kesel *et al.* (2020).

Collections examined from Denmark

On *Cillenus lateralis* Samouelle, 1819 (Col. Carabidae)

DENMARK – **Fyn (F)** • Sprogø; 55°20.012′ N, 10°58.263′ E; PG23; 7 Sep. 2013; *JP 101*; JP det.; ZMUC C-F-122576. – **Sydjylland (SJ)** • Sønderstrand på Rømø; 55°6.373′ N, 8°29.380′ E; MG60; 14 Mar. 2020; *JP 1615*; JP det.; ZMUC C-F-124364.

Remarks

First record from Denmark. *Laboulbenia lichtensteinii* is related to other species of the *L. pedicellata*-complex. The appendage is the more remarkable characteristic, similar to the appendage of *L. egens* (Santamaria 1998). It is a rare species that should only be sought where its particular host is found.

Laboulbenia littoralis De Kesel & Haelew.
MB#801461
Fig. 36E–F

Mycologia 106 (3): 409 (De Kesel & Haelewaters 2014a). – **Type**: "Holotype.– BELGIUM, WEST-VLAANDEREN: Knokke-Heist, Zwin estuary, 28 Apr. 2012, parasite on tibia of male *Cafius xantholoma* (Gravenhorst, 1806) (Coleoptera, Staphylinidae, Staphylininae, Staphylinini, Philonthina), A. De Kesel 5152b (BR–MYCO 171396-94)"; BR.

Diagnostic features

Cell V trapezoidal, similar in size and shape to cell IV. Septum IV–V vertical, connected with septum III–IV. Basal cell of outer appendage swollen and similar or slightly longer than cell IV, twice as long as the basal cell of inner appendage, separated from the outer branch by a thick, black and constricted septum. Appendages not exceeding the tip of perithecium, crowded in mature thalli with a few distinctively brown antheridia (Fig. 36F, an). Dorsal side of the receptacle bent outwards at the junction of cells II and III. Perithecium with large black preostiolar spots.

Distribution and hosts

Only known from the original description (De Kesel & Haelewaters 2014a), on *Cafius* (Col. Staphylinidae) from Belgium, the Netherlands, France and Italy.

Collections examined from Denmark

On *Cafius xantholoma* (Gravenhorst, 1806) (Col. Staphylinidae Staphylininae)
DENMARK – **Fyn (F)** • Knudshoved; 55°18.212′ N, 10°49.828′ E; PG13; 11 Nov. 2018; *JP 1225*; JP det.; ZMUC C-F-123752 • Sprogø; 55°20.012′ N, 10°58.263′ E; PG23; 7 Sep. 2013; *JP 100*; JP det.; ZMUC C-F-122575. – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.305′ N, 12°17.042′ E; UB20; 2 May 2018; *JP 1102*; JP det.; ZMUC C-F-123620. – **Nordøstsjælland (NEZ)** • Liseleje; 56°1.048′ N, 11°58.454′ E; PH81; 7 Oct. 2018; *JP 1203*; JP det.; ZMUC C-F-123730. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 23 Sep. 2018; *JP 1177*; JP det.; ZMUC C-F-123701 • Klinteby Klint; 55°11.579′ N; 11°32.489′ E; PG61; 10 Sep. 2016; *JP 121*; JP det.; ZMUC C-F-122598.

Remarks

First record from Denmark. A photo of this species is given here for the first time. According to De Kesel & Haelewaters (2014a), *Laboulbenia littoralis* is a sister species of *L. slackensis* and may be distinguished from it by (1) the stouter thallus, (2) the swollen outer appendage basal cell which is equal to or taller than cell IV and twice as long as the inner appendage basal cell, and (3) the outwards bent receptacle. *Laboulbenia littoralis* seems to be restricted to *Cafius xantholoma*, whereas *L. cafii* occurs on species of the genus *Remus*. Our observations with Danish specimens agree with this statement (see under *L. cafii*).

Fig. 36. *Laboulbenia* spp. **A**–**B**. *L. leisti* J.Siemaszko & Siemaszko. **A**. Mature thallus with lower area of appendages in detail (B) with labelled antheridia (an). – **C**–**D**. *L. lichtensteinii* F.Picard. **C**. Mature thallus. **D**. Upper part of an immature thallus showing the young appendage. – **E**–**F**. *L. littoralis* De Kesel & Haelew. **E**. Mature thallus. **F**. Antheridia (an) in detail. – **G**–**I**. *L. luxurians* Peyr. **G**–**H**. Mature thalli with labelled cells III, IV, insertion cell (ic), and the black spot on the upper dorsal side of cell I (arrow). **I**. Appendage from an immature thallus in detail. Scale bars: A–C, E, G–I = 50 µm; D, F = 25 µm. Photographs from slides ZMUC C-F-122760 (A–B), ZMUC C-F-122576 (C–D), ZMUC C-F-123730 (E–F), ZMUC C-F-123642 (G–H), ZMUC C-F-123515 (I).

Laboulbenia luxurians Peyr.
MB#193932
Fig. 36G–I

Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1 68: 248 (Peyritsch 1873). – **Type**: [Type lost?!] "Auf *Bembidium varium* Oliv., und zwar sowohl den Flügeldecken als den Extremitäten". [Austria, according to Balazuc 1974c]

Laboulbenia compacta Thaxt. (Thaxter 1892: 37) [MB#242044]
Laboulbenia confusa Thaxt. (Thaxter 1895: 476) [MB#241977]
Laboulbenia marvinii Huldén (Huldén 1985: 8) [MB#104412]

Diagnostic features

Thallus stocky. Cell II broad and enlarged distally. Cell III flattened, strongly oblique. Cells IV and V larger; the outer margin of cell IV longer than the outer margin of cell III. Basal cells of primary appendage flattened. The two lower septa in the outer appendage dark and constricted. Insertion cell not blackened, with the same colour as surrounding cells (Fig. 36H, ic). [Detailed descriptions: Huldén 1985; Majewski & Sugiyama 1985; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Reported on *Bembidion* (Col. Carabidae), usually on members of the subgenus *Notaphus*. Widespread in **Europe**: Austria, France, Germany, Hungary, Italy, Poland, Romania, Spain, Switzerland, Russia (Santamaria *et al.* 1991), Latvia (De Kesel & Krastina De Kesel 2006), Slovakia (Rossi & Máca 2006), the Netherlands (Haelewaters *et al.* 2014); **Africa**: Algeria (Maire 1920); **America**: USA (Thaxter 1892), Argentina (Thaxter 1912a); and **Asia**: Japan (Majewski & Sugiyama 1985).

Collections examined from Denmark

On *Bembidion dentellum* (Thunberg, 1787) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14 45.096′ E; VB80; 13 Jun. 1991; *V. Mahler Dry0057*; V. Mahler det.; ZMUC C-F-124123.

On *Bembidion varium* (Olivier, 1795) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.270′ N, 12°15.392′ E; UB20; 6 Jun. 2018; *JP 1121*; JP det.; ZMUC C-F-123642. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1008*; JP det.; ZMUC C-F-123515 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1587*; JP det.; ZMUC C-F-124348.

Remarks

First record from Denmark. Often confused and sometimes synonymized with *Laboulbenia pedicellata*, however clearly differs from it by several features as: (1) the black spot on the upper dorsal side of cell I (Fig. 36G–H, arrows), (2) the cell III is distinctly shorter than cell IV (Fig. 36H), and (3) the insertion cell is not blackened as it usually occurs in most species of *Laboulbenia* (Fig. 36H, ic). In immature thalli, the typically crowded appendages appear to be leaning on the young perithecium where the trichogyne is found (Fig. 36I). Not all the diagnostic features reported here are present in the drawings associated with the short original description, i.e., cell III is not flattened and strongly oblique in Peyritsch (1873: fig. 10), which is the only mature thallus in which this cell is visible.

Laboulbenia manubriolata Thaxt.
MB#190687
Figs 37A–B, 105A

Proceedings of the American Academy of Arts and Sciences 51: 44 (Thaxter 1915). – **Type**: "On various parts of a small Carabid allied to *Tachys*. No. 2081d (Type) on elytra. Samarang. Java"; FH.

Diagnostic features

Cell II and upper part of cell I tuberculate (Fig. 37A). Cell V obtriangular, twice as long as cell IV, not connected with cell III. Outer appendage unbranched, with the basal cell forming a distinctive blunt outgrowth on its outer margin (Fig. 37A–B, arrows). Inner appendage consisting of 2–3 once divided branches arising directly from the basal cell and terminated by solitary antheridia which in overmature thalli degenerate to develop sterile, variably elongated branches. [Detailed descriptions: Santamaria 1998; Majewski 2006]

Distribution and hosts

On *Perigona nigriceps* (Col. Carabidae) (sometimes as *Tachys* in old literature), an invasive ground beetle introduced by timber trade in **Europe**: Finland (Huldén 1983), Portugal (Santamaria 1998), United Kingdom (Weir 1996), and Poland (Majewski 2006); **Asia**: Sri Lanka, Indonesia (Thaxter 1915), China (Rossi 1982b), Korea (Lee 1986), Japan (Terada 2000), Taiwan (Terada *et al.* 2004), Thailand (Rossi & Bernardi 2018), and Cambodia (Kong *et al.* 2020).

Collections examined from Denmark

On *Perigona nigriceps* (Dejean, 1831) (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 824*; JP det.; ZMUC C-F-123318. – **Nordøstsjælland (NEZ)** • Nærum; 55°48.616′ N, 12°32.706′ E; UB48; 13 Nov. 2016; *JP 127*; JP det.; ZMUC C-F-122604 • ibid.; 23 Mar. 2017; *JP 238*; JP det.; ZMUC C-F-122718.

Remarks

First record from Denmark.

Laboulbenia melanaria Thaxt.
MB#219945
Fig. 37C–D

Proceedings of the American Academy of Arts and Sciences 35: 186 (Thaxter 1899). – **Type**: "On *Diachromus germanus* Linn., Hope Coll. No. 319, Portugal"; FH. [type according to Thaxter 1908: 338]

Laboulbenia heroica Speg. (Spegazzini 1914: 60) [MB#226172]

Diagnostic features

Cell V rounded in outline, broader than long, paler than surroundings, half or less of the length of cell IV, not connected with cell III. Insertion cell separated from the perithecium. Outer appendage once divided above the suprabasal cell into two elongate, up to 450 µm long, branches; dorsal margins often shaded in the basal portion. Inner appendage of immature thalli consisting of two simple branches bearing solitary terminal antheridia. Perithecium blackened, subopaque, free. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 1998]

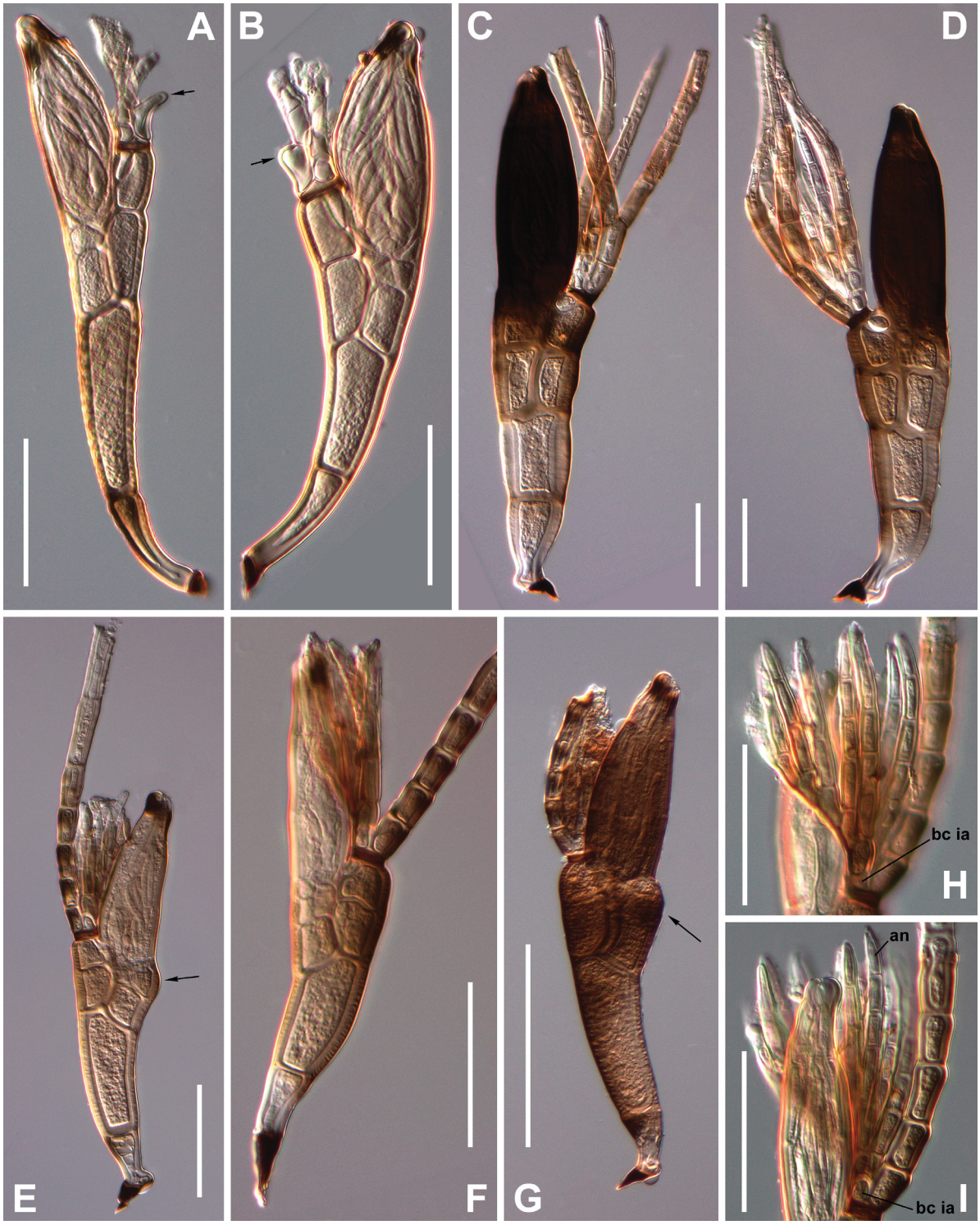

Fig. 37. *Laboulbenia* spp. **A**–**B**. *L. manubriolata* Thaxt. Mature thalli with labelled outgrowth on basal cell of outer appendage (arrows). – **C**–**D**. *L. melanaria* Thaxt. Mature thalli. – **E**–**I**. *L. metableti* Scheloske. **E**–**G**. Mature thalli with protuberant cell VII labelled with arrows in E and G. **H**–**I**. Inner appendage in detail with two focus levels, near in H, far in I; "bc ia" is the basal cell of inner appendage, "an" is an antheridium. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122604 (A–B), ZMUC C-F-124124 (C–D), ZMUC C-F-123103 (E), ZMUC C-F-123072 (F), ZMUC C-F-123384 (G), ZMUC C-F-122626 (H–I).

Distribution and hosts

Mostly on *Diachromus germanus* (Col. Carabidae), but also reported on other carabids belonging to the Harpalinae like *Anisodactylus*, *Ophonus* and *Pseudophonus*. The record on *Bembidion* (Hoess & Senn-Irlet 2009) require confirmation. Recorded from **Europe**: Italy, France, Portugal, Switzerland, Russia, Poland, Romania, former Czechoslovakia, Austria, Spain, Bulgaria (Majewski 2008), and the Netherlands (Haelewaters *et al.* 2012); **Africa**: Morocco (Maire 1916a); **Asia**: Turkey (Balazuc 1974c), and Korea (Lee *et al.* 2011). The record from Belgium by De Kesel (1998) should be removed from this country according to De Kesel *et al.* (2020) because it corresponds to a sample collected in France.

Collections examined from Denmark

On *Diachromus germanus* (Linnaeus, 1758) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Nykøbing Falster; 54°46.434′ N, 11°51.911′ E; PF87; 1865; *E. Benzon Dry0058*; E. Benzon det.; ZMUC C-F-124124.

Remarks

First record from Denmark. This is a well-distinguished and widespread species but appears to be very uncommon in Denmark where the record is from a collection of 1865. Moreover, this apparent rarity is primarily due to the fact that the host (*Diachromus*) is considered extinct in Denmark and has not been found for more than 150 years.

Laboulbenia metableti Scheloske
MB#332780
Fig. 37E–I

Parasitologische Schriftenreihe 19: 124 (Scheloske 1969). – **Type**: "Auf den Elytren sowie der Unterseite von Thorax und Abdomen von *Metabletus* (= *Blechrus*) *foveatus* und *M. truncatellus*, zwei kleinen, auf sandingen, trockenen Wiesen und Feldern lebenden Laufkäfern (Col. Carabidae), die ich bei Schwand/Nürnberg und Erlangen erbeutete. Deutschland. Holotypus Abb. 29". [Germany]

Diagnostic features

Cell V obtriangular, minute, usually paler than its surroundings, half or less of the length of cell IV, not connected with cell III. Outer appendage unbranched, with the 4–5 lower cells (including the basal) slightly bulging, darkened towards the dorsal and upper margins. Inner appendage consisting of two branches directly arising from the basal cell; each branch with 5–6 superposed cells which, pointing towards the same side, bear each simple 2–3 celled branches terminated with elongated slender antheridia (Fig. 37H–I). Basal cell of inner appendage half the length of the outer. Cell VII typically protuberant under the perithecium (Fig. 37E–G, arrows).

Distribution and hosts

This species occurs on species of *Syntomus* (=*Metabletus* Schmidt-Goebel, 1846, =*Blechrus* Motschulsky, 1847) (Col. Carabidae) from Germany (type), Poland (Majewski 1972a), Italy (Rossi & Cesari Rossi 1976), Finland, Russia (Huldén 1983), France (Balazuc 1990), Belgium (De Kesel & Rammeloo 1992), and the Netherlands (Haelewaters & De Kesel 2020). Records referring of *Laboulbenia notiophili* Cépède & Picard or *Laboulbenia casnoniae* Thaxt. from *Metabletus* and *Syntomus* should be included here; this concerns records from Hungary (Bánhegyi 1950), Andorra (Balazuc *et al.* 1982), Spain (Santamaria 1989), United Kingdom (Weir 1996), Austria, Morocco (Rossi & Santamaria 2006), Switzerland (Hoess & Senn-Irlet 2009), and Sweden (Huggert 2010).

Collections examined from Denmark

On *Syntomus foveatus* (Geoffroy, 1785) (Col. Carabidae)

DENMARK – **Fyn (F)** • Bagenkop; 54°45.201′ N, 10°40.616′ E; PF06; 5 Oct. 2016; *JP 147*; JP det.; ZMUC C-F-122626 • Knudshoved Marina; 55°17.781′ N, 10°50.542′ E; PG12; 18 Oct. 2017; *JP 586*; JP det.; ZMUC C-F-123072. – **Lolland, Falster, Møn (LFM)** • Bøtø Plantage; 54°37.629′ N, 11°57.661′ E; PF95; 17 May 2017; *JP 416*; JP det.; ZMUC C-F-122900 • Gedser Odde; 54°33.588′ N, 11°58.187′ E; PF95; 19 Jul. 2011; *JP 152*; JP det.; ZMUC C-F-122632 • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 458*; JP det.; ZMUC C-F-122943 • Nykøbing; 54°46.279′ N, 11°52.845′ E; PF87; 17 May 2017; *JP 410*; JP det.; ZMUC C-F-122894 • Ulvshale; 55°2.301′ N, 12°16.244′ E; UB20; 25 Sep. 2016; *JP 144*; JP det.; ZMUC C-F-122622. – **Nordøstsjælland (NEZ)** • Nordøst for Bispebjerg Station; 55°42.508′ N, 12°32.786′ E; UB47; 18 Aug. 2016; *JP 116*; JP det.; ZMUC C-F-122593. – **Nordvestsjælland (NWZ)** • Sandflugtsplantage ved Rørvig; 55°57.126′ N, 11°43.060′ E; PH60; 4 Nov. 2017; *JP 712*; JP det.; ZMUC C-F-123202. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1006*; JP det.; ZMUC C-F-123513.

On *Syntomus truncatellus* (Linnaeus, 1761) (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Stenholtsvang; 55°57.439′ N, 12°21.204′ E; UC30; 28 Oct. 2017; *JP 615*; JP det.; ZMUC C-F-123103. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 886*; JP det.; ZMUC C-F-123384 • Sonnerup Skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 259*; JP det.; ZMUC C-F-122739.

Remarks

First record from Denmark. After the review of *Laboulbenia casnoniae* Thaxt. (Rossi & Santamaria 2006), *L. metableti* was included among the synonyms of *L. notiophili*. Reported as a separate species by De Kesel & Rammeloo (1992), it was later neglected, being included within the scope of *L. casnoniae* or *L. notiophili* even though in most references it was mentioned as a peculiar, perhaps separate species. De Kesel *et al.* (2020) reinstated *L. metableti* as a separate species. We agree with this judgement after the study of the abundant material from Denmark. Certainly, it is well-characterized by several features as the arrangement of the appendage system, especially by the inner appendage (Fig. 37H–I), which matches that described and illustrated by De Kesel *et al.* (2020). Even at the low magnification of a dissecting microscope the species stands out because of the characteristic way the inner set of appendages appears to wrap the perithecia (Fig. 37F).

Laboulbenia murmanica Huldén
MB#108114
Fig. 38A–D

Karstenia 23: 57 (Huldén 1983). – **Type**: "Holotype. Slide L. Huldén 4, Collecting data of the host: U.S.S.R. Murmansk Region: Konozero, leg. Edgren. Host. *Bembidion transparens* (Gebler) (Coleoptera, Carabidae). The parasite was found on the right elytron of the host"; MZH. [Russia]

Diagnostic features

Receptacle distinctly constricted at the septum between cell II and cells III/VI (Fig. 38A–C, arrows). Cell II inflated and broadest halfway up. Cell V oval, large, shorter than cell IV, not connected with cell III. Outer appendage simple to slightly branched, not exceeding the perithecial apex, with the basal cell separated from cells above by a moderately darkened septum. Inner appendage consisting of a few branches terminated by solitary antheridia (Fig. 38D). Basal cell of inner appendage shorter or similar than basal cell of outer appendage, which also has a darkened septum above. [Detailed description: Majewski 1994b]

Distribution and hosts

After its description from Russia, *L. murmanica* has been found on species of *Bembidion* (Col. Carabidae) from Poland (Majewski 1990b), United Kingdom (Weir 1996), Belgium (De Kesel 1998), Lithuania (Markovskaja 2004), and Denmark (Høier 2009).

Collections examined from Denmark

On *Bembidion assimile* Gyllenhal, 1810 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 656*; JP det.; ZMUC C-F-123145 • ibid.; 4 Jun. 2018; *JP 1128*; JP det.; ZMUC C-F-123651 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1320*; JP det.; ZMUC C-F-123856. – **Nordøstsjælland (NEZ)** • Munkholmbroen; 55°67.361′ N, 11°80.738′ E; PG77; 4 May 2019; *L. Kjær-Thomsen & L. Thomas 1471*; JP det.; ZMUC C-F-124051 • Nivå Bugt Strandenge; 55°55.737′ N, 12°31.267′ E; UC40; 9 Dec. 2018; *L. Kjær-Thomsen & L. Thomas 1245*; JP det.; ZMUC C-F-123773 • Nordhavnstippen på Københavns Nordhavn; 55°43.091′ N, 12°37.088′ E; UB57; 29 Apr. 2018; *JP 1092*; JP det.; ZMUC C-F-123609 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1056*; JP det.; ZMUC C-F-123573. – **Nordvestjylland (NWJ)** • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 776*; JP det.; ZMUC C-F-123271. – **Nordvestsjælland (NWZ)** • Halleby Å ved Bjerge Sydstrand; 55°33.194′ N, 11°10.079′ E; PG35; 24 Oct. 2018; *JP 1210*; JP det.; ZMUC C-F-123737. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1368*; JP det.; ZMUC C-F-123908 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1448*; JP det.; ZMUC C-F-123997 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1286*; JP det.; ZMUC C-F-123818.

On *Bembidion biguttatum* (Fabricius, 1779) (Col. Carabidae)

DENMARK – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1588*; JP det.; ZMUC C-F-124349.

On *Bembidion doris* (Panzer, 1796) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *H. Liljehult 1169*; JP det.; ZMUC C-F-123694.

On *Bembidion varium* (Olivier, 1795) (Col. Carabidae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 709*; JP det.; ZMUC C-F-123199. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1321*; JP det.; ZMUC C-F-123857. – **Nordvestjylland (NWJ)** • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 778*; JP det.; ZMUC C-F-123273. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1369*; JP det.; ZMUC C-F-123910 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1289*; JP det.; ZMUC C-F-123821.

Remarks

This species seems very common in Denmark. May coexist on the same host with *L. vulgaris* or *L. pedicellata*.

Laboulbenia notiophili Cépède & F.Picard
MB#148452
Fig. 38E–G

Bulletin Scientifique de la France et de la Belgique 42: 259 (Cépède & Picard 1908). – **Type**: [Type lost!] "Sur les élytres, le prothorax et la tête de *Notiophilus semipunctatus* F., Mortain (Manche). Exemplaires recueillis par M. l'abbé Pasquet". [France]

Laboulbenia baetica Balazuc, Espadaler & Girbal (Balazuc *et al.* 1982: 416) [MB#114237]
Laboulbenia blanchardii Cépède (Cépède 1914: 373; as *L. blanchardi*) [MB#222483]
Laboulbenia cymindicola Speg. (Spegazzini 1914: 37) [MB#250379]
Laboulbenia pulchella Speg. (Spegazzini 1914: 39) [MB#145851]

Diagnostic features

Thallus dark except for cell I and, sometimes, cell V. Cell V obtriangular, small, half or less of the length of cell IV, not connected with cell III. Outer appendage unbranched, with the lower cells (including the basal cell) variably darkened, especially towards the dorsal margin. Inner appendage consisting of two branches directly arising from the basal cell, terminated by solitary or a cluster of slender antheridia (Fig. 38F, an). [Detailed descriptions: Weir 1994; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Widespread in Europe and North Africa on Col. Carabidae of the genera *Notiophilus*, *Cymindis*, *Demetrias*, *Dromius*, *Pseudotrechus* Rosenhauer, 1856, *Philorhizus*, *Metadromius*, *Calodromius* Reitter, 1905, *Ophionea*? Klug, 1821, *Homethes*? Newman, 1842 and *Aeptomus*? Found in **Europe**: Andorra, Austria, Bulgaria, Finland, France, Germany, Hungary, Italy, Norway, Poland, Romania, Russia, Spain, Sweden, Switzerland, United Kingdom, former Yugoslavia (Santamaria *et al.* 1991), Portugal (Santamaria 1992b), Belgium (De Kesel 1998), Czech Republic (Rossi & Máca 2006), Denmark (Høier 2009), the Netherlands (Haelewaters *et al.* 2012), and **Africa**: Algeria and Morocco (Santamaria *et al.* 1991).

Collections examined from Denmark

On *Demetrias imperialis* (Germar, 1824) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1310*; JP det.; ZMUC C-F-123845. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1280*; JP det.; ZMUC C-F-123811.

On *Notiophilus aestuans* Dejean, 1826 (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 141*; JP det.; ZMUC C-F-122618.

On *Notiophilus biguttatus* (Fabricius, 1779) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 12 May 1993; *S. Langemark & O.E. Meyer 900*; JP det.; ZMUC C-F-123398 • ibid.; 7 Jun. 1993; *S. Langemark & O.E. Meyer 899*; JP det.; ZMUC C-F-123397 • ibid.; 16 Jun. 1993; *S. Langemark & O.E. Meyer 915*; JP det.; ZMUC C-F-123413 • ibid.; 8 Jul. 1993; *S. Langemark & O.E. Meyer 905*; JP det.; ZMUC C-F-123403 • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 548*; JP det.; ZMUC C-F-123034 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1307*; JP det.; ZMUC C-F-123842. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 928*; JP det.; ZMUC C-F-123428 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 938*; JP det.; ZMUC C-F-123440 • Havgranerne i Tofte Skov; 56°50.576′ N, 10°15.552′ E; NJ70; 19 Sep.–2 Oct. 2013; *I.*

Fig. 38. *Laboulbenia* spp. **A**–**D**. *L. murmanica* Huldén. **A**–**C**. Mature thalli showing constriction at septum II–VI/III (arrows). **D**. Immature thallus showing undamaged appendage. – **E**–**G**. *L. notiophili* Cépède & F.Picard. **E**, **G**. Mature thalli. **F**. Inner appendage in detail showing antheridia (an) and basal cell of inner appendage (bc ia). – **H**–**I**. *L. olisthopi* Speg. **H**. Mature thallus. **I**. Two immature thalli with labelled cell V. Scale bars: A–E, G–I = 50 µm; F = 25 µm. Photographs from slides ZMUC C-F-123145 (A–B), ZMUC C-F-123271 (C), ZMUC C-F-123651 (D), ZMUC C-F-122541 (E–F), ZMUC C-F-122545 (G), ZMUC C-F-122637 (H–I).

Aggerholm 924; JP det.; ZMUC C-F-123422. – **Nordøstsjælland (NEZ)** • Brønshøj; 55°42.234′ N, 12°30.135′ E; UB47; 8 May 2016; *JP 64*; JP det.; ZMUC C-F-122541 • Gribskov, Nederste Koppel; 56°2.749′ N, 12°20.077′ E; UC31; 1–31 May 2014; *J. Heilmann-Clausen et al. 162*; P. Jørum det.; ZMUC C-F-122641 • Tokkekøb Hegn; 55°52.334′ N, 12°22.229′ E; UB39; 6 May 2013; *JP 330*; JP det.; ZMUC C-F-122808. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1373*; JP det.; ZMUC C-F-123914 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1274*; JP det.; ZMUC C-F-123804.

On *Notiophilus germinyi* Fauvel, 1863 (Col. Carabidae)

DENMARK – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 929*; JP det.; ZMUC C-F-123429.

On *Notiophilus palustris* (Duftschmid, 1812) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1308*; JP det.; ZMUC C-F-123843. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 942*; JP det.; ZMUC C-F-123446. – **Nordøstsjælland (NEZ)** • Asserbo Plantage; 56°1.984′ N, 12°0.817′ E; UC11; 28 Apr. 2019; *JP 1456*; JP det.; ZMUC C-F-124007. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1416*; JP det.; ZMUC C-F-123962 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1275*; JP det.; ZMUC C-F-123805.

On *Notiophilus rufipes* Curtis, 1829 (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Nordøst for Bispebjerg Station; 55°42.508′ N, 12°32.786′ E; UB47; 18 Aug. 2016; *JP 114*; JP det.; ZMUC C-F-122591 • Rådvad; 55°48.338′ N, 12°33.589′ E; UB48; 13 Nov. 2016; *JP 126*; JP det.; ZMUC C-F-122603 • Vanløse; 55°41.443′ N, 12°28.058′ E; UB47; 15 Jan. 2018; *J. Søgaard Hansen 995*; J. Søgaard Hansen det.; ZMUC C-F-123502.

On *Paradromius linearis* (Olivier, 1795) (Col. Carabidae)

DENMARK – **Fyn (F)** • Bagenkop; 54°45.201′ N, 10°40.616′ E; PF06; 5 Oct. 2016; *JP 149*; JP det.; ZMUC C-F-122628 • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 694*; JP det.; ZMUC C-F-123183. – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 3 Aug. 2019; *JP 1487*; JP det.; ZMUC C-F-124072 • Ulvshale; 55°2.636′ N, 12°15.638′ E; UB20; 26 May 2018; *JP 1110*; JP det.; ZMUC C-F-123628. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; JP 737; JP det.; ZMUC C-F-123230 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 406*; JP det.; ZMUC C-F-122890 • Syd for Veddelev; 55°40.346′ N, 12°4.915′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 335*; JP det.; ZMUC C-F-122814 • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 138*; JP det.; ZMUC C-F-122614. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 572*; JP det.; ZMUC C-F-123058. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 878*; JP det.; ZMUC C-F-123375 • Halleby Å ved Bjerge Sydstrand; 55°33.194′ N, 11°10.079′ E; PG35; 24 Oct. 2018; *JP 1209*; JP det.; ZMUC C-F-123735. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1279*; JP det.; ZMUC C-F-123810 • ibid.; 54°59.421′ N, 12°6.435′ E; UA19; 19 Aug. 2019; *JP 1500*; JP det.; ZMUC C-F-124087.

On *Paradromius longiceps* (Dejean, 1826) (Col. Carabidae)

DENMARK – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1585*; JP det.; ZMUC C-F-124346.

On *Philorhizus melanocephalus* (Dejean, 1825) (Col. Carabidae)

DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 16 Feb. 2018; *JP 976*; JP det.; ZMUC C-F-123483. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 695*; JP det.; ZMUC C-F-123184. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1311*; JP det.; ZMUC C-F-123846. – **Nordøstsjælland (NEZ)** • Ejby Ådal; 55°42.292′ N, 11°50.465′ E; PG77; 16 Feb. 2019; *L. Kjær-Thomsen & L. Thomas 1395*; JP det.; ZMUC C-F-123938 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 15 Jun. 2013; *JP 229*; JP det.; ZMUC C-F-122710. – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 17 May 2019; *JP 1468*; JP det.; ZMUC C-F-124048 • Stold Skydeterræn; 55°45.124′ N, 11°17.634′ E; PG48; 25 May 2014; *JP 377*; JP det.; ZMUC C-F-122860 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 643*; JP det.; ZMUC C-F-123131. – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 965*; JP det.; ZMUC C-F-123472. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1258*; JP det.; ZMUC C-F-123786.

On *Philorhizus sigma* (Rossi, 1790) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Dueodde; 54°59.442′ N, 15 4.510′ E; WA09; 2 Jul. 2007; *JP 69*; JP det.; ZMUC C-F-122545. – **Østjylland (EJ)** • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015; *JP & H. Liljehult 516*; JP det.; ZMUC C-F-122999 • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; 24 Nov. 2019; *JP 1546*; JP det.; ZMUC C-F-124307. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP & H. Liljehult 696*; JP det.; ZMUC C-F-123185. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1312*; JP det.; ZMUC C-F-123847. – **Nordøstsjælland (NEZ)** • Strødam; 55°58.056′ N, 12°16.273′ E; UC20; 4 Oct. 2014; *JP 40*; JP det.; ZMUC C-F-122515. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 219*; JP det.; ZMUC C-F-122700. – **Sydjylland (SJ)** • Sølsted Mose; 55°1.829′ N, 8°50.351′ E; MF89; 2 Jun. 2013; *JP 486*; JP det.; ZMUC C-F-122970. – **Sydsjælland (SZ)** • Bimose i Broby Overdrev; 55°23.921′ N, 11°35.499′ E; PG64; 5 Aug. 2014; *JP 41*; JP det.; ZMUC C-F-122516 • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Apr. 2019; *H. Liljehult 1470*; JP det.; ZMUC C-F-124050 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 966*; JP det.; ZMUC C-F-123473.

Remarks

Species of *Laboulbenia* on European Lebiini were a true taxonomical problem until Rossi & Santamaria (2006) proposed that *L. casnoniae* should be regarded as an exclusively American species occurring only on *Colliuris* De Geer, 1774 (Col. Carabidae Lebiinae). Moreover, all previous European and North African records of *L. casnoniae* should be named with the prioritary name *L. notiophili*, including other species as synonyms (see above). De Kesel *et al.* (2020) suggested the need for a molecular analysis to confirm this status, especially for the material on *Demetrias* that could belong to *L. blanchardii* as a separate species.

Laboulbenia olisthopi Speg.

MB#243319

Fig. 38H–I

Redia 10: 55 (Spegazzini 1914; as *L. olistopi*). – **Type**: "On *Olistopus sturmii* from Saxony in Germany"; LPS. [Type according to Balazuc 1975a]

Diagnostic features

Thallus olive brown. Cell V oval, similar in length but half as broad as cell IV, connected with septum III–IV (Fig. 38I). Outer appendage unbranched. Inner appendage consisting of several short branches terminated by solitary or paired antheridia (Fig. 38I) which may be replaced by elongated sterile appendages in old thalli (Fig. 38H). Basal cell of inner appendage slightly smaller than basal cell of outer appendage. [Detailed descriptions: Balazuc 1975a; Santamaria 1998]

Distribution and hosts

On species of the genus *Olisthopus* (= *Odontonyx* Stephens, 1827) (Col. Carabidae) in Europe, Canary Islands (Arndt & Santamaria 2004), and Madeira (Balazuc 1975a). Records from **Europe**: Germany (type), Italy (Spegazzini 1914), Switzerland (Baumgartner 1923), France (Balazuc 1975a), and Spain (Santamaria 1989). Records from Poland (Majewski 2006) and Ukraine (Majewski 2008) may correspond to *L. polyphaga* (see below).

Collections examined from Denmark

On *Olisthopus rotundatus* (Paykull, 1790) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 15 Nov. 2010; *JP 158*; JP det.; ZMUC C-F-122637. – **Sydsjælland (SZ)** • Vordingborg; 55°0.395′ N, 11°54.682′ E; PF89; 23 Apr. 1990; *JP Dry0050*; JP det.; ZMUC C-F-124116.

Remarks

First record from Denmark. The distinctiveness of this species has been subject of debate. In the original description, Spegazzini (1914) offered a too brief diagnosis and blurred photographs of four deeply darkened thalli. Neither with the description nor with the images, the shape and layout of cell V was well-defined. Balazuc (1975a) and Santamaria (1998) described *L. olisthopi* including a cell V as large as cell IV and connected with septum III–IV.

Polish and Ukrainian thalli depicted by Majewski (2006) seem to be different from those by Balazuc and Santamaria, but according to the Polish author they are much closer to Spegazzini's species, supporting his argument with the identity of the host, *Olisthopus sturmii* (Duftschmid, 1812), which was the same as for the type from nearby Germany, whereas thalli from the hosts mentioned by Balazuc and Santamaria according to Majewski should belong, to other species, also because they were from Madeira and Southern European areas, far from the Central European type.

Among the studied Danish material, some thalli found on *Amara apricaria* (Paykull, 1790) have given us a clue to the mess involving three species: *L. olisthopi*, *L. polyphaga* and *L. ophoni*. Thus, Majewski (1994b) classified under *L. polyphaga* some Polish thalli found on *Amara* (including *A. apricaria*). To check Majewski's determination we proceeded to request a loan of the *L. polyphaga* type from the Farlow Herbarium. The type slide of *Laboulbenia polyphaga* from FH (see explanation under *L. ophoni*) includes six thalli in poor condition (Fig. 39C). The study of these thalli convinced us that the material published by Majewski (2006) as *L. olisthopi* belongs to *L. polyphaga*. Furthermore, as we will explain in the paragraphs devoted to *L. ophoni*, the thalli on *Amara* which Majewski classified as *L. polyphaga* instead correspond to *L. ophoni*.

Laboulbenia oodiphila Huldén
MB#108115
Fig. 39A–B

Karstenia 23: 57 (Huldén 1983). – **Type**: "Holotype. Slide L. Huldén 5, Collecting data of the host: Finland. Al: Finström, 30.VI.1943, leg. Hakan Lindberg. Host. *Oodes helopiodes* (Fabricius) (Coleoptera, Carabidae). The parasite occurs on the anterior margin of the left elytron and the left mesofemur, accidentally on the coxae or other parts of the elytra"; MZH.

Diagnostic features

Lower receptacle (cells I and II) forming a long pedicel where cell II is 3–4 times as long as broad. Cell V small, obtriangular to oval, about half the length or less of cell IV, not connected with cell III. Outer appendage unbranched or once ramified above the second cell. Inner appendage consisting of a large basal cell bearing 1–2 antheridial branchlets which later proliferate into sterile appendages. [Detailed description: Majewski 1994b]

Distribution and hosts

Known from the carabid genus *Oodes* in Finland (type), Poland, Ukraine (Majewski 1994b), Switzerland (Hoess & Senn-Irlet 2009), Bulgaria, Italy, China (Rossi *et al.* 2019a), and Austria (Rossi & Christian 2020).

Collections examined from Denmark

On *Oodes helopioides* (Fabricius, 1792) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Bastemose i Almindingen; 55°7.554′ N, 14°56.560′ E; VB90; 28 Jun. 1994; *JP Dry0053*; JP det.; ZMUC C-F-124119. – **Nordøstsjælland (NEZ)** • Trørød Mose; 55°50.383′ N, 12°32.598′ E; UB49; 19 Jun. 1955; *Johs. Petersen Dry0052*; Johs. Petersen det.; ZMUC C-F-124118.

Remarks

First record from Denmark. The distribution of this species is patchy, from Southern Europe to far China, probably by lack of exploration, but the record from Denmark is not surprising because of its previous records from neighbouring countries.

Laboulbenia ophoni Thaxt.
MB#236083
Fig. 39D–G

Proceedings of the American Academy of Arts and Sciences 35: 190 (Thaxter 1899). – **Type**: "On *Harpalus sulphuripes* Germ. from Italy"; FH. [type according to Majewski 2008]

Diagnostic features

Thallus pale yellowish brown. Cell V oval, similar in length to cell IV, connected with septum III–IV (Fig. 39D–F) or, very rarely, short and then not connected (Fig. 39G). Outer appendage once or twice divided from the suprabasal cell. Inner appendage consisting of a basal cell bearing one to several branches terminated by clustered antheridia (Fig. 39F). Basal cell of inner appendage half as long than basal cell of outer appendage. Perithecium with two preostiolar spots merged in a contrasting black ring. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 1998]

Fig. 39. *Laboulbenia* spp. **A**–**B**. *L. oodiphila* Huldén. Mature thalli. – **C**. *L. polyphaga* Thaxt. Broken mature thallus from type slide kept in FH, collected on *Olisthopus parmatus*. – **D**–**G**. *L. ophoni* Thaxt. **D**–**E**. Mature thalli from *Harpalus* and *Ophonus*, respectively. **F**. Immature thallus showing appendages in detail and labelled basal cell of inner appendage (bc ia). **G**. Mature thallus from *Amara apricaria*. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124118 (A–B), FH8460 (C) (lectotype), ZMUC C-F-122500 (D), ZMUC C-F-124115 (E–F), ZMUC C-F-122776 (G).

Distribution and hosts

The typical hosts belong to Col. Carabidae of the genera *Ophonus*, *Carterus* Dejean & Boisduval, 1829 and *Harpalus*, but this fungus has been also reported on *Amara*, *Dolichus* Bonelli, 1810, *Scybalicus* Schaum, 1862, *Europhilus* Chaudoir, 1859 and *Agonum* (Majewski 2008). Known from **Europe**: Finland, France, Germany, Hungary, Italy, Poland, Romania, Spain, Sweden, Switzerland, Russia (Santamaria *et al.* 1991), United Kingdom (Cannon *et al.* 1985), Belgium (De Kesel 1998), Lithuania (Markovskaja 2000), Sweden (Huggert 2010), and Slovakia (Rossi *et al.* 2010). Also in North **Africa** from Algeria (Thaxter 1899).

Collections examined from Denmark

On *Amara apricaria* (Paykull, 1790) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Botanisk Have i København; 55°41.214′ N, 12°34.289′ E; UB47; 18–25 Jul. 2013; *JP & O. Karsholt 297*; JP det.; ZMUC C-F-122776.

On *Harpalus affinis* (Schrank, 1781) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Brønshøj; 55°42.234′ N, 12°30.135′ E; UB47; 18 Aug. 2018; *JP 1170*; JP det.; ZMUC C-F-123695.

On *Harpalus rubripes* (Duftschmid, 1812) (Col. Carabidae)
DENMARK – **Sydsjælland (SZ)** • Klinteby Klint; 55°11.579′ N, 11°32.489′ E; PG61; 19 Apr. 2015; *H. Liljehult 27*; JP det.; ZMUC C-F-122500.

On *Ophonus melletii* (Heer, 1837) (Col. Carabidae)
DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 700*; JP det.; ZMUC C-F-123189.

On *Ophonus puncticeps* Stephens, 1828 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.569′ N, 11°21.958′ E; PF55; 18 Aug. 2018; *JP 1171*; JP det.; ZMUC C-F-123696.

On *Ophonus rufibarbis* (Fabricius, 1792) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°59.171′ N, 12°31.954′ E; UA49; 12 May 2018; *J. Kypke et al. Dry0049*; JP det.; ZMUC C-F-124115 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1316*; JP det.; ZMUC C-F-123852.

On *Ophonus rupicola* (Sturm, 1818) (Col. Carabidae)
DENMARK – **Sydsjælland (SZ)** • Klinteby Klint; 55°11,579′ N, 11 32,489′ E; PG61; 19 Apr. 2015; *H. Liljehult 26*; JP det.; ZMUC C-F-122499.

Other material examined

Lectotype of *Laboulbenia polyphaga* (here designated) (MycoBank MBT10002233)
UNITED STATES • "*Laboulbenia polyphaga*, slide from FH, #8460, barcode 00313730, "type", on *Olisthopus parmatus* Say., from York, Maine, York County (USA), 29–06–1892"; lectotype: FH[00313730] (here designated) (MycoBank MBT10002233). [consists of six mature thalli in poor condition. (Fig. 39C)]

Remarks

First record from Denmark. In species of the genus *Laboulbenia* the trait "septum IV–V connected with septum III–IV" versus "… not connected…" is considered mostly invariable and exclusive, and exceptions to this rule have rarely been documented. However, *L. ophoni* is one of these species, where in some, but not all specimens septum IV–V does not reach septum III–IV.

Thalli we have found on *Amara apricaria* [C-F-122777] are relevant for this discussion. The species of *Laboulbenia* reported on *Amara* are: *L. aubryi*, *L. flagellata*, *L. polyphaga*, and *L. ophoni*. The latter was reported on *Amara* by Weir (1996) from Great Britain and by Rossi *et al.* (2010) from Slovakia, although in the latter case with the reservation of "to be confirmed" because of the variability observed in septum IV–V. Danish thalli on *Amara* agree with Slovakian thalli and also vary in this feature but the remaining characters fit very well with the description of typical *L. ophoni* (Fig. 39G).

Of the three remaining species found on *Amara*, *L. polyphaga* deserves our special attention because it is significant to the discussion of *L. ophoni*. The status and distinctiveness of *L. polyphaga* is a real headache. *Laboulbenia polyphaga* was loosely described by Thaxter (1893, 1896) who wrote: "this form, although presenting no striking peculiarities of structure, seems sufficiently well defined to warrant its separation as a distinct species". Furthermore, Thaxter added the sentence "it is nearly allied to *L. pterostichi*", which indeed is highly surprising, even shocking. Thaxter described *L. polyphaga* from a very diverse material without specifying a type, i.e., on *Olisthopus*, *Stenolophus* (including *Agonoderus*, sometimes treated as a separate genus), *Badister*, *Harpalus*, *Bradycellus*, and *Amara*. Over the years, the list of records and hosts for *L. polyphaga* increased significantly, becoming absolutely overwhelming (Santamaria *et al.* 1991; Majewski 2008). Balazuc (1974e) also wrote an extensive explanation about the confusion concerning this taxon. Lastly, Majewski (1994b) related this species with others having simple outer appendage like *L. benjaminii*, *L. notiophili* (as *L. casnoniae*), and *L. eubradycelli*, and suggested the possibility of a collective species. Although some Polish thalli on *Amara* show an outer appendage once divided above the second cell, Majewski (1994b) classified his thalli from *Amara* and *Trichotichnus* Morawitz, 1863 as *L. polyphaga* in line with other records (Bánhegyi 1940; Balazuc 1974e; Sugiyama 1973; De Kesel & Rammeloo 1992), defining its own characteristics in contradiction to some parts of Thaxter's description but accepting others like that where a ± copiously branched appendage is mentioned. Majewski's Polish and our Danish thalli on *Amara* are identical.

Trying to solve this confusion, we decided to request from FH the loan of Thaxter's original slides (see above under other material examined). According to curatorial staff in that herbarium, only one slide labelled as the "type" of *L. polyphaga* exists. Probably remaining material published by Thaxter has not been registered under the name *L. polyphaga*. One explanation we can think of is that Thaxter was not absolutely convinced about its determination and never labelled his slides as *L. polyphaga*, so that these are difficult to find in FH databases. With the single slide received, we decided for the lectotypification of *L. polyphaga* because some of the included thalli seem to be the same as those illustrated by Thaxter (1896: pl. XV, figs 18–21), especially that of fig. 18 which is similar to, if not the very same that we have photographed from the borrowed slide (Fig. 39C).

In conclusion, we suggest that *L. polyphaga* should be restricted to thalli growing on *Olisthopus*, with dark brown thalli, unbranched outer appendage, inner appendage bearing a tuft of few antheridia lacking sterile branches, and a small, bright coloured cell V, located in the inner-upper corner of cell IV and separated from this by an oblique septum not reaching the septum III–IV. For comparison of these thalli with *L. olisthopi*, also on *Olisthopus*, refer above to the proper paragraph of this species.

Laboulbenia parriaudii Balazuc ex Santam.
MB#446188
Fig. 40A–B

Flora Mycologica Iberica 4: 122 (Santamaria 1998). – **Type**: "Balazuc herbarium. Sur *Bledius* (*Blediodes*) *arenarius* (Paykull), France, Dept. Gironde: Gujan [No.68.14]"; PC.

Laboulbenia parriaudii Balazuc (Balazuc 1974d: 257) (nom. inval.) [MB#316145]

Diagnostic features

Cell V trapezoidal, similar in size and shape to cell IV, connected with septum III–IV. Outer appendage simple or once branched, with the distal septum of the basal cell darkened and constricted (Fig. 40A–B, arrows). Inner appendage deteriorating with maturation of the thallus. Basal cell of inner appendage shorter than basal cell of outer appendage. [Detailed description: Santamaria 1998]

Distribution and hosts

Only known on *Bledius* (Col. Staphylinidae Oxytelinae) from France and Spain (Santamaria 1989).

Collections examined from Denmark

On *Bledius fergussoni* Joy, 1912 (Col. Staphylinidae Oxytelinae)

DENMARK – **Bornholm (B)** • Dueodde; 54°59.442′ N, 15°4.510′ E; WA09; 2 Jul. 2007; *JP 67*; JP det.; ZMUC C-F-122543. – **Lolland, Falster, Møn (LFM)** • Busemarke Mose; 54°57.459′ N, 12°27.054′ E; UA39; 28 Aug. 2019; *JP 1508*; JP det.; ZMUC C-F-124096. – **Nordøstsjælland (NEZ)** • Hornbæk Strand; 56°5.602′ N, 12°28.504′ E; UC41; Jun. 1898; *F. de Tengnagel Dry0133*; M. Hansen det.; ZMUC C-F-124200.

Remarks

First record from Denmark. *Laboulbenia parriaudii* is similar to *L. pedicellata* and *L. luxurians*. An accurate description of appendages is not yet available because they deteriorate with thalli ageing, and the required immature thalli have not yet been found. Therefore, antheridia are unknown and remain undescribed.

Laboulbenia pedicellata Thaxt.
MB#219334
Fig. 40C–H

Proceedings of the American Academy of Arts and Sciences 27: 44 (Thaxter 1892). – **Type**: "On *Bembidium* sp., Maine"; FH. [USA]

Laboulbenia gracilipes Cépède & F.Picard. (Cépède & Picard 1907: 780) [MB#182939]
Laboulbenia gibbulosa Speg. (Spegazzini 1915b: 55) [MB#183213]
Laboulbenia tapirina R.K.Benj. & Shanor (Benjamin & Shanor 1952: 126) [MB#299202]

Diagnostic features

Cell V variably oval, as long as cell IV, connected with septum III–IV. Outer appendage variably branched above the suprabasal cell; septa at the lower side in outer branch thick and dark, with blackened suffusion spreading through the dorsal margin (Fig. 40G, arrow). Inner appendage consisting of numerous branches bearing lateral solitary antheridia. Basal cell of inner appendage slightly shorter than basal cell of outer appendage. [Detailed descriptions: Thaxter 1896; Huldén 1985; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Common on many species of the genus *Bembidion* in a broad sense, and on *Dyschirius* (Col. Carabidae). Occurrence on other hosts are likely wrong or require verification. Widespread, only unknown in Oceania (Santamaria *et al.* 1991; Majewski 2008). Recent records are from Denmark (Høier 2009), Switzerland (Hoess & Senn-Irlet 2009), Slovakia (Rossi *et al.* 2010), Sweden (Huggert 2010), the Netherlands (Haelewaters *et al.* 2012), Israel, Ecuador (Barragán *et al.* 2013), Bulgaria, Cyprus (Rossi *et al.* 2019a), Ukraine (Haelewaters *et al.* 2019b), and Cambodia (Kong *et al.* 2020).

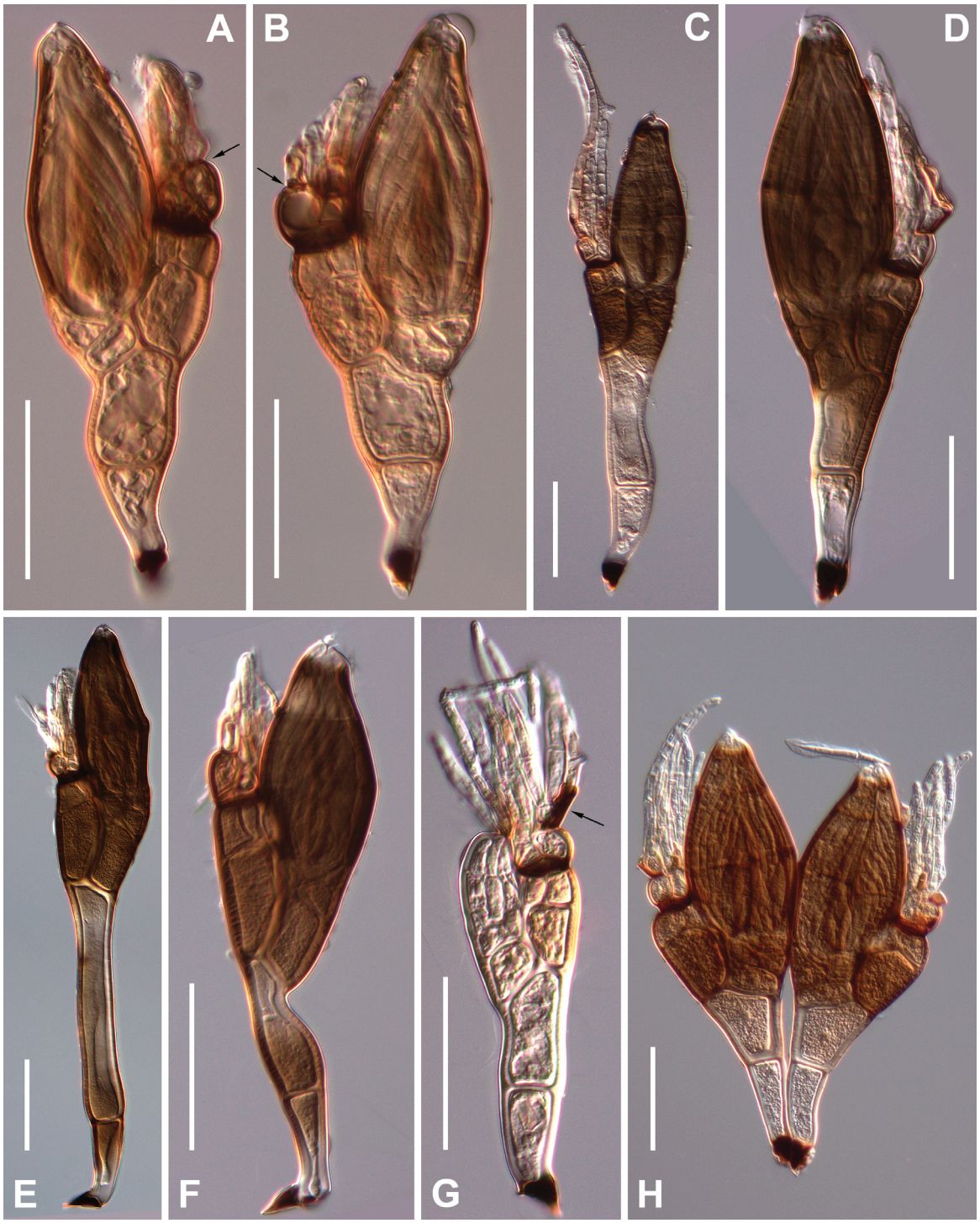

Fig. 40. *Laboulbenia* spp. **A**–**B**. *L. parriaudii* Balazuc ex Santam. Mature thalli showing the distal septum of the basal cell darkened and constricted (arrows), a diagnostic character. – **C**–**H**. *L. pedicellata* Thaxt. Mature thalli, except the immature one represented in G showing the septum at the lower side in outer branch thick and dark, with blackened suffusion spreading through the dorsal margin (arrow). **C**–**D**. From *Bembidion aeneum*. **E**. From *Bembidion doris*. **F**. From *Bembidion minimum*. **G**–**H**. From *Bembidion mannerheimi*. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124096 (A–B), ZMUC C-F-122506 (C–D), ZMUC C-F-122492 (E), ZMUC C-F-123118 (F), ZMUC C-F-123132 (G), ZMUC C-F-123391 (H).

Collections examined from Denmark

On *Bembidion aeneum* Germar, 1824 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Resle Skov; 54°56.359′ N, 11°43.437′ E; PF79; 25 Sep. 2006; *H. Liljehult 1461*; JP det.; ZMUC C-F-124012. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 740*; JP det.; ZMUC C-F-123234 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 409*; JP det.; ZMUC C-F-122893 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 628*; JP det.; ZMUC C-F-123117. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 573*; JP det.; ZMUC C-F-123059 • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *K.B. Nielsen 218*; JP det.; ZMUC C-F-122699 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 779*; JP det.; ZMUC C-F-123274. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 873*; JP det.; ZMUC C-F-123369 • ibid.; 30 Dec. 2013; *K.B. Nielsen 30*; JP det.; ZMUC C-F-122506. – **Sydjylland (SJ)** • Ballum Sluse; 55°7.866′ N, 8°41.125′ E; MG70; 26 Oct. 2017; *H. Liljehult 872*; JP det.; ZMUC C-F-123368.

On *Bembidion assimile* Gyllenhal, 1810 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1128*; JP det.; ZMUC C-F-123651. – **Nordøstsjælland (NEZ)** • Nordhavnstippen på Københavns Nordhavn; 55°43.091′ N, 12°37.088′ E; UB57; 29 Apr. 2018; *JP 1092*; JP det.; ZMUC C-F-123609 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1056*; JP det.; ZMUC C-F-123573. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1448*; JP det.; ZMUC C-F-123996.

On *Bembidion biguttatum* (Fabricius, 1779) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Skelsmyre i Rønne Plantage; 55°4.375′ N, 14°45.096′ E; VB80; 25 Apr. 2014; *JP 508*; JP det.; ZMUC C-F-122991. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1129*; JP det.; ZMUC C-F-123652 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 837*; JP det.; ZMUC C-F-123332 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1322*; JP det.; ZMUC C-F-123858. – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 22 Apr. 2018; *JP 1038*; JP det.; ZMUC C-F-123554. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1287*; JP det.; ZMUC C-F-123819.

On *Bembidion doris* (Panzer, 1796) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Ravnsholt; 54°57.415′ N, 11°15.306′ E; PF49; 24 Aug. 2018; *L. Kjær-Thomsen 1176*; JP det.; ZMUC C-F-123700 • Ulvshale; 55°3.218′ N, 12°15.801′ E; UB20; 10 Jun. 2017; *JP 429*; JP det.; ZMUC C-F-122914. – **Nordøstsjælland (NEZ)** • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1223*; JP det.; ZMUC C-F-123750 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 19*; JP det.; ZMUC C-F-122492.

On *Bembidion gilvipes* Sturm, 1825 (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Stålmosen, Vindinge; 55°37.379′ N, 12°8.322′ E; UB16; 12 Apr. 1979; *H.J. Petersen Dry0055*; H.J. Petersen; ZMUC C-F-124121. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1288*; JP det.; ZMUC C-F-123820 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1589*; JP det.; ZMUC C-F-124350.

On *Bembidion guttula* (Fabricius, 1792) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 627*; JP det.; ZMUC C-F-123116 • Syd for Veddelev; 55°40.346′ N, 12°4.915′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 333*; JP det.; ZMUC C-F-122811. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 574*; JP det.; ZMUC C-F-123060 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 777*; JP det.; ZMUC C-F-123272. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 611*; JP det.; ZMUC C-F-123099 • Halleby Å ved Bjerge Sydstrand; 55°33.194′ N, 11°10.079′ E; PG35; 24 Oct. 2018; *JP 1211*; JP det.; ZMUC C-F-123738. – **Sydjylland (SJ)** • Brede Ådal; 55°3.184′ N, 8°54.138′ E; MG90; 24 Oct. 2013; *H. Liljehult 500*; JP det.; ZMUC C-F-122984. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1370*; JP det.; ZMUC C-F-123911 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 967*; JP det.; ZMUC C-F-123474.

On *Bembidion illigeri* Netolitzky, 1914 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Rødbyhavn; 54°39.072′ N, 11°21.809′ E; PF55; 4 Jun. 2018; *JP 1120*; JP det.; ZMUC C-F-123640.

On *Bembidion lunulatum* (Geoffroy, 1785) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1323*; JP det.; ZMUC C-F-123859. – **Nordøstsjælland (NEZ)** • Brønshøj (Degnemosen); 55°42.043′ N, 12°30.352′ E; UB47; 26 May 2016; *JP 290*; JP det.; ZMUC C-F-122769.

On *Bembidion mannerheimii* Sahlberg, 1827 (Col. Carabidae)
DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 710*; JP det.; ZMUC C-F-123200 • Kohaveskov ved Landkildegård; 55°22.750′ N, 10°27.979′ E; NG93; 24 Aug. 2001; *H. Liljehult 1398*; JP det.; ZMUC C-F-123942, C-F-123944. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 23 Sep. 1993; *S. Langemark & O.E. Meyer 893*; JP det.; ZMUC C-F-123391 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1324*; JP det.; ZMUC C-F-123863. – **Nordøstjylland (NEJ)** • Syd for Krogsagergård; 56°37.534′ N, 9°45.551′ E; NH47; 24 Nov. 2019; *JP 1555*; JP det.; ZMUC C-F-124316. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 741*; JP det.; ZMUC C-F-123235. – **Nordvestsjælland (NWZ)** • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 644*; JP det.; ZMUC C-F-123132. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1449*; JP det.; ZMUC C-F-123999 • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 546*; JP det.; ZMUC C-F-123032.

On *Bembidion minimum* (Fabricius, 1792) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 629*; JP det.; ZMUC C-F-123118. – **Vestjylland (WJ)** • Sneum Sluse; 55°43.303′ N, 8°60.710′ E; MG74; 24 Mar. 2019; *L. Kjær-Thomsen & L. Thomas 1403*; JP det.; ZMUC C-F-123949.

On *Bembidion normannum* Dejean, 1831 (Col. Carabidae)
DENMARK – **Fyn (F)** • Sprogø; 55°20.012′ N, 10°58.263′ E; PG23; 7 Sep. 2013; *JP 213*; JP det.; ZMUC C-F-122692.

On *Bembidion quadrimaculatum* (Linnaeus, 1761) (Col. Carabidae)
DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 711*; JP det.; ZMUC C-F-123201.

On *Bembidion varium* (Olivier, 1795) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°3.218′ N, 12°15.801′ E; UB20; 10 Jun. 2017; *JP 430*; JP det.; ZMUC C-F-122915.

On *Dyschirius globosus* (Herbst, 1784) (Col. Carabidae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; JP 693; JP det.; ZMUC C-F-123181. – **Lolland, Falster, Møn (LFM)** • Busemarke Mose; 54°57.459′ N, 12°27.054′ E; UA39; 28 Aug. 2019; *JP 1507*; JP det.; ZMUC C-F-124094 • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1127*; JP det.; ZMUC C-F-123650 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1305*; JP det.; ZMUC C-F-123840. – **Nordøstjylland (NEJ)** • Vandplasken ved Kærsgård Strand; 57°31.199′ N, 9°53.070′ E; NJ57; 21 Nov. 2017; *JP 802*; JP det.; ZMUC C-F-123297. – **Nordøstsjælland (NEZ)** • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; JP 269; JP det.; ZMUC C-F-122748 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 623*; JP det.; ZMUC C-F-123112 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1054*; JP det.; ZMUC C-F-123570. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 215*; JP det.; ZMUC C-F-122695 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 769*; JP det.; ZMUC C-F-123264. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 610*; JP det.; ZMUC C-F-123098 • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 713*; JP det.; ZMUC C-F-123205 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 854*; JP det.; ZMUC C-F-123349 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; JP 756; JP det.; ZMUC C-F-123250. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1363*; JP det.; ZMUC C-F-123901 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1441*; JP det.; ZMUC C-F-123989 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1272*; JP det.; ZMUC C-F-123802 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 962*; JP det.; ZMUC C-F-123469.

On *Dyschirius tristis* Stephens, 1827 (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 743*; JP det.; ZMUC C-F-123237. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1364*; JP det.; ZMUC C-F-123903.

Remarks

This is a very variable and may be a collective species in need of a thorough revision (Haelewaters *et al.* 2019b). Attempts have been made to isolate some species with more or less luck (Benjamin & Shanor 1952; Santamaria *et al.* 2020a). An example of this may be *L. tenera* which was described on *Bembidion dentellum* (Thunberg, 1787) by Majewski (1994b) from Poland. It has been separated from *L. pedicellata* by several characters, especially related to the branching of outer appendage. We have found similar thalli to *L. tenera* on *Bembidion aeneum* (Fig. 40C). Distinguishing characteristics seem not to be very robust; furthermore, normal thalli of *L. pedicellata* have been found on the same host together with that *tenera*-like forms.

This species gives the name to a morphologically related group of species that share some characteristics such as: IV and V cells of the same height, and the presence of at least a first constricted and dark septum in the outer appendage.

Laboulbenia philonthi Thaxt.
MB#147868
Fig. 41A–B

Proceedings of the American Academy of Arts and Sciences 28: 174 (Thaxter 1893). – **Type**: "USA, Massachusetts, Belmont/Waltham, Waverley neighborhood, "April 23, 1813" [sic], no collector, on *Philonthus* sp., slide FH 00313494 (5 adult thalli)"; FH. [lectotype designated in Haelewaters *et al.* 2015b: 468]

Diagnostic features

Often, cell I bears a blackish lateral swelling above the foot (Fig. 41A–B, arrows). Cell V oval, as long as cell IV, connected with septum III–IV. Outer appendage simple or branched, with the lower 2–3 cells short, inflated, and separated with thick blackened septa. Inner appendage profusely branched unilaterally above the basal cell, with branches similar to those of the outer appendage. Basal cells of inner and outer appendages similar. [Detailed descriptions: Thaxter 1896; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Infects Col. Staphylinidae of the genus *Philonthus* and relatives (e.g., *Spatulonthus*, *Paragabrius* Coiffait, 1963, *Oligotergus* Bierig, 1937) from **Europe**: Spain, United Kingdom, France, the Netherlands, Italy, Germany, Austria, Czech Republic, Poland, Lithuania, Latvia, Greece; **America**: USA, Mexico, Guatemala, Uruguay, Argentina; **Asia**: Turkey and Korea (Majewski 2008). Recently recorded also from Ecuador (Proaño Castro & Rossi 2008), Trinidad & Tobago, Venezuela, Panama, Grenada, Canada (Haelewaters *et al.* 2015b), Bulgaria, Hungary (Rossi *et al.* 2019a), Slovakia (Rossi *et al.* 2019b), Slovenia (Rossi & Christian 2020), and Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Philonthus salinus* Kiesenwetter, 1844 (Col. Staphylinidae Staphylininae)
DENMARK – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 605*; JP det.; ZMUC C-F-123094. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1301*; JP det.; ZMUC C-F-123835.

Remarks

First record from Denmark. Because of its presence in the surrounding countries, the finding of *L. philonthi* in Denmark is far from surprising. The bulging of cell I is not found in all the thalli reported in the literature; so far we lack explanations of what factors favour its presence.

Laboulbenia picardii Maire
MB#148121
Fig. 41C–D

Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 7: 28 (Maire 1916a). – **Type**: [Type lost?!] "Sur les élytres de *Tachys bisulcatus* Nic.: Larache (Maroc), marais de Bou-Charren, 4/5 1910 (P. de Peyerimhoff)".

Diagnostic features

Cell II up to eight times as long as broad, showing a corrugated surface (Fig. 41D). Cell V oval, half of the length of cell IV, not connected with cell III. Outer appendage unbranched, straight. Inner appendage consisting of two short branches borne from the basal cell and each giving rise to a solitary lateral antheridium. [Detailed description: Santamaria 1998]

Distribution and hosts

This species seems exclusive on carabids of the genus *Porotachys* (often as *Tachys*) and allied genera of the subtribe Tachyina; from Morocco (type), Greece (Balazuc 1974e), Italy (Rossi 1975), Lebanon (Huldén 1985), and Spain (Santamaria 1989). The record from Japan on *Macrotachys* Kult, 1961 (Terada 1998a) was unexpected.

Collections examined from Denmark

On *Porotachys bisulcatus* (Nicolai, 1822) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Stensø ved Nakskov; 54°49.465′ N, 11°7.254′ E; PF37; 7 Jan. 2018; *JP 950*; JP det.; ZMUC C-F-123456.

Remarks

First record from Denmark. Although the Danish material consists of only one immature thallus, its classification leave no doubt because of the unique characters of cell II (see the corrugation of its margins in Fig. 41D) and outer appendage.

Laboulbenia pseudomasei Thaxt.
MB#243962
Fig. 41E–G

Proceedings of the American Academy of Arts and Sciences 35: 196 (Thaxter 1899; as *L. pseudomasci*). – **Type**: "On *Pseudomaseus nigrita* Fab., Paris Museum, No. 201, Mongolia. Near upper inferior margin of prothorax on left side"; FH.

Laboulbenia matheyi Baumgartner (Baumgartner 1923: 263) [MB#270636]

Diagnostic features

Cell V obtriangular, half of the length of cell IV, often divided and proliferating into a branch of variable length (Fig. 41F, arrow) which may support some antheridia. Insertion cell separated from the perithecium. Outer appendage once or twice branched above the basal cell, sometimes bearing solitary, lateral antheridia. Inner appendage, in young thalli, consisting of two branches bearing paired antheridia arising from the basal cell; in mature thalli replaced with long sterile appendages, similar to the outers. Basal cell of inner appendage half as long and as broad than basal cell of outer appendage. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Typically grows on species of *Pterostichus* of the subgenus *Melanius* (often as *Pseudomaseus* Chaudoir, 1838 or *Platysma*), but also reported on other Col. Carabidae like *Patrobus*, *Lagarus*, *Elaphrus*, *Stomis*, *Loricera*, *Anchomenus*, *Oxycentrus* Chaudoir, 1854, and *Nebria*. Known in Europe, North and Central America, and Asia. Given the confusion with *L. pterostichi* Thaxt. for years, it is wise to refer to the work of Rossi & Weir (1997) who unravelled the problem, and we agree with them that the number of misidentifications makes it impossible to determine its geographical distribution with certainty. Recently reported from Austria (Rossi & Christian 2020) and the Netherlands (Haelewaters & De Kesel 2020).

Collections examined from Denmark

On *Pterostichus minor* (Gyllenhal, 1827) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14 55.777′ E; VA99; 22 Jun. 2018; *JP 1149*; JP det.; ZMUC C-F-123673. – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41;

Fig. 41. *Laboulbenia* spp. **A**–**B**. *L. philonthi* Thaxt. Mature thalli showing blackish lateral swelling above the foot (arrows). – **C**–**D**. *L. picardii* Maire. **C**. Immature thallus. **D**. Corrugation of cell II margins in detail. – **E**–**G**. *L. pseudomasei* Thaxt. **E**, **G**. Mature thalli. **F**. Branch (arrow) from cell V in detail. Scale bars: A–C, E–G = 50 µm; D = 25 µm. Photographs from slides ZMUC C-F-123094 (A–B), ZMUC C-F-123456 (C–D), ZMUC C-F-122782 (E), ZMUC C-F-122742 (F), ZMUC C-F-122740 (G).

20 May 2013; *JP 368*; JP det.; ZMUC C-F-122851. – **Fyn (F)** • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1075*; JP det.; ZMUC C-F-123593. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1124*; JP det.; ZMUC C-F-123646. – **Nordøstsjælland (NEZ)** • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 263*; JP det.; ZMUC C-F-122742 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 16*; JP det.; ZMUC C-F-122489 • ibid.; 19 Mar. 2017; *JP 663*; JP det.; ZMUC C-F-123152. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 860*; JP det.; ZMUC C-F-123355. – **Sydjylland (SJ)** • Draved Skov; 55°0.964′ N, 8°58.395′ E; MF99; 1 Jun. 2013; *JP 303*; JP det.; ZMUC C-F-122782. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1420*; JP det.; ZMUC C-F-123966.

On *Pterostichus nigrita* (Paykull, 1790) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14 55.777′ E; VA99; 22 Jun. 2018; *JP 1150*; JP det.; ZMUC C-F-123674. – **Nordøstsjælland (NEZ)** • Strødam; 55°57.558′ N, 12°16.638′ E; UC20; 24–25 Sep. 2006; *J. Høier 1577*; P. Jørum det.; ZMUC C-F-124338. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1419*; JP det.; ZMUC C-F-123965.

On *Pterostichus rhaeticus* Heer, 1837 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 658*; JP det.; ZMUC C-F-123147 • ibid.; 4 Jun. 2018; *JP 1123*; JP det.; ZMUC C-F-123645. – **Nordøstsjælland (NEZ)** • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 261*; JP det.; ZMUC C-F-122740 • Jonstrup Vang ved Store Sejben Mose; 55°45.452′ N, 12°22.217′ E; UB38; 1–12 Jul. 2004; *J. Høier 1576*; P. Jørum det.; ZMUC C-F-124337 • Storø i Gurre Sø; 56°2.208′ N, 12°29.057′ E; UC41; 7 Apr. 2020; *JP 1634*; JP det.; ZMUC C-F-124367. – **Nordvestjylland (NWJ)** • Gammelgård på Fur; 56°50.314′ N, 8°58.971′ E; MH99; 22 Nov. 2013; *JP 419*; JP det.; ZMUC C-F-122903. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Jun. 2019; *JP 1474*; JP det.; ZMUC C-F-124054 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 26 Apr. 2020; *JP 1605*; JP det.; ZMUC C-F-124359.

Remarks

First record from Denmark. Often confused with *L. flagellata*, *L. proliferans* Thaxt. and *L. pterostichi* (Majewski 1994b). The latter probably does not exist in Europe (Rossi & Weir 1997).

Laboulbenia pygidicola Santam. sp. nov.
MB#840605
Fig. 42

Diagnosis

Thallus slender. Outer appendage elongated and dark at least in the basal portion. Inner appendage consisting of 2(–3) branches borne directly on the basal cell. Each of these branches once divided above first cell in three-celled appendages, where each terminal cell is an elongated antheridium (Fig. 42D–F, an). Perithecial apex obtuse, yet truncated, with a prominent dorsal lip.

Etymology

The species epithet refers to the "pygidium" (last abdominal segment of arthropods), where the fungus grows.

Type material

Holotype

DENMARK – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; on *Syntomus truncatellus* (Linnaeus, 1761) (Col. Carabidae); 10 Dec. 2013; *JP 886*; JP det.; ZMUC C-F-123384.

Paratype

DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; on *S. truncatellus*; 14 Jan. 2012; *JP 541*; JP det.; ZMUC C-F-123025.

Description

Thallus brown, especially darker at the appendages and perithecial apex, paler around the basal portions of the thallus and distal outer appendage. Basal cell of the receptacle (I) slender, narrowly elongated, up to five times as long as broad, with ± parallel margins, hyaline even in darker thalli. Suprabasal cell of the receptacle (II) shorter, darker and broader than cell I, somewhat gradually broadened towards the distal end, up to 3–4 times as long as broad. Cell III slightly longer than broad, almost rectangular in section. Cell IV shorter than III. Cell V very small, situated at the upper-inner corner of cell IV and separated from it by an oblique, curved septum that does not reach septum III–IV (Fig. 42E). Insertion cell brown but neither opaque nor deeply darkened or blackened, instead similar in colour to, or paler than its surroundings.

Outer appendage unbranched, consisting of up to 14 variably elongated cells, very long, as long as the length from foot to insertion cell; uniformly dark brown to gradually paler upwards. Inner appendage not exceeding the perithecial apex, consisting of a short basal cell about three times shorter than the outer but similar in width, giving rise to 2(–3) branches. Each of these branches includes a lowermost cell bearing two three-celled appendages, consisting of elongated and narrow cells where the terminal functions as an antheridium (Fig. 42D–F, an).

Perithecial stalk cell (VI) rhomboidal, as long as broad, slightly shorter than adjacent cell III. Perithecium ovate-fusiform, broadest between tiers w_1 and w_2, gradually tapering into an indistinct neck and a truncate, flattened, slightly bent, darker apex, where preostiolar spots appear ± blurred.

Length from foot to apex of perithecium 194–302 µm. Perithecium (including basal cells) 95–120 × 24–34 µm. Length from foot to tip of outer appendage (when undamaged) 419–489 µm.

Thalli were found on the elytra of the hosts. The hosts were sifted from fresh flood debris on a coastal meadow and from old, mouldy and decomposed *Phragmites* piles on moist, sun-exposed ground.

Remarks

This species should be compared with *L. metableti* with which it coexists on the same host in the two samples studied. Both species may be distinguished by the cell arrangement of the inner appendage, by the elongation and slenderness of its receptacle and the outer appendage, and by the truncated perithecial apex of *L. pygidicola* sp. nov., among other characteristics. The status of this species could be compared with that of *L. hyalopoda* and *L. notiophili*. *Laboulbenia notiophili* and *L. metableti* have been found on many other parts of host bodies without undergoing important morphological changes, therefore *L. hyalopoda* and *L. pygidicola* sp. nov. seem to be good species instead of growth forms. *Laboulbenia pygidicola* sp. nov. seems extremely rare according to the large quantities of samples of infested *Syntomus* we have studied.

Fig. 42. *Laboulbenia pygidicola* Santam. sp. nov. **B**–**C**. Mature thalli. **A**, **D**–**F**. Inner appendage and surrounding areas in detail with labelled antheridia (an) and cell V. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123384 (A–E) (holotype), ZMUC C-F-123025 (F).

Laboulbenia rougetii Mont. & C.P.Robin
MB#245803
Fig. 43A–B

Histoire naturelle des végétaux parasites qui croissent sur l'homme et sur les animaux vivants: 622 (Robin 1853). – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "In antennis, thorace, pedibus et elytris *Brachini crepitantis* L., *B. explodentis* Duftschmidt, et *B. sclopetae* Fabricius".

Laboulbenia europaea Thaxt. (Thaxter 1893: 167) [MB#186192]

Diagnostic features

Thallus reddish-brown. Cell V oval or obtriangular, half the length of cell IV, not connected with cell III. Outer appendage with the dorsal margin of lower part variably darkened, once branched above the suprabasal cell. Inner appendage of immature thalli consisting of a basal cell and a suprabasal cell which supports two simple branches bearing each a pair of antheridia which as the thallus matures will be replaced with sterile and fertile elongate branches bearing lateral solitary or paired darkened antheridia (Fig. 43B, an). Basal cell of inner appendage half as long than basal cell of outer appendage. [Detailed descriptions: Thaxter 1896; Sugiyama & Yamamoto 1982; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Occurs mostly on *Brachinus*, *Anchomenus*, *Aptinus* Bonelli, 1810, *Chlaenius* and other genera. Common and widespread in Europe (including Denmark, by Rostrup 1935), Africa, Asia as well as in Oceania (New Zealand) (Santamaria *et al.* 1991; Majewski 2008). Records from America probably belong to *L. flagellata* because it is broadly accepted that *L. rougetii* does not exist in America. Recent new records are from Sweden (Huggert 2010), Turkey (Rossi 2016), Bulgaria (Rossi *et al.* 2019a), Slovakia (Rossi *et al.* 2019b), Cambodia, and Kenya (Kong *et al.* 2020).

Collections examined from Denmark

On *Brachinus crepitans* (Linnaeus, 1758) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Sose; 55°2.801′ N, 14°50.722′ E; VB90; 4 Aug. 2008; *Mo. Hansen Dry0051*; Mo. Hansen det.; ZMUC C-F-124117.

Remarks

Laboulbenia rougetii is the type of the genus and the first species of Laboulbeniales to be described. Does not differ greatly from *L. flagellata* and seems to have been confused with it by some authors, at least those records of *L. rougetii* on carabids like e.g., *Agonum* spp. Indeed, the differences between both species are few, and without knowing the identity of the hosts they are not easily distinguished. *Laboulbenia rougetii* shows thalli with reddish shades whereas *L. flagellata* lacks this colour. The ecological niche that *L. rougetii* occupies on *Brachinus* in most of the world is replaced by *L. texana* Thaxt. in America.

Laboulbenia slackensis Cépède & F.Picard
MB#239158
Fig. 43C–D

Compte Rendu, Association Française pour l'Avancement des Sciences (part 2): 780 (Cépède & Picard 1907). – **Type**: [Type lost!] "*Pogonus chalceus* Marsh. Bords de la Slack, Ambleteuse (Pas-de-Calais)". [France]

Diagnostic features

Cell V trapezoidal to obtriangular, similar in size and shape to cell IV. Septum IV–V vertical, connected with septum III–IV. Basal cell of outer appendage shorter than cell IV, slightly inflated outward and twice as long as the basal cell of inner appendage, separated from the outer branch by a thick, black and constricted septum (Fig. 43D, arrow). Appendages, if undamaged, exceeding the tip of the perithecium. Dorsal side of the receptacle straight to slightly concave. [Detailed descriptions: Balazuc 1974e; De Kesel 1989; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Occurs on the genus *Pogonus* (Col. Carabidae) from **Europe**: Belgium, France, Germany, Greece, Italy, Poland, Spain (Santamaria *et al.* 1991), the Netherlands (Meijer 1975), and United Kingdom (Weir 1996); **Africa**: Morocco (Maire 1916a), Algeria (Maire 1920), and Comores (Balazuc 1982); and **Asia**: Japan (Terada 1998a).

Collections examined from Denmark

On *Pogonus chalceus* (Marsham, 1802) (Col. Carabidae)

DENMARK – **Fyn (F)** • Ristinge; 54°49.793′ N, 10°38.242′ E; PF07; ca 1870; *Schiødte Dry0153*; Schiødte det.; ZMUC C-F-124219. – **Sydjylland (SJ)** • Råhede; 55°16.263′ N, 8°39.392′ E; MG72; 31 May 2013; *JP 154*; JP det.; ZMUC C-F-122634.

Remarks

First record from Denmark. Sister species of *L. littoralis* which occurs on *Cafius* (Col. Staphylinidae). Both species were distinguished by biometric, morphological and ecological characteristics by De Kesel & Haelewaters (2014a).

Laboulbenia sphaerii Santam.

MB#239158

Fig. 43E–F

Nova Hedwigia 56(3): 414 (Santamaria 1993a). – **Type**: "Spain. Barcelona: Mura, 31TDG11, spread over the entire body of *Sphaerius acaroides* Waltl (Coleoptera Sphaeriidae) captured on the soft mud of Mura river, S. Santamaria, BCB-Mycotheca SS·1047b [holotypus]"; BCB.

Diagnostic features

Thallus diminutive, up to 85 µm in total length. Receptacle four-celled, because cells III and IV remain undivided and form a single cell (III–IV) (Fig. 43E–F). Lower receptacle consisting only of cell I. Cell V oval or obtriangular, half of the length of cell III–IV, not connected with cell II. Outer appendage unbranched, with a hooked apex. Inner appendage consisting of 1–3 simple branches arising from a flattened basal cell and bearing some solitary antheridium. [Detailed descriptions: Santamaria 1998; Majewski 1999]

Distribution and hosts

Exclusively on the mud beetle *Sphaerius acaroides* (Col. Sphaeriusidae) [= *Microsporus acaroides* (Waltl, 1838), Col. Microsporidae]. Reported from Spain (type), Poland (Majewski 1999), and Sweden (Huggert 2010, not named).

Fig. 43. *Laboulbenia* spp. **A**–**B**. *L. rougetii* Mont. & C.P.Robin. **A**. Mature thallus. **B**. Two young thalli showing antheridia (an). – **C**–**D**. *L. slackensis* Cépède & F.Picard. In D, the black and constricted septum separating the basal cell of outer appendage from outermost branch is labelled (arrow). – **E**–**F**. *L. sphaerii* Santam. **E**. A pair of two immature thalli. **F**. Mature thallus from holotype. Both images with undivided cells III and IV being labelled. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124117 (A–B), ZMUC C-F-124219 (C), ZMUC C-F-122634 (D), ZMUC C-F-124098 (E), BCB SS1047b (holotype) (F).

Collections examined from Denmark

On *Sphaerius acaroides* Waltl, 1838 (Col. Sphaeriusidae)

DENMARK – **Nordøstsjælland (NEZ)** • Søndersø, Jonstrup Vang; 55°46.278′ N, 12°22.010′ E; UB38; 1 Apr. 1872; *leg. unknown Dry0028*; det. unknown; ZMUC C-F-124098.

Remarks

First record from Denmark. The Danish material consists of two immature thalli from a dry-preserved beetle captured in 1872 (Fig. 43E). Despite the scarcity and age of the material, the specimens are perfectly classifiable given the distinctive characteristics and ecology. For comparison and for documentary interest we reproduce a photograph of a mature thallus from the Spanish holotype (Fig. 43F).

Although most species in the genus *Laboulbenia* have a typically five-celled receptacle (namely cells from I to V), some species show undivided cells III+IV or III+IV+V. Song *et al.* (2019) listed 23 species with these characteristics but omitted *L. sphaerii* which is the only Danish species of the genus having undivided cells III+IV. These species have been reported to grow on hosts belonging to three insect orders (Coleoptera, Diptera, and Heteroptera) and eight families (Song *et al.* 2019); it will remain unknown whether this character evolved independently on multiple occasions until most of the species have been sequenced.

Laboulbenia stenolophi Speg.
MB#242700
Fig. 44A–E

Redia 10: 65 (Spegazzini 1914). – **Type**: "Abbastanza raro e scarso sulle elitre dello *Stenolophus teutonus* nei dintorni di Conegliano, settembre ed ottobre 1912"; LPS. [Italy]

Laboulbenia acupalpi Speg. (Spegazzini 1915a: 458) [MB#159040] **syn. nov.**

Diagnostic features

Thallus pale brownish-yellow. Septum IV–V oblique, strongly curved, not connected with septum III–IV. Cell IV protruding at the outer margin. Cell V distant from cell VII. Cell VI shorter than cell III. Outer appendage straight, without dark septa, once or barely branched from the basal or suprabasal cells. Basal cell of inner appendage small, half as long than basal cell of outer appendage, usually supporting two short branches terminated by a few to numerous antheridia, rarely with long sterile appendages. Perithecium typically with a ventral prominence formed by the junction of outer wall cell tiers w_1 and w_2 (Fig. 44A, C, arrows). [Detailed descriptions: Terada 1976; Lee & Sugiyama 1984; Terada 2001]

Distribution and hosts

Laboulbenia acupalpi has been reported on species of the genus *Acupalpus* (Col. Carabidae) in France, Hungary, Italy, Poland, Spain, United Kingdom (Majewski 2008), Switzerland (Hoess & Senn-Irlet 2009, on *Stenolophus*), Algeria (Santamaria *et al.* 1991), Argentina (Spegazzini 1917), Japan (Sugiyama 1978b), Korea (Kang *et al.* 1983), and China (Lee & Lim 2000, on *Stenolophus* and *Abacetus* Dejean, 1828). Majewski (2008) also reports it on *Stenolophus* from Poland.

Laboulbenia stenolophi occurs on *Stenolophus* (Col. Carabidae) from Italy (type), France (Spegazzini 1915a), Tunisia (Maire 1916a), Hungary (Bánhegyi 1944), Germany (Scheloske 1969), Taiwan (Terada 1976), Indonesia (Lee & Sugiyama 1984), Japan (Terada 2001), China (Shen & Ye 2006), and Poland (Majewski 2008). Also recorded on *Acupalpus* from Ukraine and Poland (Majewski 2008). Probably

also on *Chlaeminus* Motschulsky, 1865 and *Abacetus* (Col. Carabidae) from Malaysia (Terada 2001, by emendation of previous records of *L. anoplogenii* by Sugiyama & Majewski 1985b). Records on other hosts are doubtful or require verification like those on *Bembidion* from India (Kaur *et al.* 1993), on *Philonthus* (Col. Staphylinidae) from Korea (Lee & Na 1998), and on *Sphodrus* Clairville, 1806 from Poland (Majewski 2008).

Some records of *L. anoplogenii* on *Stenolophus* or Stenolophini may be considered *L. stenolophi*. This concerns those from USA (Thaxter 1908), Switzerland (Baumgartner 1923), Madagascar, Iran, France (Balazuc 1974a), Comores (Balazuc 1982), Thailand (Sugiyama & Phanichapol 1984), Spain (Santamaria 1992b), United Kingdom (Weir 1996), Belgium (De Kesel 1998), Korea (Lee & Na 1999), the Netherlands (Haelewaters *et al.* 2012), and Turkey (Rossi 2016). The same is probably true for the records of *L. anoplogenii* on *Abacetus* from India, France and Sri Lanka (Thaxter 1908), France again (Balazuc 1974a), Guinea (Santamaria *et al.* 1991), China (Lee & Lim 2000); also the records of *L. anoplogenii* on *Acupalpus* from Japan (Santamaria *et al.* 1991) and Poland (Majewski 1999) should belong in *L. stenolophi*.

Collections examined from Denmark

On *Acupalpus exiguus* Dejean, 1829 (Col. Carabidae)

DENMARK – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 569*; JP det.; ZMUC C-F-123055.

On *Acupalpus flavicollis* (Sturm, 1825) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Robbedale; 55°4.738′ N, 14°45.569′ E; VB80; 2 Jul. 2006; *H. Liljehult 68*; H. Liljehult det.; ZMUC C-F-122544. – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 834*; JP det.; ZMUC C-F-123329 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1315*; JP det.; ZMUC C-F-123850. – **Nordøstsjælland (NEZ)** • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 863*; JP det.; ZMUC C-F-123358 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1028*; JP det.; ZMUC C-F-123538. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 570*; JP det.; ZMUC C-F-123056. – **Nordvestsjælland (NWZ)** • Eriksminde syd for Korshage; 55°57.744′ N, 11°46.504′ E; PH70; 27 Oct. 2019; *JP 1536*; JP det.; ZMUC C-F-124296. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 490*; JP det.; ZMUC C-F-122974.

On *Acupalpus parvulus* (Sturm, 1825) (Col. Carabidae)

DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 706*; JP det.; ZMUC C-F-123196. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1314*; JP det.; ZMUC C-F-123849. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 571*; JP det.; ZMUC C-F-123057 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 774*; JP det.; ZMUC C-F-123269. – **Nordvestsjælland (NWZ)** • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 607*; JP det.; ZMUC C-F-123096 • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 717*; JP det.; ZMUC C-F-123209 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 638*; JP det.; ZMUC C-F-123127. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1372*; JP det.; ZMUC C-F-123913 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1282*; JP det.; ZMUC C-F-123814.

On *Stenolophus mixtus* (Herbst, 1784) (Col. Carabidae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1148*; JP det.; ZMUC C-F-123672. – **Østjylland (EJ)** • Havnen i Randers; 56°27.687′ N, 10°3.546′ E;

NH65; 19 May 2013; *JP 371*; JP det.; ZMUC C-F-122854. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 661*; JP det.; ZMUC C-F-123150 • Mandemarke; 54°58.014′ N, 12°29.479′ E; UA39; 22-23 Jun. 2016; *O. Karsholt 130*; JP det.; ZMUC C-F-122606 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 828*; JP det.; ZMUC C-F-123322. – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 714*; JP det.; ZMUC C-F-123206.

On *Stenolophus teutonus* (Schrank, 1781) (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Karlstrup Kalkbrud syd for Karlstrup; 55°32.863′ N, 12°12.385′ E; UB25; 28 May 2016; *JP 226*; JP det.; ZMUC C-F-122707.

Remarks

First record from Denmark. *Laboulbenia anoplogenii*, *L. stenolophi* and *L. acupalpi* show major morphological resemblances, to the point that they may be hardly separable. The three species have been reported on the same or allied hosts as, for example, *Acupalpus* and *Stenolophus*. Balazuc (1974a) regarded *L. stenolophi* as a synonym of *L. anoplogenii.* Majewski (1999) reported *L. anoplogenii* on *Acupalpus* (*Stenolophus*) *teutonus* from Poland, and compared it with *L. acupalpi*; according to this author, *Laboulbenia anoplogenii* differs from *L. acupalpi* by the strong branching of the outer and inner appendages, by the very numerous clustered antheridia, and by the non-elongate outer appendage basal cell. Furthermore, the same author mentioned thalli not differing from *L. acupalpi* being collected on representatives of *Acupalpus* subgenus *Stenolophus* (according to the entomological systematics used by Majewski) in Poland.

Terada (2001) restricted *L. anoplogenii* to parasites on *Anoplogenius* Chaudoir, 1852 from China (type locality), Taiwan (Sugiyama & Shazawa 1977), and Japan (Sugiyama 1973), with these distinctive characteristics: (1) no crowded antheridia in young thalli, but many sterile long branches; (2) cell IV divides even in early stages of development; (3) cell V extends downward to the level of cell VII; (4) cell VI is taller and extends farther distally than cell III; (5) the level of the insertion cell is slightly above the perithecial base; and (6) the basal cell of the outer appendage is similar in size to the basal cell of the inner appendage. According to Terada, the name *L. anoplogenii* was misapplied to specimens occurring on *Stenolophus* and mentioned several features which should characterize *L. stenolophi*: (1) cell IV variably protruding or bulging at the outer corner; (2) cell IV division not observed in young thalli but rarely in mature (Fig. 44B, arrow); (3) cell V distant from cell VII; (4) cell VI variably shorter than cell III; (5) insertion cell situated far above the base of the perithecium; and (6) inner appendage consists of a short branchlet with antheridia. According to the mentioned work by Terada, specimens on *Astigis* Rambur, 1838, and maybe those on *Abacetus* and *Chlaeminus* remain in an uncertain position.

Our conclusions: (1) *Laboulbenia acupalpi* and *L. stenolophi* should be considered inseparable by morphological traits and therefore we place them in synonymy, (2) the presence of *L. anoplogenii* in Europe needs to be reconsidered, (3) features of appendages do not seem good enough to distinguish *L. anoplogenii* from *L. stenolophi*, and (4) characteristics related to the comparative size of cells VI and III as well as the position of cell V in relation to cell VII are invariable and valuable for separating *L. stenolophi* and *L. anoplogenii*.

Laboulbenia stilicicola Speg.
MB#242534
Fig. 44F–G

Redia 10: 41 (Spegazzini 1914). – **Type**: “Abbondante sulle elitre di *Stilicus fragilis* raccolto a Lévico, G. Doria, X, 1884 (Coll. Mus. Civ. Genova, n. 71)”; LPS. [Italy]

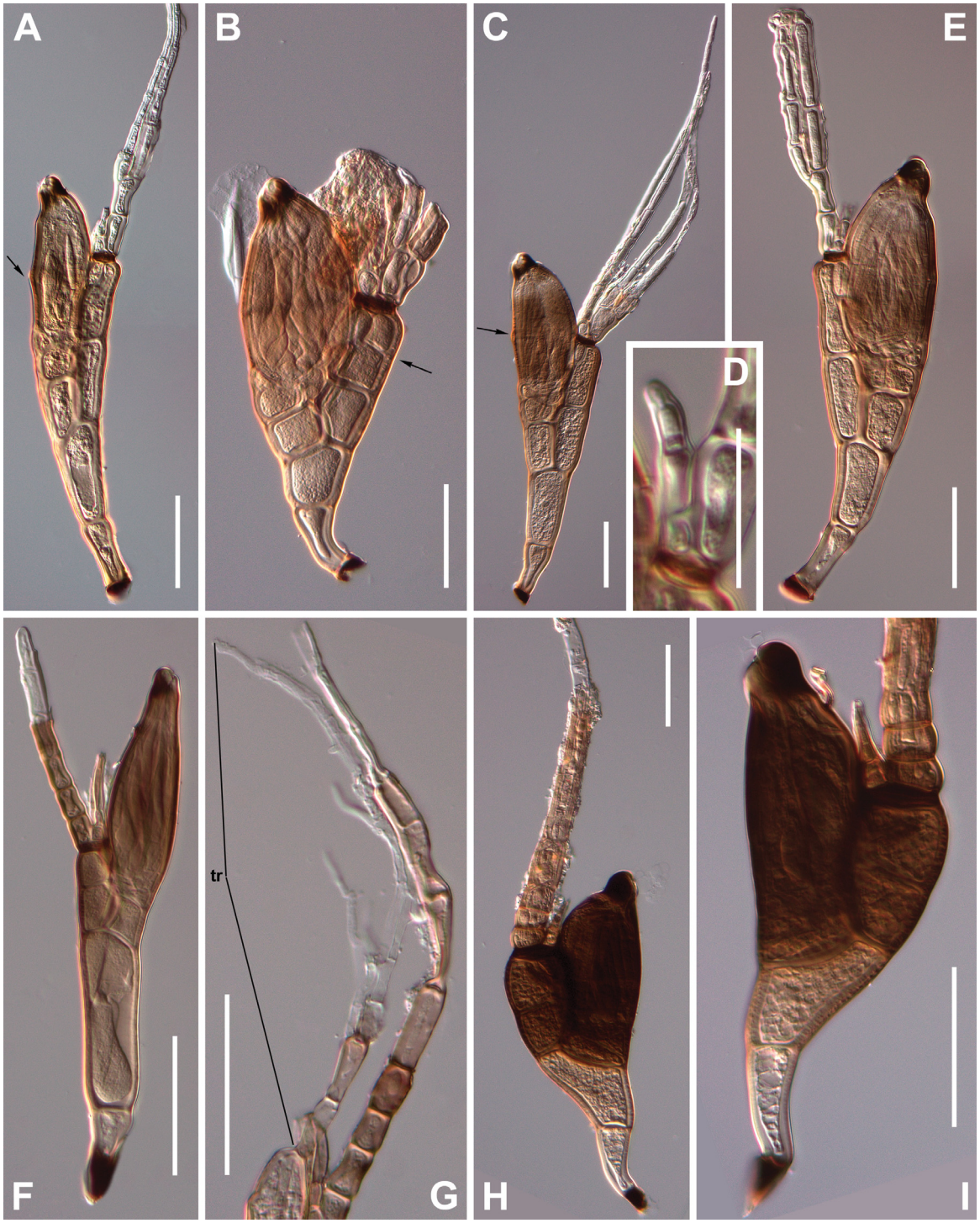

Fig. 44. *Laboulbenia* spp. **A**–**E**. *L. stenolophi* Speg. Mature thalli except fig. D which represents a detail of the inner appendage. A and C show the perithecial ventral prominence formed by the junction of outer wall cell tiers w_1 and w_2 (arrows). **B**. Cell IV subdivision is shown (arrow). **A**–**B**. From *Stenolophus mixtus*. **C**. From *Stenolophus teutonus*. **D**–**E**. From *Acupalpus flavicollis*. – **F**–**G**. *L. stilicicola* Speg. **F**. Mature thallus. **G**. Upper part of an immature thallus showing an elongate trichogyne (tr). – **H**–**I**. *L. thaxteri* Cépède & F.Picard. Mature thalli. Scale bars: A–C, E–I = 50 µm; D = 25 µm. Photographs from slides ZMUC C-F-122606 (A), ZMUC C-F-123150 (B), ZMUC C-F-122707 (C), ZMUC C-F-122974 (D–E), ZMUC C-F-123727 (F–G), ZMUC C-F-123102 (H–I).

Laboulbenia atroseptata T.Majewski (Majewski 1990a: 45) [MB#128601]

Diagnostic features

Cell V obtriangular, minute, half or less of the length of cell IV, not connected with cell III. Outer appendage unbranched, with the lower cells flattened, darkened, inflated, and separated with moderately thick, dark and constricted septa. Inner appendage consisting of a simple or once divided branch terminated by solitary or paired antheridia. Basal cell of inner appendage half as long and narrower than basal cell of outer appendage. [Detailed descriptions: Majewski 1994b; Santamaria 1998]

Distribution and hosts

On *Rugilus* (= *Stilicus* Berthold, 1827) (Col. Staphylinidae Paederinae) from **Europe**: Finland, France, Italy, the Netherlands, Poland, Spain, Switzerland, United Kingdom (Santamaria *et al.* 1991), Belgium (De Kesel & Haghebaert 1991), Greece (Castaldo *et al.* 2004), and Sweden (Huggert 2010); and from USA (Balazuc 1974e).

Collections examined from Denmark

On *Rugilus rufipes* (Germar, 1836) (Col. Staphylinidae Paederinae)

DENMARK – **Nordøstsjælland (NEZ)** • Husum; 55°42.851′ N, 12°29.061′ E; UB47; 6 Oct. 2018; *JP 1201*; JP det.; ZMUC C-F-123727. – **Nordvestsjælland (NWZ)** • Klinteskov ved Tissø; 55°34.569′ N, 11°18.882′ E; PG46; 24 Oct. 2018; *JP 1214*; JP det.; ZMUC C-F-123740.

Remarks

First record from Denmark. A rather variable species by thallial length and perithecium width/length ratio, resulting in a slenderer to somewhat stocky species. In Fig. 44G (tr) a very elongate and branched trichogyne is illustrated.

Laboulbenia thaxteri Cépède & F.Picard
MB#142449
Fig. 44H–I

Bulletin Scientifique de la France et de la Belgique 42: 260 (Cépède & Picard 1908). – **Type**: [Type lost?!] "*Tachypus flavipes* L., surtout sur le dessus du corps. Andrésy (Seine-et-Marne), collection Surcouf". [France]

Diagnostic features

Cell V obtriangular, large, half of the length of cell IV, not connected with cell III. Outer appendage unbranched, with the lower cells inflated, and separated with somewhat dark and constricted septa. Inner appendage unbranched, consisting of three cells, the basal, the suprabasal, and a terminal large antheridium. Basal cell of inner appendage much smaller than basal cell of outer appendage. [Detailed descriptions: Bechet & Bechet 1984; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Occurs on *Asaphidion* (= *Tachypus* Stephens, 1828) (Col. Carabidae) from **Europe**: Spain, France, United Kingdom, Belgium, Italy, Switzerland, Austria, Poland, Greece, Romania, Latvia, Lithuania (Majewski 2008), Russia (Huldén 1985), Denmark (Høier 2009), Sweden (Huggert 2010), and Bulgaria (Rossi *et al.* 2019a); and from Northern **Africa**: Algeria (Maire 1920).

Collections examined from Denmark

On *Asaphidion curtum* (Heyden, 1870) (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 12 May 1993; *S. Langemark & O.E. Meyer 102*; JP det.; ZMUC C-F-122577 • ibid.; *S. Langemark & O.E. Meyer 902*; JP det.; ZMUC C-F-123400 • ibid.; 7 Jun. 1993; *S. Langemark & O.E. Meyer 897*; JP det.; ZMUC C-F-123395 • ibid.; 28 Jul. 1993; *S. Langemark & O.E. Meyer 920*; JP det.; ZMUC C-F-123418. – **Nordøstsjælland (NEZ)** • Stenholtsvang; 55°57.439′ N, 12°21.204′ E; UC30; 28 Oct. 2017; *JP 614*; JP det.; ZMUC C-F-123102.

Remarks

First record from Denmark. Its presence in Denmark is not surprising considering its existence in neighbouring countries.

Laboulbenia vulgaris Peyr.
MB#237743
Fig. 45

Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1 68: 248 (Peyritsch 1873). – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "Scheint in der Wiener Umgebung die gemeinste Art zu sein; ich fand sie auf *Bembidium littorale* Pz., *B. fasciolatum* Duft., *B. punctulatum* Drapiez, *B. lunatum* Duft., *B. obsoletum* Dej. und auf *Deleaster dichrous* Grav.". [Austria]

Laboulbenia chilensis Speg. (Spegazzini 1910: 71) [MB#237513]
Laboulbenia abyssalis Maire (Maire 1916a: 21) [MB#169522]
Laboulbenia rauraciae Baumgartner (Baumgartner 1923: 264) [MB#276168]
Laboulbenia mattiroloi S.Colla (Colla 1925: 258) [Not registered in MycoBank]
Laboulbenia picardi Lepesme (Lepesme 1939: 150) [MB#486749]
Laboulbenia villiersi Lepesme (Lepesme 1944: 67) [Not registered in MycoBank]
Laboulbenia lepesmei Maire (Maire 1945: 40) [MB#287395]
Laboulbenia hastiana Huldén (Huldén 1983: 55) [MB#108112]

Diagnostic features

Cell V obtriangular, half of the length of cell IV, not connected with cell III. Outer appendage unbranched or once divided above the second or third cell, with the lower cells variably darkened and/or constricted at the septa. Inner appendage not exceeding the perithecial apex, usually consisting of two branchlets bearing few antheridia. Basal cell of inner appendage trapezoidal to wedge-shaped, much smaller than basal cell of outer appendage and typically enchased and underlying it (Fig. 45A, bc ia). [Detailed descriptions: Thaxter 1896; Sugiyama 1973; Balazuc 1974e; Majewski 1994b; Santamaria 1998]

Distribution and hosts

Laboulbenia vulgaris is a very common species infecting species of *Bembidion* in a broad sense (Col. Carabidae Bembidiina) and *Trechus* (Col. Carabidae Trechiina), but also reported on many other carabids and even staphylinids on an endless and quite confusing list. Widespread, known even from the most remote and extreme places of the planet (as the Crozet Islands and the Himalaya, Lepesme 1947), although absent in Oceania. For an extensive list of countries see Santamaria *et al.* (1991) and Majewski (2008). Recently newly recorded from Croatia, Slovenia, and Slovakia (Haelewaters *et al.* 2019b).

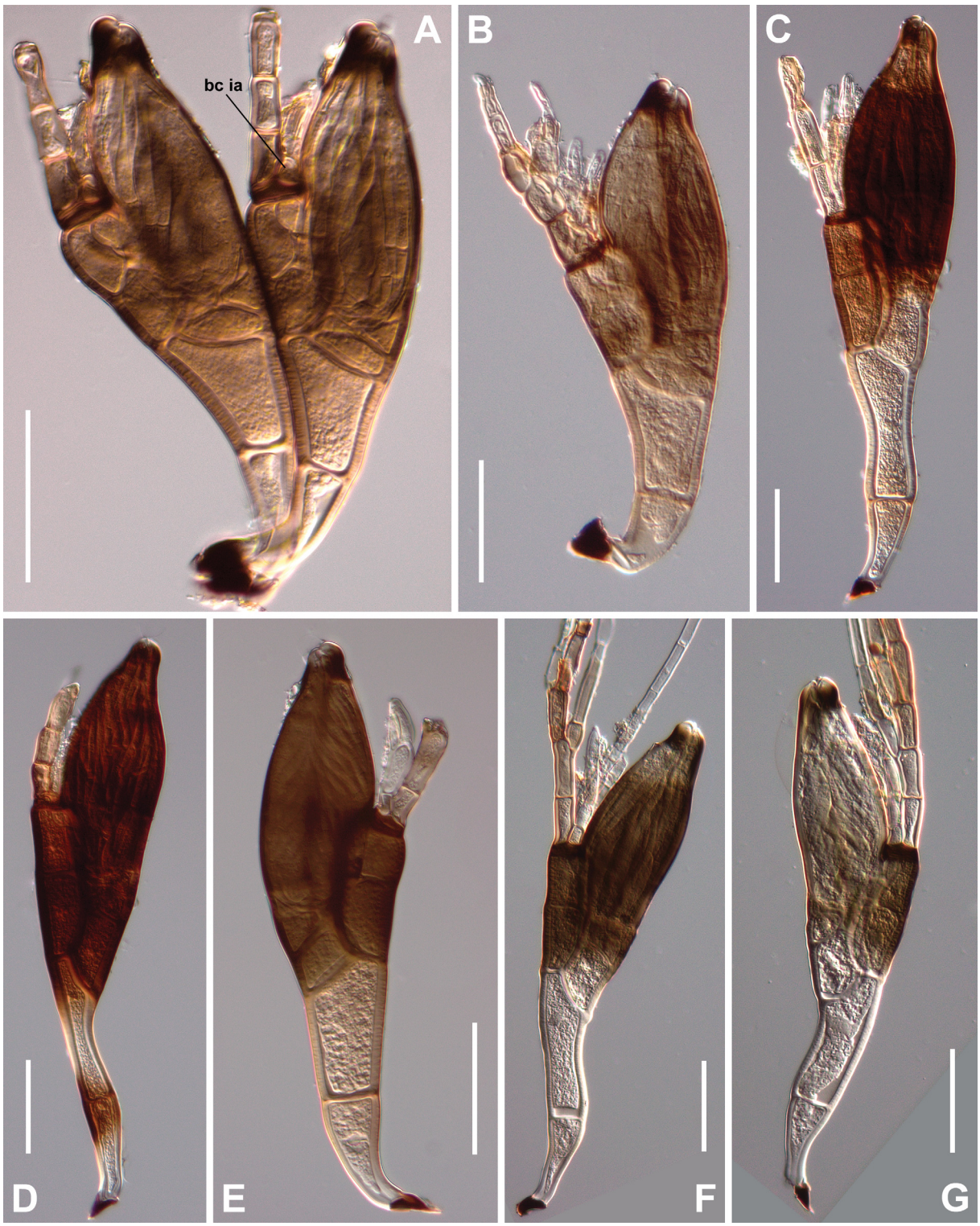

Fig. 45. *Laboulbenia vulgaris* Peyr. Mature thalli. In A the basal cell of the inner appendage has been labelled. **A**. From *Trechus quadristriatus*. **B**. From *Epaphius secalis*. **C**–**D**, **F**–**G**. From *Bembidion mannerheimi*. **E**. From *Bembidion obtusum*. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122615 (A), ZMUC C-F-123439 (B), ZMUC C-F-123392 (C), ZMUC C-F-123404 (D), ZMUC C-F-123734 (E), ZMUC C-F-123861 (F–G).

Collections examined from Denmark

On *Bembidion aeneum* Germar, 1824 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Resle Skov; 54°56.359′ N, 11°43.437′ E; PF79; 25 Sep. 2006; *H. Liljehult 1461*; JP det.; ZMUC C-F-124012.

On *Bembidion assimile* Gyllenhal, 1810 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 835*; JP det.; ZMUC C-F-123330. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 742*; JP det.; ZMUC C-F-123236 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 408*; JP det.; ZMUC C-F-122892 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 626*; JP det.; ZMUC C-F-123115. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 217*; JP det.; ZMUC C-F-122698. – **Sydjylland (SJ)** • Sønderstrand på Rømø; 55°6.373′ N, 8°29.380′ E; MG60; 25 Oct. 2017; *H. Liljehult 618*; JP det.; ZMUC C-F-123106.

On *Bembidion biguttatum* (Fabricius, 1779) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1322*; JP det.; ZMUC C-F-123858. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.469′ N, 11°23.147′ E; PG47; 18 Feb. 2017; *JP 341*; JP det.; ZMUC C-F-122820.

On *Bembidion bruxellense* Wesmaël, 1835 (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Gedser Odde; 54°33.588′ N, 11°58.187′ E; PF95; 19 May 2000; *H. Liljehult 273*; JP det.; ZMUC C-F-122752. – **Nordøstsjælland (NEZ)** • Bognæs Storskov; 55°41.242′ N, 12°1.678′ E; UB17; 1 Aug. 2013; *JP 365*; JP det.; ZMUC C-F-122848.

On *Bembidion dentellum* (Thunberg, 1787) (Col. Carabidae)
DENMARK – **Bornholm (B)** • Rønne Plantage; 55°4.375′ N, 14 45.096′ E; VB80; 13 Jun. 1932; *E. Suenson Dry0056*; E. Suenson; ZMUC C-F-124122.

On *Bembidion femoratum* Sturm, 1825 (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Karlstrup Kalkbrud syd for Karlstrup; 55°32.863′ N, 12°12.385′ E; UB25; 28 May 2016; *JP 227*; JP det.; ZMUC C-F-122708.

On *Bembidion guttula* (Fabricius, 1792) (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 980*; JP det.; ZMUC C-F-123487. – **Nordvestjylland (NWJ)** • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 777*; JP det.; ZMUC C-F-123272. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1007*; JP det.; ZMUC C-F-123514.

On *Bembidion lampros* (Herbst, 1784) (Col. Carabidae)
DENMARK – **Nordøstsjælland (NEZ)** • Gentofte; 55°44.005′ N, 12°33.020′ E; UB48; 23 Sep. 2017; *H. Enghoff 501*; JP det.; ZMUC C-F-122985.

On *Bembidion lunulatum* (Geoffroy, 1785) (Col. Carabidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1323*; JP det.; ZMUC C-F-123860.

On *Bembidion mannerheimii* Sahlberg, 1827 (Col. Carabidae)
DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 746*; JP det.; ZMUC C-F-123240. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 5 May 1993; *S. Langemark & O.E. Meyer 894*; JP det.; ZMUC C-F-

123392 • ibid.; 25 May 1993; *S. Langemark & O.E. Meyer 910*; JP det.; ZMUC C-F-123408 • ibid.; 16 Jun. 1993; *S. Langemark & O.E. Meyer 916*; JP det.; ZMUC C-F-123414 • ibid.; 8 Jul. 1993; *S. Langemark & O.E. Meyer 906*; JP det.; ZMUC C-F-123404 • ibid.; 16-24 Aug. 1993; *S. Langemark & O.E. Meyer 913*; JP det.; ZMUC C-F-123411 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1324*; JP det.; ZMUC C-F-123861, C-F-123862. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 20*; JP det.; ZMUC C-F-122493. – **Nordvestsjælland (NWZ)** • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 644*; JP det.; ZMUC C-F-123132. – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.235′ N, 12°6.280′ E; UA19; 14 Jan. 2012; *JP 546*; JP det.; ZMUC C-F-123030, C-F-123031.

On *Bembidion obtusum* Audinet-Serville, 1821 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 836*; JP det.; ZMUC C-F-123331 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1319*; JP det.; ZMUC C-F-123855. – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 140*; JP det.; ZMUC C-F-122617. – **Nordvestsjælland (NWZ)** • Bjerge Sydstrand; 55°34.046′ N, 11°9.459′ E; PG35; 24 Oct. 2018; *JP 1208*; JP det.; ZMUC C-F-123734 • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 874*; JP det.; ZMUC C-F-123370.

On *Bembidion stephensii* Crotch, 1866 (Col. Carabidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Hjelm Kobbel; 54°54.863′ N, 12°14.918′ E; UA28; 28 Aug. 2019; *JP 1505*; JP det.; ZMUC C-F-124092.

On *Bembidion tetracolum* Say, 1823 (Col. Carabidae)

DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 745*; JP det.; ZMUC C-F-123239. – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 16 Jun. 1993; *S. Langemark & O.E. Meyer 918*; JP det.; ZMUC C-F-123416 • Hobyskov; 54°44.069′ N, 11°15.296′ E; PF46; 7 Jan. 2018; *JP 954*; JP det.; ZMUC C-F-123460. – **Nordøstsjælland (NEZ)** • Espergærde; 56°0.591′ N, 12°33.074′ E; UC40; 24 May 2016; *M.H. Post 357*; JP det.; ZMUC C-F-122839 • Naturcenter Amager; 55°36.862′ N, 12°34.575′ E; UB46; 13 Jun. 2011; *C. Theilgaard 151*; JP det.; ZMUC C-F-122631 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1238*; JP det.; ZMUC C-F-123765. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 857*; JP det.; ZMUC C-F-123352 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 758*; JP det.; ZMUC C-F-123252. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1371*; JP det.; ZMUC C-F-123912 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 25 Apr. 2019; *JP 1447*; JP det.; ZMUC C-F-123995 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1375*; JP det.; ZMUC C-F-123916.

On *Epaphius secalis* (Paykull, 1790) (Col. Carabidae)

DENMARK – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 941*; JP det.; ZMUC C-F-123445 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 937*; JP det.; ZMUC C-F-123439.

On *Trechus obtusus* Erichson, 1837 (Col. Carabidae)

DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 16 May 2014; *JP 313*; JP det.; ZMUC C-F-122792. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 703*; JP det.; ZMUC C-F-123193 • Knudshoved Marina; 55°17.781′ N, 10°50.542′ E; PG12; 18 Oct. 2017; *JP 587*; JP det.; ZMUC C-F-123074. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 927*; JP

det.; ZMUC C-F-123427, C-F-123443 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 936*; JP det.; ZMUC C-F-123437 • Havgranerne i Tofte Skov; 56°50.576′ N, 10°15.552′ E; NJ70; 5–19 Sep. 2013; *I. Aggerholm 925*; JP det.; ZMUC C-F-123424 • Knarmod i Tofte Skov; 56°51.824′ N, 10°15.470′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 948*; JP det.; ZMUC C-F-123454 • Toftgården i Tofte Skov; 56°50.789′ N, 10°12.918′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 945*; JP det.; ZMUC C-F-123450 • Vandplasken ved Kærsgård Strand; 57°31.199′ N, 9°53.070′ E; NJ57; 21 Nov. 2017; *JP 803*; JP det.; ZMUC C-F-123298. – **Nordøstsjælland (NEZ)** • Kagsmose; 55°42.698′ N, 12°27.378′ E; UB47; 19 Sep. 2013; *H. Liljehult 1397*; JP det.; ZMUC C-F-123941 • Syd for Veddelev; 55°40.346′ N, 12°4.915′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 334*; JP det.; ZMUC C-F-122812. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 879*; JP det.; ZMUC C-F-123376.

On *Trechus quadristriatus* (Schrank, 1781) (Col. Carabidae)

DENMARK – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 139*; JP det.; ZMUC C-F-122615.

Remarks

Laboulbenia vulgaris should be regarded as a collective species showing very variable characteristics (Lepesme 1947), like other species such as *L. pedicellata* and *L. luxurians* with which it often coexists on the same host individual. Accordingly, up to 13 infraspecific forms have been described, including ranks as forms, varieties, subspecies and even an aberration, difficult to recognize at the very least and lacking any taxonomical value. A good candidate for further molecular analysis (Haelewaters & De Kesel 2020). In the figures included, we show the wide range of variation in this species, even with some doubtful forms, such as those of Fig. 45F–G collected on *Bembidion mannerheimii*.

Subtribe Stigmatomycetinae (Thaxt.) I.I.Tav.

Genus ***Acompsomyces*** Thaxt.
MB#45

Proceedings of the American Academy of Arts and Sciences 37: 37 (Thaxter 1901b). – Type species: *A. corticariae* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cells II and III separated by an oblique or vertical septum, adnate on top of the cell I (Fig. 46B). Primary appendage free, its cells giving rise to three or 7–8 antheridia showing free efferent necks; the terminal antheridium bears a dorsal spinous process (the original spore apex, sx). Perithecium with 5(–6) cells in each vertical row of outer wall cells; the perithecial tip showing four terminal lobes surrounding a well-defined conical apex. Trichogyne three-celled, consisting of a basal cell bearing two divergent, papillate cells (Fig. 46B, tr).

Remarks

The genus consists of eight species, of which six in Europe, one in Denmark. The most recently described species is *A. ootypi* (Santamaria 1993c). Six of the eight species occur on Col. Cryptophagidae and Lathridiidae, forming a consistent group with distinctive characteristics (Benjamin 1989; Santamaria 2003). The other two species, *A. decarthricola* Speg. on Pselaphinae (Col. Staphylinidae) from Argentina (Benjamin 2001) and *A. stenichni* (Scheloske) I.I.Tav. on Scydmaeninae (Col. Staphylinidae) need further revision for a certain generic allocation.

Acompsomyces stenichni (Scheloske) I.I.Tav.
MB#105014
Fig. 46A–C

Mycologia Memoirs 9: 131 (Tavares 1985). – **Basionym**: *Stigmatomyces stenichni* Scheloske, *Parasitologische Schriftenreihe* 19: 149 (Scheloske 1969) [MB#339712]. – **Type**: "Auf den Elytren von *Stenichnus scutellaris* (Col., Scydmaenidae), den ich in Bruchwäldern bei Schwand/Nürnberg erbeutete. Deutschland. Holotypus Abb. 50". [Germany]

Diagnostic features

Appendage consisting of around seven superposed cells, each of them bearing a solitary lateral, flask-shaped antheridium, except for the uppermost which bears a pair of antheridia. [Detailed descriptions: Weir 1994; Majewski 1994b]

Distribution and hosts

Associated with species of the genus *Stenichnus* Thomson, 1859 (Col. Staphylinidae Scydmaeninae) from Germany (type), Poland (Majewski 1973c), United Kingdom (Weir 1994), and France (Santamaria & Rossi 1999). The record from Mexico on an undetermined scydmaenid (Benjamin 1989) requires verification.

Collections examined from Denmark

On *Stenichnus collaris* (Müller & Kunze, 1822) (Col. Staphylinidae Scydmaeninae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup; 54°46.408′ N, 11°39.955′ E; PF77; 26 Jun. 1901; *F. de Tengnagel Dry0168*; F. de Tengnagel det.; ZMUC C-F-124234 • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 553*; JP det.; ZMUC C-F-123039.

Remarks

First record from Denmark. The generic assignment of this species is questionable. Formerly described in the genus *Stigmatomyces*, Tavares (1985) suggested its transfer to the genus *Acompsomyces*, but Benjamin (1989) questioned this statement. The arrangement of cells in the receptacle as well as the trichogyne morphology agree with most typical species of *Acompsomyces* on Cryptophagidae and Lathridiidae, but characters of the appendage and perithecial apex argue with this advice. Study of more material of this apparently rare species may lead to the creation of a new genus.

Genus ***Aphanandromyces*** W.Rossi
MB#244

Mycologia 74 (3): 520 (Rossi 1982a). – Type species: *A. audisioi* W.Rossi (by monotypy)

Brief description

Monoecious. Receptacle three-celled (Fig. 46D). Cells II and III adnate on the top of cell I. Primary appendage consisting of a wedge-shaped basal cell, a suprabasal cell with a rounded protuberance on the outer, lower side, and a collapsing third cell above which supports two cells and four antheridia, although this portion typically falls off at maturity. Perithecium with five cells in each vertical row of outer wall cells.

Remarks

Monotypic. Tavares (1985) compared this genus with *Synandromyces* and *Autophagomyces*. The latter similarity was also mentioned by Rossi (1982a). Although appendage loss is common in other genera,

Fig. 46. A–**C**. *Acompsomyces stenichni* (Scheloske) I.I.Tav. **A**, **C**. Submature thalli. **B**. Immature thallus showing the trichogyne (tr) and cells of receptacle (I, II, III). – **D**–**E**. *Aphanandromyces audisioi* W.Rossi. Mature thalli. D. With labelled cells of receptacle (I, II, III). **E**. With labelled primary appendage (pa), and antheridia (an). – **F**–**H**. *Bordea denotata* Haelew. & De Kesel. Mature thalli. Different parts of the thallus are labelled. Abbreviations: a = primary septum; an = antheridium; sx = spinous process or remains of the original spore apex; I, II, III = cells of primary receptacle. Arrows = cytoplasmatic constraint or septum-like marking above septum II–VI. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123039 (A–C), ZMUC C-F-122509 (D), ZMUC C-F-122633 (E), ZMUC C-F-122556 (F–H).

the break off of the appendage by the collapse of one of its cells represents a unique characteristic among the Laboulbeniales.

Aphanandromyces audisioi W.Rossi
MB#110475
Fig. 46D–E

Mycologia 74 (3): 520 (Rossi 1982a). – **Type**: "On all parts of the body of many specimens of *Brachypterus urticae* (F.) (Insecta, Coleoptera, Nitidulidae) collected on *Urtica dioica* L. Northern Italy: Arigna, 1100 m, and Canali di Trivigno"; RO.

Diagnostic features

See genus description. [Detailed descriptions: Majewski 1994b; Santamaria 2003; De Kesel & Gerstmans 2011]

Distribution and hosts

Exclusive on *Brachypterus urticae* (Col. Kateretidae), a beetle commonly found on male flowers of *Urtica* spp. Described from Italy (Rossi 1982a), has been later reported from Poland (Majewski 1986b), Spain (Santamaria 1989), France (Balazuc 1990), Sweden (Santamaria *et al.* 1991), United Kingdom (Weir 1996), Lithuania (Markovskaja 2000), Greece (Castaldo *et al.* 2004), Latvia (De Kesel & Krastina De Kesel 2006), Belarus (Majewski 2008), and Belgium (De Kesel & Gerstmans 2011).

Collections examined from Denmark

On *Brachypterus urticae* (Fabricius, 1792) (Col. Kateretidae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14°55.777′ E; VA99; 22 Jun. 2018; *JP 1144*; JP det.; ZMUC C-F-123667. – **Nordøstsjælland (NEZ)** • Åsen ved Lellinge; 55°27.948′ N, 12°8.785′ E; UB15; 26 Jun. 2019; *JP 1483*; JP det.; ZMUC C-F-124068 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 15 Jun. 2013; *JP 230*; JP det.; ZMUC C-F-122711 • Karlstrup Kalkbrud syd for Karlstrup; 55°32.863′ N, 12°12.385′ E; UB25; 28 May 2016; *JP 98*; JP det.; ZMUC C-F-122573 • Rødovre; 55°39.663′ N, 12°27.490′ E; UB37; 8°Jun. 2018; *JP 1139*; JP det.; ZMUC C-F-123663. – **Nordvestjylland (NWJ)** • Krabbesholm Skov; 56°34.471′ N, 9°2.886′ E; NH06; 20 Jun. 2012; *JP 34*; JP det.; ZMUC C-F-122509. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 9 Jun. 2013; *JP 153*; JP det.; ZMUC C-F-122633. – **Sydsjælland (SZ)** • Bimose i Broby Overdrev; 55°23.921′ N, 11°35.499′ E; PG64; 28 Jun. 2013; *JP 326*; JP det.; ZMUC C-F-122804 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 27 Jun. 2013; *JP 389*; JP det.; ZMUC C-F-122872.

Remarks

First record from Denmark. This species is present from north to south and from west to east in Europe, therefore its presence in Denmark is not surprising. We have been fortunate to find a mature thallus retaining the primary appendage with antheridia (Fig. 46E, pa, an).

Genus *Arthrorhynchus* Kolen.
MB#337

Wiener Entomologische Monatsschrift 1: 67 (Kolenati 1857). – Type species: *A. diesingii* Kolen.

Helminthophana Peyr., *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1* 68: 250 (Peyritsch 1873) [MB#2262]

Brief description

Monoecious. Receptacle three-celled. Cell I extending within the host body into a conspicuous non-septate haustorium. Blackened foot absent. Primary appendage free, consisting of several superposed cells. Each of these cells, except the lowermost basal, give rise to four or more antheridia arranged in whorls. The terminal antheridium bears a dorsal spinous process (the original spore apex, sx). Perithecium with 5–6 cells in each vertical row of outer wall cells; the perithecial tip showing four terminal lobes surrounding the ostiole.

Remarks

This genus consists of 3–6 species depending on the authors (Majewski 1994b). We count six species if *A. eucampsipodae* Thaxt. is separated from *A. diesingii* Kolenati (Haelewaters *et al.* 2020).

Arthrorhynchus nycteribiae (Peyr.) Thaxt.
MB#353725

Proceedings of the American Academy of Arts and Sciences 36: 408 (Thaxter 1901a). – **Basionym**: *Laboulbenia nycteribiae* Peyr., *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Wien. Mathematisch-naturwissenschaftliche Classe. Abteilung 1* 64: 451 (Peyritsch 1871) [MB#148528]. – *Helminthophana nycteribiae* Peyr. (Peyritsch 1873: 250) [MB#177180]. – **Type**: [Ind. loc.] "Ich fand drei mit *Laboulbenia* behaftete Exemplare, das eine war als *Nycteribia Montaguei* bestimmt und stammte aus Österreich, und zwei unbestimmte Nycteribien aus dem Banat". [Austria]

Reported from Denmark by Ryberg (1947) on undetermined Nycteribiidae. The hosts, possible carriers of this species, were thoroughly examined but without the finding of any infected individuals although well over a hundred specimens were studied.

Genus ***Bordea*** Maire
MB#628

Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 7: 15 (Maire 1916a). – Type species: *B. coronata* Maire

Brief description

Monoecious. Receptacle three-celled (Fig. 46F). Cell III separated from cell II by an oblique septum; not in contact with cell I and laterally adnate to the base of the perithecial stalk-cell (VI). Primary appendage free, consisting of two superposed cells and a terminal, usually spinose (Fig. 46H, sx), flask-shaped antheridium (Fig. 46F, an). Perithecium with five cells in each vertical row of outer wall cells.

Remarks

The genus consists of 15 species, of which two in Europe, one in Denmark. The most recently described species is *B. denotata* (Haelewaters *et al.* 2014). Benjamin (2001) redefined the genus *Autophagomyces*, transferring some species to *Bordea* and describing the genus *Rossiomyces*.

Bordea denotata Haelew. & De Kesel
MB#804337
Fig. 46F–H

Nova Hedwigia 98 (1–2): 114 (Haelewaters *et al.* 2014). – **Type**: "On *Bibloporus bicolor* (Denny, 1825) (Coleoptera, Staphylinidae, Pselaphinae), collected in Haren, Harener Wildernis (Groningen), N 53°10′ E 6°38′, 2.ix.2000, under bark of standing dead *Alnus glutinosa* tree, leg. and det. O.Vorst (cOV), D.Haelewaters 60d (HOLOTYPE, 1 mature thallus, found on elytra, BR MYCO 173758–31)"; BR.

Diagnostic features

Cell II separated from cell III by a strongly oblique septum. Basal part of cell VI not or slightly constricted, showing a cytoplasmatic constraint or septum-like marking above septum II–VI (Fig. 46G–H, arrows). Perithecial apex rounded.

Distribution and hosts

Only known from the type, on *Bibloporus bicolor* (Denny, 1825) (Col. Staphylinidae Pselaphinae) from the Netherlands.

Collections examined from Denmark

On *Bibloporus minutus* Raffray, 1914 (Col. Staphylinidae Pselaphinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Løgnor; 54°46.987′ N, 11°48.999′ E; PF87; 16 Dec. 2014; *K.B. Nielsen 81*; JP det.; ZMUC C-F-122556.

Remarks

First record from Denmark. Related to *Bordea strangulata* (Thaxt.) R.K.Benj. which occurs on *Euconnus*-like beetles (Col. Staphylinidae Scydmaeninae) from Guatemala (Benjamin 2001). Constriction of cell VI is present in both species, although it is different. The Danish record is the first for this species after its original description. A photo of this species is given here for the first time.

Genus ***Corethromyces*** Thaxt.
MB#1245

Proceedings of the American Academy of Arts and Sciences 27: 36 (Thaxter 1892). – Type species: *C. cryptobii* Thaxt.

Eucorethromyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 35: 433 (Thaxter 1900) [MB#1919]

Brief description

Monoecious. Receptacle three-celled. Primary appendage free, consisting of several superposed cells bearing lateral branches, some of them giving rise to intercalary but also terminal antheridia. Cells II and VI superposed, separated by a ± horizontal or oblique septum. Perithecium with four cells in each vertical row of outer wall cells.

Remarks

This is a large genus consisting of 92 species, of which 13 in Europe, three in Denmark. The most recently described species are *C. gibbosus* and *C. marshallii* (Rossi *et al.* 2020). Hughes (2008) reported two undescribed species from Ptiliidae and Byrrhidae. Although Tavares (1985) redefined the too broad

generic characteristics of the original description (Thaxter 1892), it is still a genus with poorly defined limits. *Corethromyces subsigmoideus* Speg. (Spegazzini 1917) is included here among the 92 species, although Tavares (1985) suggests that it could be a *Cryptandromyces*. Most species are associated with Col. Staphylinidae, but also with Carabidae, Leiodidae, Heteroptera Lygaeidae (De Kesel & Haelewaters 2019), and Diptera Sphaeroceridae (Rossi *et al.* 2020). The number of perithecial wall cells may be questioned according to Weir & Hughes (2002) who mentioned five tiers instead of four at least in *C. diochi* Thaxt. (Thaxter 1931); moreover, these authors suggested that the genus might be separated into two subgroups.

Key to the Danish species (partially following Santamaria 2003)

1. Basal cell of the receptacle (I) blackish brown, extending laterally into a black outgrowth. On *Rugilus* (Col. Staphylinidae) ..... ***C. stilici*** Thaxt.
– Basal cell of the receptacle (I) not fully darkened, without a lateral expansion 2

2. Basal cell of the appendage dark, supporting a few-celled axis bearing lateral slender phialides. Perithecial apex without a dark preapical spot. On *Tachyporus* Gravenhorst, 1802 (Col. Staphylinidae) ..... ***C. bialowiezensis*** T.Majewski
– Basal cell of the appendage mostly entirely pale (rarely partially darkened), carrying several crowded sterile and fertile branches, the latter bearing intercalary phialides. Perithecium with a dark preapical spot. On *Choleva* (Col. Leiodidae) ..... ***C. henrotii*** Balazuc ex Balazuc

Corethromyces bialowiezensis T.Majewski
MB#459689
Fig. 47A–B

Acta Mycologica 34 (1): 9 (Majewski 1999). – **Type**: "On *Tachyporus solutus* Erichson (Col., Staphylinidae, Tachyporinae): Bialowieza, meadow near forest (Bialowieza National Park sect. 399), 14.5.1987 (TM. 3713 – HOLOTYPE)"; KRAM. [Poland]

Diagnostic features

Cell I elongate, entirely pale except for the lower part and the darkened foot. Basal cell of primary appendage darkened, distally rounded, supporting a few-celled axis bearing lateral, slender phialides.

Distribution and hosts

Only known from the type locality in Poland, on *Tachyporus* (Col. Staphylinidae Tachyporinae).

Collections examined from Denmark

On *Tachyporus chrysomelinus* (Linnaeus, 1758) (Col. Staphylinidae Tachyporinae)
DENMARK – **Sydjylland (SJ)** • Juvre; 55°11.050′ N, 8°33.568′ E; MG71; 8 Mar. 2020; *JP 1642*; JP det.; ZMUC C-F-124370.

Remarks

First record from Denmark and second after the original description. There is no doubt that *Tachyporus chrysomelinus* is very common and widespread in Denmark and often occurs in large numbers when found. Nevertheless, *C. bialowiezensis* probably is a very rare species although the absence of citations may also be due to a lack of research. A photo of this species is given here for the first time.

Corethromyces henrotii Balazuc ex Balazuc
MB#283407
Fig. 47C–D

Bulletin Mensuel de la Société Linnéenne de Lyon 42 (10): 283 (Balazuc 1973b, as *henroti*). – **Type**: "Sur *Choleva oblonga* Latreille (Coleoptera, Leiodidae) de Mouthier-Hautepierre (Doubs), H. Henrot leg."; PC. [France] [No. 74.34, Santamaria 2003]

Corethromyces henrotii Balazuc (Balazuc 1971c: 252) (nom. inval.) [MB#541473]

Diagnostic features

Cell I small, with the dark pigmentation of the foot sometimes extending upwards. Appendage consisting of a rather large basal cell III bearing crowded fertile and sterile branches (Fig. 47C). Fertile branches slender, including intercalary antheridia. Cell VI inflated. Perithecium showing a shaded preapical region with a dark spot on the posterior side (Fig. 47C, arrow). [Detailed descriptions: Santamaria 2003; De Kesel & Haelewaters 2019]

Distribution and hosts

Only on *Choleva* (Col. Leiodidae) from Belgium, Czech Republic, Finland, France, Italy, Spain, and the Netherlands (De Kesel & Haelewaters 2019).

Collections examined from Denmark

On *Choleva agilis* (Illiger, 1798) (Col. Leiodidae)
DENMARK – **Nordøstsjælland (NEZ)** • Hillerød; 55°55.714′ N, 12°18.383′ E; UC30; Oct. 1904; *J.P. Johansen Dry0059*; J.P. Johansen det.; ZMUC C-F-124125.

On *Choleva fagniezi* Jeannel, 1922 (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Skærbro Kær; 56°4.588′ N, 9°46.314′ E; NH41; 24 Apr. 1998; *V. Mahler Dry0060*; V. Mahler det.; ZMUC C-F-124126.

On *Choleva jeanneli* Britten, 1922 (Col. Leiodidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lindeskov ved Nykøbing; 54°44.747′ N, 11°53.917′ E; PF87; 14 May 1994; *JP Dry0061*; JP det.; ZMUC C-F-124127. – **Nordvestsjælland (NWZ)** • Yderby Lyng; 55°59.039′ N, 11°19.178′ E; PH40; 12 Apr. 2020; *JP 1596*; JP det.; ZMUC C-F-124356.

On *Choleva oblonga* Latreille, 1807 (Col. Leiodidae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 12 Mar. 2017; *JP 278*; JP det.; ZMUC C-F-122757.

Remarks

First record from Denmark. Some of the studied thalli belong to the unusual forms described by De Kesel & Haelewaters (2019), which are characterized by having a darkened cell III (Fig. 47D), a feature not considered enough important by those authors to separate them as a new species; our material is not in a good enough condition to be adequately studied, but the option of a new species should not be ruled out.

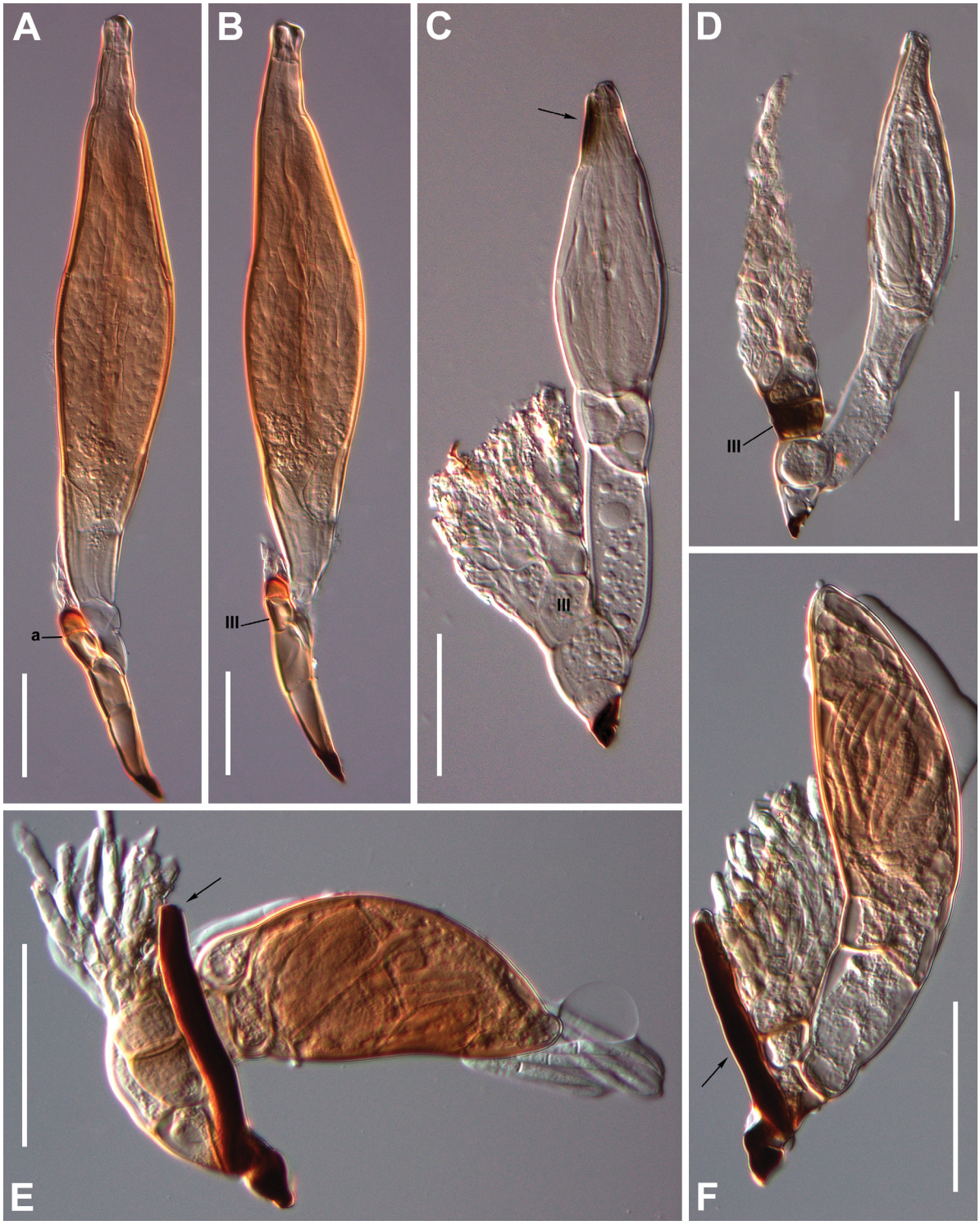

Fig. 47. *Corethromyces* spp. – **A**–**B**. *C. bialowiezensis* T.Majewski. Mature thalli, with labelled primary septum (a) and cell III. – **C**–**D**. *C. henrotii* Balazuc ex Balazuc. **C**. Typical mature thallus showing cell III and shaded preapical region with a dark spot on the perithecial posterior side (arrow). **D**. Mature thallus of a unusual form having a darkened cell III. – **E**–**F**. *C. stilici* Thaxt. Mature thalli from abdominal tergites (E) or sternites (F), both showing a labelled cell I blackened outgrowth (arrows). Scale bars: 50 µm. Photographs from slides ZMUC C-F-124370 (A–B), ZMUC C-F-124127 (C), ZMUC C-F-124125 (D), ZMUC C-F-122735 (E–F).

Corethromyces stilici Thaxt.
MB#183854
Fig. 47E–F

Proceedings of the American Academy of Arts and Sciences 37: 42 (Thaxter 1901b). – **Type**: [Not designated] [Ind. loc.] "On the abdomen of *Stilicus* sp., Interlaken, Switzerland. On *Stilicus rufipes* Germ., Berlin Museum, No. 836. Europe"; FH.

Diagnostic features

Cell I small, dark, laterally extending into a ± straight, stout, blackened outgrowth (Fig. 47E–F, arrows). Perithecial wall consisting of four vertical, spirally arranged rows of cells (Fig. 47E). [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 2003]

Distribution and hosts

On species of *Rugilus* (= *Stilicus*) (Col. Staphylinidae Paederinae) from **Europe**: Germany, the Netherlands, Italy, Poland, Spain, Switzerland (Santamaria *et al.* 1991), Hungary (Bánhegyi *et al.* 1985), Belgium (De Kesel & Haghebaert 1991), France (Duverger 1995), Denmark (Høier 2009), Sweden (Huggert 2010); **America**: USA (Thaxter 1908), Argentina, Chile, Uruguay (Santamaria *et al.* 1991); and **Asia**: Sumatra (Tavares 1985).

Collections examined from Denmark

On *Rugilus rufipes* (Germar, 1836) (Col. Staphylinidae Paederinae)

DENMARK – **Østjylland (EJ)** • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 797*; JP det.; ZMUC C-F-123292 • Høgdal; 56°6.449′ N, 9°36.941′ E; NH31; 11 Mar. 2017; *JP 353*; JP det.; ZMUC C-F-122835. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 685*; JP det.; ZMUC C-F-123173. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1334*; JP det.; ZMUC C-F-123873. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 933*; JP det.; ZMUC C-F-123433 • ibid.; *I. Aggerholm 944*; JP det.; ZMUC C-F-123448 • Engskoven i Tofte Skov; 56°51.525′ N, 10°15.065′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 939*; JP det.; ZMUC C-F-123441 • Toftgården i Tofte Skov; 56°50.789′ N, 10°12.918′ E; NJ70; 22 Aug.–5 Sep. 2013; *I. Aggerholm 947*; JP det.; ZMUC C-F-123452 • Vesterskoven i Tofte Skov; 56°50.346′ N, 10°13.361′ E; NJ70; 7 Aug. 2013; *JP 317*; JP det.; ZMUC C-F-122796 • ibid.; 8–22 Aug. 2013; *I. Aggerholm 926*; JP det.; ZMUC C-F-123425. – **Nordøstsjælland (NEZ)** • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 596*; JP det.; ZMUC C-F-123085 • Husum; 55°42.851′ N, 12°29.061′ E; UB47; 6 Oct. 2018; *JP 1201*; JP det.; ZMUC C-F-123728 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 4*; JP det.; ZMUC C-F-122474, C-F-122475 • ibid.; 19 Mar. 2017; *JP 669*; JP det.; ZMUC C-F-123158 • Klinten ved Selsø; 55°44.158′ N, 11°59.634′ E; PG88; 11 Mar. 2007; *JP 518*; JP det.; ZMUC C-F-123001 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 1 Dec. 2019; *JP 1564*; JP det.; ZMUC C-F-124324 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 23 Mar. 2017; *JP 469*; JP det.; ZMUC C-F-122953 • ibid.; 14 Apr. 2013; *JP 786*; JP det.; ZMUC C-F-123281 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1242*; JP det.; ZMUC C-F-123769 • Tokkekøb Hegn; 55°52.334′ N, 12°22.229′ E; UB39; 12 Apr. 2018; *JP 1026*; JP det.; ZMUC C-F-123536. – **Nordvestsjælland (NWZ)** • Klinteskov ved Tissø; 55°34.569′ N, 11°18.882′ E; PG46; 24 Oct. 2018; *JP 1214*; JP det.; ZMUC C-F-123741 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 846*; JP det.; ZMUC C-F-123341 • Sonnerup Skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 255*; JP det.; ZMUC C-F-122735. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1379*; JP det.; ZMUC C-F-123920 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1297*; JP det.; ZMUC

C-F-123830 • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; 17 Feb. 2019; *JP 1388*; JP det.; ZMUC C-F-123931 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1591*; JP det.; ZMUC C-F-124352. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1260*; JP det.; ZMUC C-F-123788.

Remarks

This species is extremely common in Denmark. Thalli are more frequent on both sides of the abdomen of its hosts, where they show a strongly curved perithecial stalk cell (VI) which forces the perithecia to project laterally (Fig. 47E); thalli from legs show a more straight habitus (Fig. 47F).

Genus ***Cryptandromyces*** Thaxt.
MB#1307

Proceedings of the American Academy of Arts and Sciences 48: 173 (Thaxter 1912a) emend. Santam. (hoc opus). – Type species: *C. geniculatus* Thaxt.

Peyerimhoffiella Maire, *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 7: 18 (Maire 1916a) [MB#3855]

Brief description

Monoecious or dioecious. Receptacle three-celled. Cells II and III separated by an oblique or vertical septum, in contact or not with cell I. Primary appendage free, consisting of several superposed cells; simple or sparsely branched, bearing lateral sessile or subsessile antheridia, or rarely functioning themselves as phialides and then with a lateral efferent neck (see *C. bibloplecti*). Perithecium with five cells in each vertical row of outer wall cells which are equal or almost equal in height (Fig. 48F).

Remarks

With the two new species here described, the genus consists of 21 species, of which six in Europe, all in Denmark. The most recently described species are *C. euplecti* (Santamaria 2001a), *C. pinguis* and *C. tricornis* (Haelewaters *et al.* 2021). Seven of the species grow on Pselaphinae (Col. Staphylinidae), viz.: *C. batrisi* (Thaxt.) I.I.Tav., *C. batrisoceni* (Thaxt.) I.I.Tav., *C. bibloplecti* T.Majewski, *C. bryaxidis* T.Majewski, *C. elegans* (Maire) W.Rossi & Castaldo, *C. euplecti* Santam., *C. zethopsi* (Thaxt.) I.I.Tav.; twelve on Scydmaeninae (Staphylinidae): *C. cauliculatus* (Thaxt.) I.I.Tav., *C. danicus* Santam. sp. nov., *C. geniculatus* Thaxt., *C. incurvatus* (Thaxt.) I.I.Tav., *C. isabellae* W.Rossi, *C. javanus* Thaxt., *C. nigromarginatus* (Thaxt.) I.I.Tav., *C. pinguis* Santam. & W.Rossi, *C. sarawakensis* (Thaxt.) I.I.Tav., *C. scydmaenarius* (Thaxt.) I.I.Tav., *C. scydmaenicola* (Thaxt.) I.I.Tav., *C. tricornis* Santam. & W.Rossi; one on Cryptophagidae: *C. cryptophagi* Santam. sp. nov., and the last on Forficulidae (Dermaptera): *C. laboulbenioides* (Thaxt.) I.I.Tav. This genus is well-recognized chiefly by two characteristics: (1) appendage consisting of cells functioning themselves as phialides or with lateral sessile or subsessile antheridia, and (2) perithecial wall cells are equal or subequal in length and five in number for each vertical row.

Key to the Danish species (partially following Santamaria 2003)

1. Appendage entirely hyaline, lacking brown suffusions 2
– Appendage with the 1–3 basal cells ± darkened, especially towards the outer margin. On several genera of Col. Staphylinidae Pselaphinae ..... ***C. euplecti*** Santam.

2. Cell III not in contact with cell I. Cells II and III superposed 3
– Cell III in contact with cell I. Cells II and III adnate, ± parallel, separated by a vertical or strongly oblique septum. On *Bibloplectus* Reitter, 1882 and *Plectophloeus* Reitter, 1891 (Col. Staphylinidae Pselaphinae) ..... ***C. bibloplecti*** T.Majewski

3. One to few stout solitary antheridia on the inner side of each of the 1–5 appendage lowermost cells, especially on the first, next above the primary septum. On several genera of Col. Staphylinidae Pselaphinae but mostly on *Brachygluta* Thomson, 1859 .... ***C. elegans*** (Maire) W.Rossi & Castaldo
– Antheridia unknown or, if present, not as above 4

4. Appendage ± elongate, consisting of several superposed globose cells. Perithecial apex with four small teeth below the conical tip. On *Bryaxis* Kugelann, 1794 (Col. Staphylinidae Pselaphinae) .... ***C. bryaxidis*** T.Majewski
– Appendage and perithecial apex different. On beetles other than pselaphids 5

5. Cell VII very large, distinctively bulging. Cell I with a thin marginal dark stripe. On *Cryptophagus* (Col. Cryptophagidae) ..... ***C. cryptophagi*** Santam. sp. nov.
– Cell VII normal. Cell I without darkening on the margin. On *Euconnus wetterhallii* (Col. Staphylinidae Scydmaeninae) ..... ***C. danicus*** Santam. sp. nov.

Cryptandromyces bibloplecti T.Majewski
MB#128600
Fig. 48

Acta Mycologica 25 (1): 43 (Majewski 1990a). – **Type**: "On *Bibloplectus ambiguus* (Reich.) (Coleoptera, Pselaphidae): Bachus (Chelm voiv.), reserve Bachus I, section 71, *Tilio–Carpinetum*, bank of woodland lake, 5.6.1986, leg. T. Majewski (TM. … 3623 – holotype)"; KRAM. [Poland]

Diagnostic features

Thallus very small, up to 100 µm long. Appendage unbranched. Cells II and III ± parallel, separated by an almost vertical septum. Cell III in contact with cell I. [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

Species known on *Bibloplectus* from the type locality (Poland) and reported here from Denmark, on *Plectophloeus* from Spain (Santamaria 2001a), and on an undetermined host from Belgium (De Kesel *et al.* 2020). Probably also on *Tychus* Leach, 1817 (here reported). Hosts belong to Col. Staphylinidae Pselaphinae.

Collections examined from Denmark

On *Bibloplectus ambiguus* (Reichenbach, 1816) (Col. Staphylinidae Pselaphinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 844*; JP det.; ZMUC C-F-123339.

On *Tychus niger* (Paykull, 1800) (Col. Staphylinidae Pselaphinae)
DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1295*; JP det.; ZMUC C-F-123827, C-F-123828.

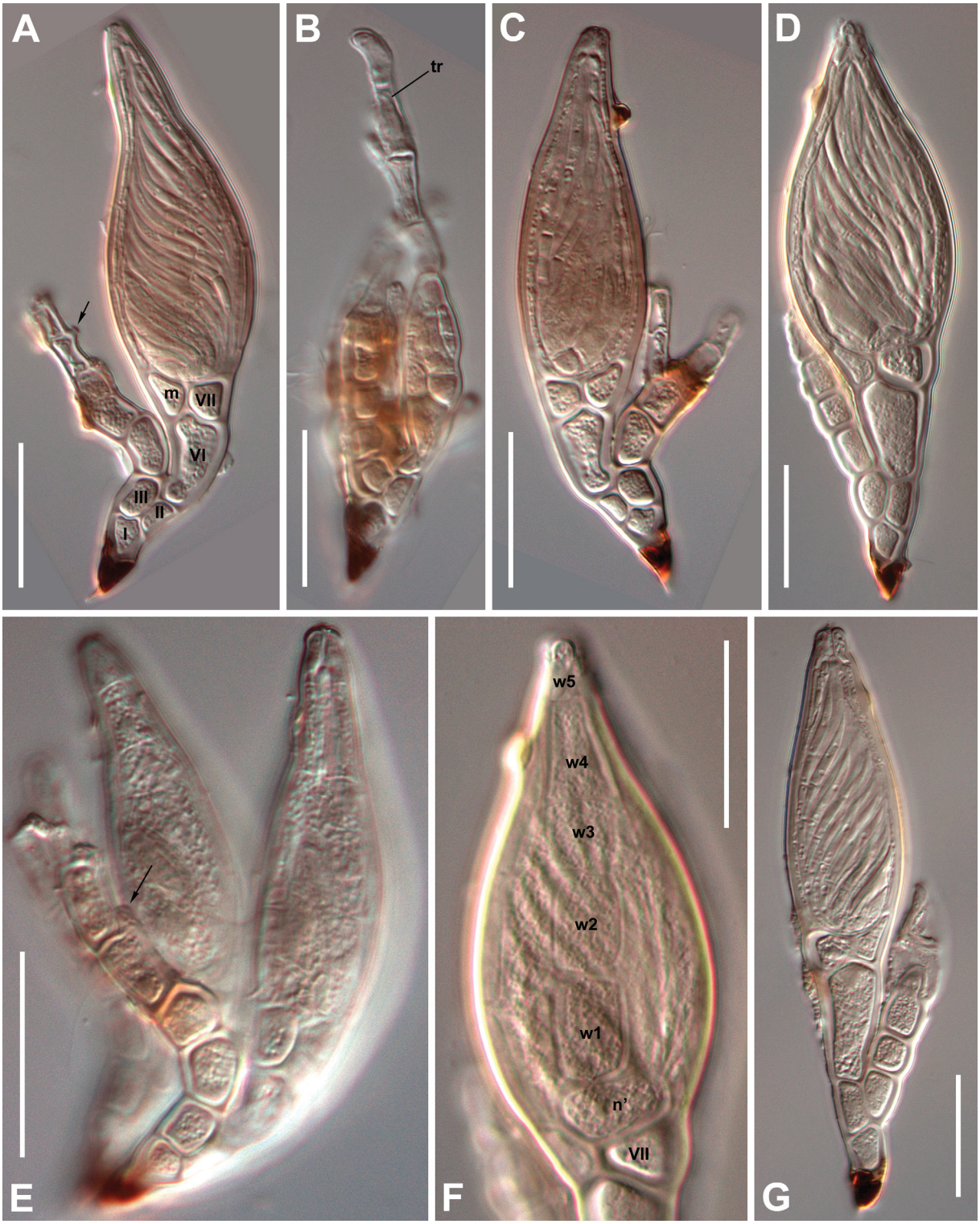

Fig. 48. *Cryptandromyces bibloplecti* T.Majewski. **A**. Mature thallus showing probable efferent necks of antheridia (arrow) and labelling of some thallial cells (I, II, III, VI, VII, and m). **B**. Immature thallus showing trichogyne (tr). **C**–**D**, **G**. Mature thalli. **E**. Paired mature thalli showing probably efferent neck of an antheridium (arrow). **F**. Perithecium in detail with labelling of cells VII, n', and w_{1-5}. **A**–**C**, **E**. From *Bibloplectus ambiguus*. **D**, **F**–**G**. From *Tychus niger*. Scale bars: 20 µm. Photographs from slides ZMUC C-F-123339 (A–C, E), ZMUC C-F-123827 (D, F–G).

Remarks

First record from Denmark. Antheridia were not described in the protologue but their presence in the form of small phialides in upper inner corner of 2nd and 3rd cells of the appendage was suggested by Majewski (1994b). In some thalli from *Bibloplectus ambiguus* (Fig. 48A, E, arrows), we have observed what seems to be efferent necks or their remains. This suggests that the appendicular cells may function directly as phialides. The occurrence of a trichogyne (Fig. 48B, tr) supports the idea of the presence of antheridia.

Thalli collected on *Tychus niger* (Fig. 48D, F–G) have been provisionally classified as *C. bibloplecti*. These fungi do not differ substantially from those described on *Bibloplectus* and *Plectophloeus*. Scheloske (1969) reported *Cryptandromyces elegans* on *Tychus* from Germany without figures.

Cryptandromyces bryaxidis T.Majewski
MB#459690
Fig. 49A–C

Acta Mycologica 34: 9 (Majewski 1999). – **Type**: "Holotypus: Poloniae, Bialowieza, sectio silvae 255C, super *Bryaxidis bulbiferis* (Reichenbach), 23.7.1998, leg. T. Majewski (KRAM, No TM 8665)"; KRAM.

Diagnostic features

Appendage unbranched, consisting of several superposed, almost globose cells separated by constricted septa. Some of these cells in middle and upper region of appendage with antheridia as corner cells in both sides. Perithecial apex showing four small teeth below the conical tip (Fig. 49C, arrows). [Detailed description: Santamaria 2003]

Distribution and hosts

Only known on *Bryaxis bulbifer* from the type in Poland, and from Spain on the same host genus (Santamaria 2001a) and later on *Bibloporus* Thomson, 1859 (Santamaria 2003). Hosts belong to Col. Staphylinidae Pselaphinae.

Collections examined from Denmark

On *Bryaxis bulbifer* (Reichenbach, 1816) (Col. Staphylinidae Pselaphinae)

DENMARK – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 730*; JP det.; ZMUC C-F-123223 • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1221*; JP det.; ZMUC C-F-123748 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 667*; JP det.; ZMUC C-F-123156. – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 1 Apr. 2017; *JP 252*; JP det.; ZMUC C-F-122732 • ibid.; 17 May 2019; *JP 1467*; JP det.; ZMUC C-F-124047. – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1413*; JP det.; ZMUC C-F-123959.

On *Bryaxis puncticollis* (Denny, 1825) (Col. Staphylinidae Pselaphinae)

DENMARK – **Østjylland (EJ)** • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 800*; JP det.; ZMUC C-F-123295 • Kjellerup; 56°17.614′ N, 9°26.106′ E; NH23; 18 Nov. 2017; *JP 818*; JP det.; ZMUC C-F-123312. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 731*; JP det.; ZMUC C-F-123224 • Stampeskov ved Rådvad; 55°48.367′ N, 12°33.322′ E; UB48; 24 Feb. 2019; *JP 1344*; JP det.; ZMUC C-F-123883. – **Sydsjælland (SZ)** • Villa Gallina i Hesede Skov; 55°16.335′ N, 11°56.850′ E; PG82; 8°Mar. 2015; *JP 480*; JP det.; ZMUC C-F-122964.

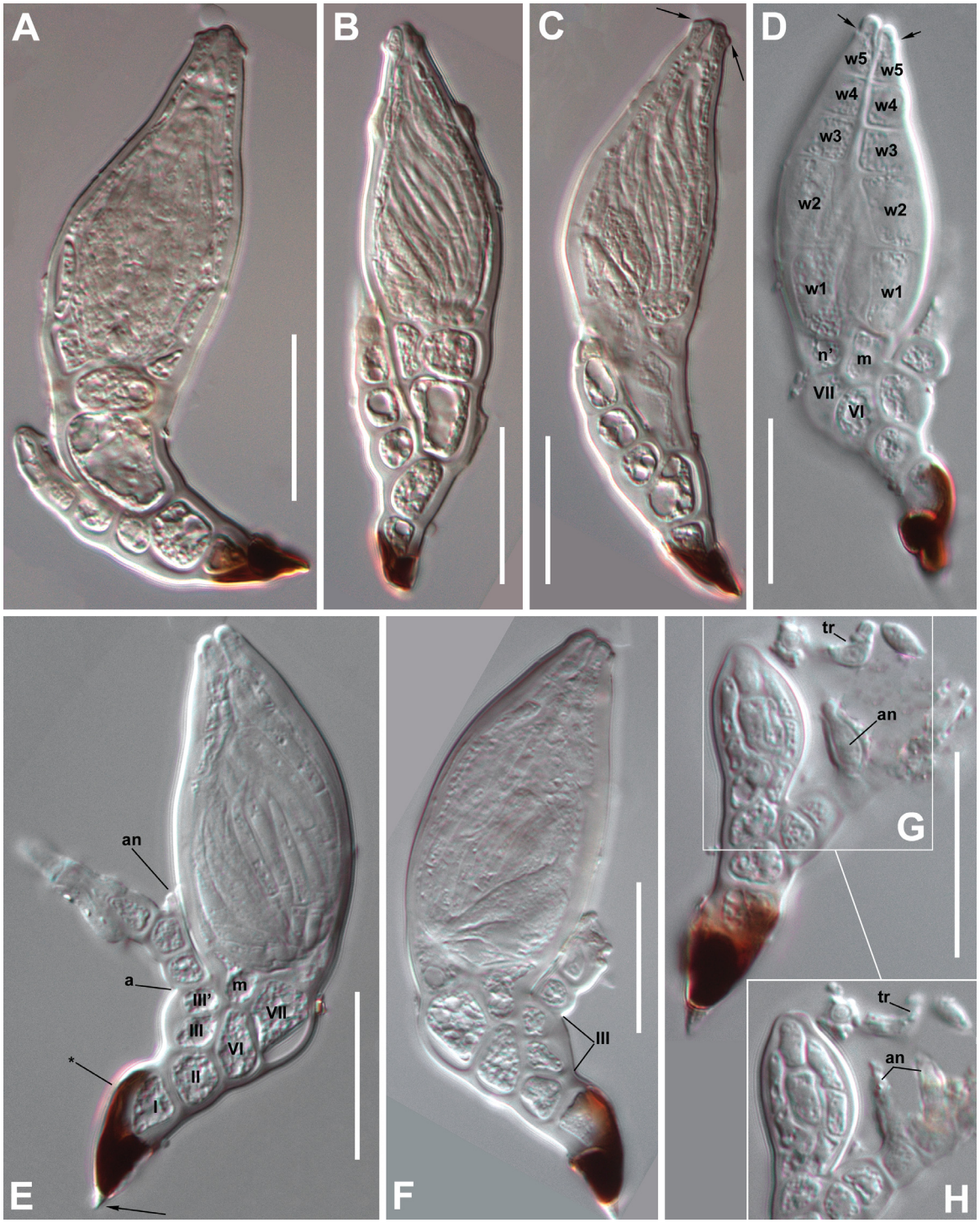

Fig. 49. *Cryptandromyces* spp. **A**–**C**. *C. bryaxidis* T.Majewski. Mature thalli. In C, arrows point to small teeth below the conical perithecial tip. – **D**–**H**. *C. cryptophagi* Santam. sp. nov. **D**. Mature thallus with labelled cells VI, VII, m, n', and two vertical rows of perithecial wall cells (w_n); arrows point to the scar through which the lips emerge. **E**. Mature thallus with labelling of cells I, II, III, III', VI, VII, m, primary septum (a), and antheridium (an); arrow points to the acute hyaline beak at the base of foot, * points to dark brown stripe on cell I. **F**. Mature thallus showing cell III. **G**–**H**. Immature thalli in detail at two focus levels to show antheridia (an), and trichogyne (tr). Scale bars: 20 µm. Photographs from slides ZMUC C-F-123224 (A–C), ZMUC C-F-123532 (D–H) (holotype).

Remarks

First record from Denmark. Before its description, *C. bryaxidis* was confused with *Cryptandromyces elegans* (Majewski 1999) but this is much larger, brightly coloured and typically bears flask-shaped phialides on the inner lower side of the appendage.

Cryptandromyces cryptophagi Santam. sp. nov.
MB#840597
Fig. 49D–H

Diagnosis

Cell I with a dorsal blackish-brown stripe. Cell VII inflated, very large, bigger than cell VI.

Etymology

The species epithet is based on the host genus *Cryptophagus*.

Type material

Holotype

DENMARK – **Nordøstsjælland (NEZ)** • Stenholtsvang; 55°57.365′ N, 12°21.254′ E; UC30; on *Cryptophagus distinguendus* Sturm, 1845 (Col. Cryptophagidae); 7 Apr. 2018; *JP 1025*; JP det.; ZMUC C-F-123532.

Isotype

DENMARK • same data as holotype; ZMUC C-F-123533, C-F-123534, C-F-123535.

Description

Thallus hyaline, except for the darkened foot and part of cell I. Basal cell of receptacle (I) obconical, with a pointed hyaline beak at base (Fig. 49E, arrow), about twice longer than broad, dorsally tinged with a dark brown stripe as a prolongation of the foot pigmentation (Fig. 49E, *). Suprabasal cell of receptacle (II) isodiametric to slightly broader than long. Cell III slightly longer than broad, above cell II and separated from it by an oblique septum; sometimes may be subdivided (Fig. 49E, III and III'; Fig. 49F, III).

Primary appendage unbranched, consisting of up to eight subequal cells, longer and narrowing towards the apex. Antheridia 1(–3) sessile, simple, bottle-shaped, borne on the inner side of the lower cells of the appendage (Fig. 49G–F, an), appearing deteriorated in mature thalli (Fig. 49E, an).

Perithecial stalk cell (VI) trapezoidal, broader than long. Cell VII very large, bigger than cell VI, with a strongly convex outer margin. Perithecium ovoidal, large, reaching half of the length of the thallus. Perithecial tip broad, with the four apical wall cells protruding like lips through a collar-like structure (Fig. 49D, arrows). Trichogyne flexuous (Fig. 49G–H, tr).

Length from foot to apex of perithecium 70–79 µm. Perithecium (not including the basal cells) 39–49 × 19–25 µm. Maximum length of primary appendage (from primary septum, when undamaged) 55 µm.

Thalli were found on the elytra of the host. The hosts were sifted from mouldy hay with many mice-nests and from moist moss and mouldy spruce needles on sun-exposed forest floor.

Remarks

This is the first species of the genus described on a beetle belonging to Cryptophagidae. It appears to be morphologically related to some species on Pselaphinae (Col. Staphylinidae) like *C. elegans* and

C. bryaxidis, but may be distinguished from them by the large, protruding cell VII, and the dark brown suffusion that extends along the outer margin of cell I. Antheridium location is similar to the arrangement in *C. elegans*, but in this species a solitary, stout antheridium is borne by the appendage basal cell, whereas in *C. cryptophagi* sp. nov. it is found on the suprabasal cell, even in cells above, becoming almost undetectable due to deterioration in the older thalli.

Lips protruding through a break near the perithecial apex is a characteristic that has been described for species of *Troglomyces*. This feature was defined as a collar-like structure or as a scar resulting from some kind of breakdown at the point where the trichogyne was attached, in the perithecial top throughout thallus development (Enghoff & Santamaria 2015).

Cryptandromyces danicus Santam. sp. nov.
MB#840598
Fig. 50

Diagnosis

Perithecium with a strongly convex margin on one side and straight to concave in the opposite side; the apex with a small rounded protuberance representing a trichogyne stump.

Etymology

The species epithet is based on Denmark.

Type material

Holotype

DENMARK – **Lolland, Falster, Møn (LFM)** • Engestofte; 54°45.767′ N, 11°33.506′ E; PF67; on *Euconnus wetterhallii* (Gyllenhal, 1813) (Col. Staphylinidae Scydmaeninae); 9 May 1952; *Johs. Andersen Dry0101*; Johs. Andersen det.; ZMUC C-F-124167.

Isotype

DENMARK • same locality and host as for holotype; 7 Jul. 1950; *F. Larsen Dry0100*; F. Larsen det.; ZMUC C-F-124166.

Description

Thallus pale yellowish, shaded in the perithecial venter. Basal cell of receptacle (I) obconical, about twice longer than broad. Suprabasal cell of receptacle (II) pentagonal, broader than long, separated from cells III and VI by oblique septa. Cell III flattened, broader than long, triangular to trapezoidal in section (Fig. 50A).

Primary appendage unbranched, rather elongate but not exceeding the perithecial apex in length, consisting of up to seven cells gradually longer upwards, but not narrowing very distinctly. Antheridia unknown.

Perithecial stalk cell (VI) two to more times as long as broad, slightly constricted towards the lower middle height. Perithecial wall cell tiers w_1 and w_2 each approximately as long as the three above (w_{3-5}) all together (Fig. 50E). Perithecium fusiform to ovoidal, with posterior margin (the side with the appendage) straight to concave, and the opposite margin quite convex. Perithecial tip subacute, variably rounded, bearing a rather conspicuous trichogyne stump on the posterior side (Fig. 50G, arrow), which may be seen when in side view as a slight rounded knob (Fig. 50C–D, arrows).

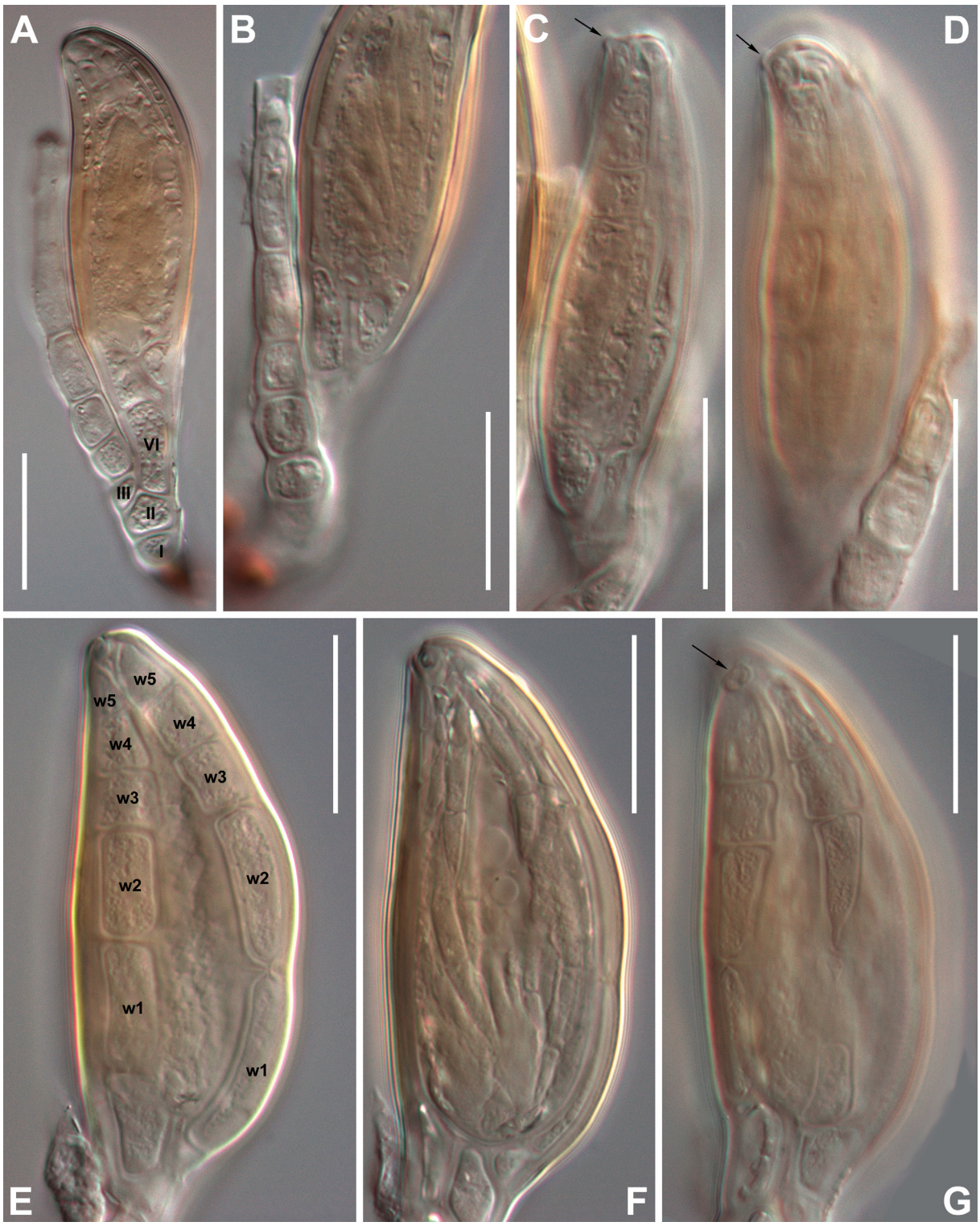

Fig. 50. *Cryptandromyces danicus* Santam. sp. nov. **A**. Submature thallus showing cells I, II, III, VI. **B**. Primary appendage in detail. **C**–**D**. Detail in side view with rounded knob at perithecial apex (arrows). **E**–**G**. Mature perithecium in detail at three focusing levels (near, middle and far, respectively) to show perithecial wall cells (w_n) and trichogyne scar (arrow). Scale bars: 20 µm. Photographs from slide ZMUC C-F-124167 (holotype).

Length from foot to apex of perithecium 86–89 µm. Perithecium (not including the basal cells) 50–60 × 19–28 µm. Maximum length of primary appendage (from primary septum, when undamaged) 52 µm.

Thalli were found on the elytra of the hosts. Nothing is known about the collecting circumstances of the hosts.

Remarks

Euconnus wetterhallii is a rarely collected ant-like stone beetle (Col. Staphylinidae Scydmaeninae) which has been reported harbouring *Stigmatomyces euconni* F.Picard (Picard 1917). A simple observation of the figure published by Picard shows us that neither the appendage with its antheridia nor the perithecia with its spiny protuberance are anything like the fungus we found. The new species reasonably fits in the genus *Cryptandromyces*. As mentioned in the genus remarks above, ten species (including the new one described here) grow on beetles of Scydmaeninae. *Cryptandromyces danicus* sp. nov. may be compared with *C. geniculatus* Thaxt., also reported on *Euconnus* (as *Connophron*) from Argentina (Thaxter 1912a) and China (Shen & Ye 2006). Although the two species are similar, the perithecium in *C. danicus* sp. nov. does not have the strong "geniculate" shape driven by some of the perithecial basal cells (probably cell VII) in *C. geniculatus*.

Cryptandromyces elegans (Maire) W.Rossi & Castaldo
MB#568984
Figs 51A–B, 105B

Plant Biosystems 138(3): 264 (Castaldo *et al.* 2004). – **Basionym**: *Peyerimhoffiella elegans* Maire, *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 7: 18 (Maire 1916a) [MB#181347]. – *Corethromyces elegans* (Maire) Thaxt. (Thaxter 1931: 366) [MB#263854]. – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "Sur les pattes et l'abdomen du Psélaphide *Brachygluta Reichei* Saulc.: Dély-Ibrahim, près Alger, 3 mars 1912 (De Borde); sur les pates de *B. dichroa* Saulc.: Djebel-Mouzaïa, juillet 1905 (P. de Peyerimhoff)". [Algeria]

Cryptandromyces brachyglutae J.Siemaszko & Siemaszko (Siemaszko & Siemaszko 1928: 205) [MB#203836]. – *Corethromyces brachyglutae* (J.Siemaszko & Siemaszko) Thaxt. (Thaxter 1931: 224) [MB#180841]

Diagnostic features

Appendage unbranched, sometimes very elongated (up to 460 µm, Majewski 1994b), consisting of several superposed and variably elongated cells. Antheridia stout, sessile or subsessile (on small supporting cells) (Fig. 51A, arrows), not rarely on a short, ramified branch (Fig. 51B, arrow) borne on the inner side of the lower cells of appendage, including cell III (Fig. 51A, III) or, less commonly, above it up to the 10th cell and even beyond. [Detailed descriptions: Majewski 1994b; Castaldo *et al.* 2004]

Distribution and hosts

Reported on Pselaphinae beetles (Col. Staphylinidae), mostly belonging to the genus *Brachygluta*, from Algeria (type) and **Europe**: Italy, Greece, Poland, France, Finland, United Kingdom, Germany (Majewski 2008), Hungary (Bánhegyi *et al.* 1985), Belgium (De Kesel & Rammeloo 1992), Sweden (Huggert 2010), the Netherlands (Haelewaters *et al.* 2014). Records on other genera different from *Brachygluta* should be checked for the identity of the fungus: *Bryaxis*, *Reichenbachia* Leach, 1826, *Rybaxis* Saulcy, 1876, *Trissemus* Jeannel, 1949, *Faronus* Aubé, 1844, *Tychus*, and *Bythinus* Leach, 1817. Records on *Bryaxis* probably refer to *Cryptandromyces bryaxidis* (Maire 1916b; Scheloske 1969; Santamaria 1989). On

Tychus we found *Cryptandromyces bibloplecti* (see above). On *Faronus*, SS has found immature thalli similar to *Cryptandromyces euplecti* from Spain (unpublished).

Collections examined from Denmark

On *Brachygluta fossulata* (Reichenbach, 1816) (Col. Staphylinidae Pselaphinae)
DENMARK – **Østjylland (EJ)** • Stidsmølle i Mattrup Skov; 55°55.455′ N, 9°33.811′ E; NG39; 19 Nov. 2017; *JP 809*; JP det.; ZMUC C-F-123304 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 983*; JP det.; ZMUC C-F-123490. – **Lolland, Falster, Møn (LFM)** • Bøtø Plantage; 54°37.629′ N, 11°57.661′ E; PF95; 17 May 2017; *JP 412*; JP det.; ZMUC C-F-122896. – **Nordøstsjælland (NEZ)** • Åsen ved Lellinge; 55°27.948′ N, 12°8.785′ E; UB15; 26 Jun. 2019; *JP 1484*; JP det.; ZMUC C-F-124069 • Lyngen ved Ølstykke; 55°47.738′ N, 12°10.253′ E; UB28; 15 May 2013; *JP 867*; JP det.; ZMUC C-F-123363 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 788*; JP det.; ZMUC C-F-123283. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 851*; JP det.; ZMUC C-F-123346. – **Sydjylland (SJ)** • Brænøre Mose; 55°23.906′ N, 9°25.714′ E; NG23; 5 Aug. 2018; JP 1165; JP det.; ZMUC C-F-123690 • Mørksø Sydøst for Kliplev; 54°52.481′ N, 9°26.561′ E; NF28; 1 Nov. 2013; *JP 355*; JP det.; ZMUC C-F-122837. – **Sydsjælland (SZ)** • Enemærket ved Næsbyholm; 55°22.429′ N, 11°36.776′ E; PG63; 17 Nov. 2019; *JP 1558*; JP det.; ZMUC C-F-124319 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1412*; JP det.; ZMUC C-F-123958 • Østerskov ved Langebæk; 54°59.421′ N, 12°6.435′ E; UA19; 19 Aug. 2019; *JP 1499*; JP det.; ZMUC C-F-124086.

On *Brachygluta helferi* (Schmidt-Goebel, 1836) (Col. Staphylinidae Pselaphinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1329*; JP det.; ZMUC C-F-123868. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 732*; JP det.; ZMUC C-F-123225 • Nord for Frederikssund; 55°51.404′ N, 12°3.534′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 404*; JP det.; ZMUC C-F-122887. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1358*; JP det.; ZMUC C-F-123896.

Remarks

First record from Denmark, where it is very common. Castaldo *et al.* (2004) brought order to the longstanding confusion between *C. brachyglutae* and *Peyerimhofiella elegans*.

Cryptandromyces euplecti Santam.
MB#474854
Fig. 51C–E

Nova Hedwigia 72 (3-4): 384 (Santamaria 2001a). – **Type**: "Spain. Barcelona: Sant Boi de Llobregat, on abdomen and elytra of *Euplectus duponti* Aubé (Coleoptera, Pselaphidae), X.1934, leg. M.Z.B., BCB-Mycotheca SS·1153d (Holotypus)"; BCB.

Diagnostic features

Appendage unbranched., with the 3–5 lower cells and cell III darkened towards the outer margin. Cells II and III ± parallel, separated by an almost vertical septum. Cell III in contact with cell I. [Detailed description: Santamaria 2003]

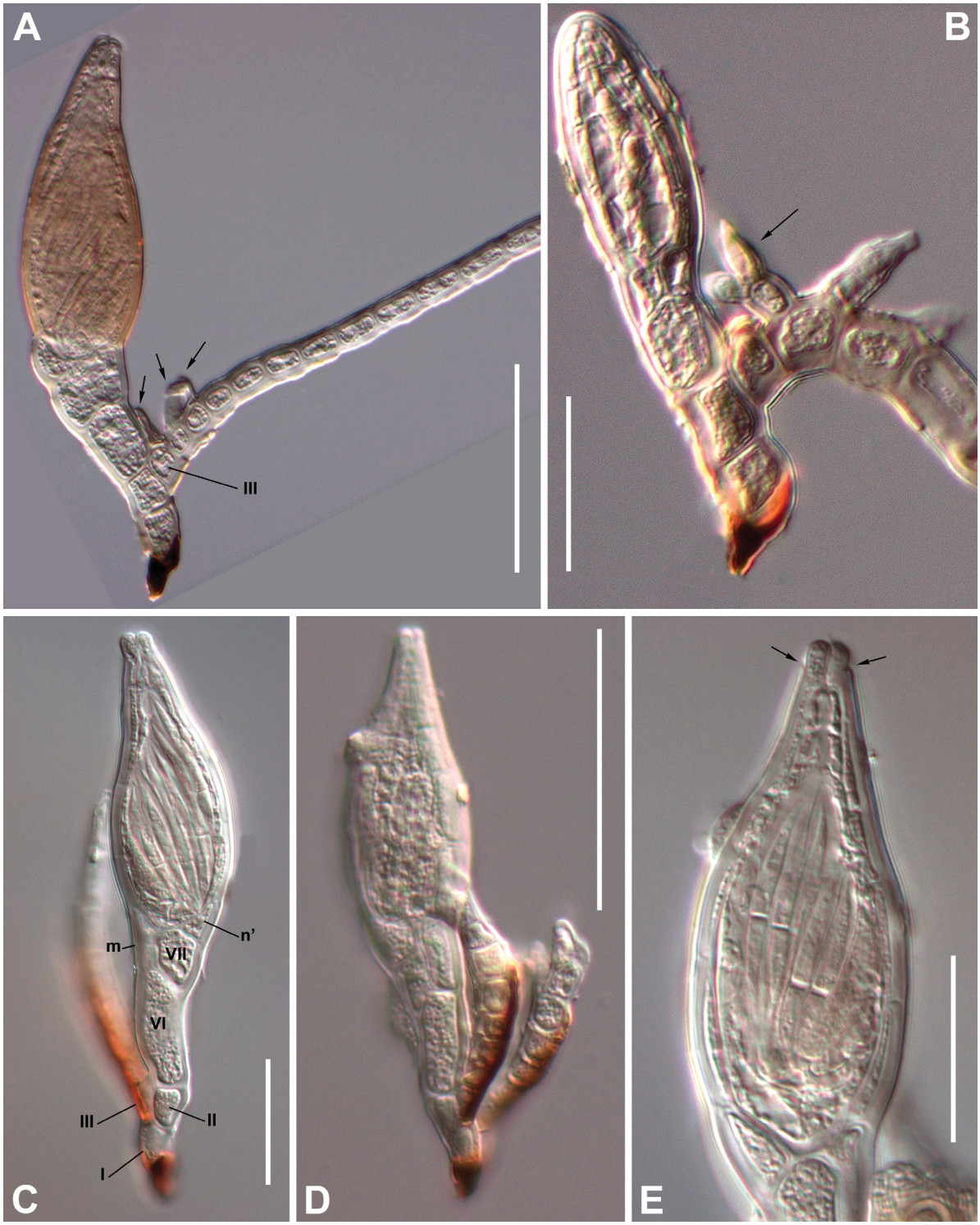

Fig. 51. *Cryptandromyces* spp. **A**–**B**. *C. elegans* (Maire) W.Rossi & Castaldo. **A**. Mature thallus showing antheridia (arrows) and cell III. **B**. Immature thallus with arrow pointing to ramified branch borne on the inner side of the lower cell of the appendage. – **C**–**E**. *C. euplecti* Santam. **C**. Mature thallus with labelled cells I, II, III, VI, VII, m and n'. **D**. A pair of thalli with primary appendages in focus. **E**. Perithecium in detail with lips protruding through a break (arrows) in apex. Scale bars: A, D = 50 µm; B = 25 µm; C, E = 20 µm. Photographs from slides ZMUC C-F-123225 (A), ZMUC C-F-122887 (B), ZMUC C-F-122946 (C–E).

Distribution and hosts

Only known from the original description on *Batrisodes* Reitter, 1882, *Euplectus* Leach, 1817 and *Plectophloeus* (Col. Staphylinidae Pselaphinae) in "Transcaucasia", Belgium, France, Spain (type) and Italy. Later, only reported once again from Belgium (De Kesel 1997).

Collections examined from Denmark

On *Bibloplectus ambiguus* (Reichenbach, 1816) (Col. Staphylinidae Pselaphinae)
DENMARK – **Nordøstsjælland (NEZ) •** Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 666*; JP det.; ZMUC C-F-123155.

On *Euplectus kirbii* Denny, 1825 (Col. Staphylinidae Pselaphinae)
DENMARK – **Lolland, Falster, Møn (LFM) •** Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 29 Nov. 2014; *JP 461*; JP det.; ZMUC C-F-122946.

Remarks

First record from Denmark. *Bibloplectus ambiguus* is a new host for the species. *Cryptandromyces euplecti* is easily distinguished by the dark brown pigmentation in the base of the appendage extending to the cell III. Antheridia are unknown. Perithecial lips protrude through a break as occurs in *C. cryptophagi* sp. nov. and species of *Troglomyces* (Fig. 51E, arrows), the latter defined by Enghoff & Santamaria (2015).

Genus ***Diphymyces*** I.I.Tav.
MB#25682

Mycologia Memoirs 9: 202 (Tavares 1985). – Type species: *D. appendiculatus* (Thaxt.) I.I.Tav.

Brief description

Monoecious. Receptacle three-celled. Cell II connected along its whole length with cell VI, thus separated by a vertical septum one from the other. Primary appendage free, consisting of several superposed cells, ± profusely branched, bearing intercalary antheridia. Perithecium with four cells in each vertical row of outer wall cells; usually with apical and/or subapical outgrowths.

Remarks

The genus consists of 26 species, of which six in Europe, one in Denmark. The most recently described species are *D. torresii* (Rossi *et al.* 2020), and *D. oryoti* (Rossi & Christian 2020). On Col. Leiodidae Cholevinae beetles with the exception of three species that occur on Col. Leiodidae Coloniinae: *D. appendiculatus* (Thaxt.) I.I.Tav., on Col. Staphylinidae: *D. penicillifer* A.Weir & W.Rossi, and on Col. Tenebrionidae: undescribed species by Hughes (2008) (see De Kesel & Haelewaters 2019).

Diphymyces niger (T.Majewski) I.I.Tav.
MB#105264
Fig. 52A–B

Mycologia Memoirs 9: 203 (Tavares 1985). – **Basionym**: *Corethromyces niger* T.Majewski, *Acta Mycologica* 9(1): 114 (Majewski 1973a) [MB#311808]. – **Type**: "On *Ptomaphagus sericatus* (Chaud.) (Col. Catopidae): Ojców near Kraków Saspowska valley, 8.6.1971, leg. A. Kosior (TM. 919 – holotype)"; KRAM. [Poland]

Laboulbenia ptomaphagi Huggert (Huggert 1973: 249) [MB#316150]

Diagnostic features

Thallus stocky, up to 80–90 µm long; entirely dark brown with the exception of paler appendage and cell I. Appendage profusely branched. Perithecial tip bearing one stout, tooth-like prominence (Fig. 52B, arrow). [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

On members of the genus *Ptomaphagus* (Col. Leiodidae) from Poland, France, Spain, United Kingdom, Czech Republic, Russia, Finland, Denmark, Sweden (Majewski 2008), Italy (Balazuc 1973b), Bulgaria and Slovenia (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Ptomaphagus sericatus* (Chaudoir, 1845) (Col. Leiodidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 3 Aug. 2019; *JP 1489*; JP det.; ZMUC C-F-124075.

On *Ptomaphagus subvillosus* (Goeze, 1777) (Col. Leiodidae)

DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1294*; JP det.; ZMUC C-F-123826.

Remarks

The recently collected specimens confirm the previous record from Denmark (Huggert 1973).

Genus ***Dipodomyces*** Thaxt.

MB#1633

Memoirs of the American Academy of Arts and Sciences 16: 267 (Thaxter 1931). – Type species: *D. monstruosus* Thaxt.

Brief description

Monoecious. Receptacle two- or three-celled. *Dipodomyces monstruosus* has a two-celled receptacle, showing an abnormal thallus development and a very unusual thallus structure (Tavares 1985). *Dipodomyces phloeocharidis* has a normal structure and will be discussed hereafter.

Remarks

The genus consists of two species, the European *D. phloeocharidis* and the type *D. monstruosus* Thaxt. from Cameroon.

Dipodomyces phloeocharidis T.Majewski

MB#110622

Fig. 52C–G

Acta Mycologica 17 (1–2): 55 (Majewski 1982). – **Type**: "On *Phloeocharis subtilissima* Mann. (Col., Staphylinidae): Pomiechówek near Nowy Dwór Mazowiecki (Warszawa voivodeship), under the bark of dry, standing *Pinus sylvestris* in a pine wood close to the Wkra river,… 21.8.1977 (TM. … 1701 – holotype), leg. T. Majewski"; KRAM. [Poland]

Diagnostic features

Primary appendage consisting of a main axis of three superposed cells (Fig. 52C, *), once to three times ramified in branches terminated by elongated antheridia. Primary septum slightly constricted and darkened (Fig. 52C, a). A spinous process (the original spore apex, sx) is found on the outer side of the 4th cell of the primary appendage (Fig. 52F, sx). Perithecium asymmetric, with a strongly convex outer margin and a straight inner margin, gradually tapering towards the pointed apex which shows three long and one short acute lips. [Detailed description: Majewski 1994b]

Distribution and hosts

Known only from the type host in Poland.

Collections examined from Denmark

On *Phloeocharis subtilissima* Mannerheim, 1830 (Col. Staphylinidae Phloeocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Liseleje; 56°1.048′ N, 11°58.454′ E; PH81; 14 Sep. 2014; *JP 39*; JP det.; ZMUC C-F-122514.

Remarks

First record from Denmark and the first outside the type country. The host is quite common and widespread in Denmark and not difficult to find under dead and dry bark of various trees (both conifers and deciduous trees), but the fungus is apparently very rarely collected. This species greatly differs from *D. monstruosus*, the type of the genus, and its inclusion in *Dipodomyces* requires an emendation of the generic diagnosis (Majewski 1982), or the description of a new genus. The trichogyne of this species shows an unusual subspherical shape (Fig. 52G, tr). Worth mentioning is the presence of reduced male thalli with apparently functional antheridia, accompanying the normal monoecious thalli (Fig. 52E). A photo of this species is given here for the first time.

Genus ***Distolomyces*** Thaxt.
MB#1674

Memoirs of the American Academy of Arts and Sciences 16: 97 (Thaxter 1931). – Type species: *D. fijianus* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cells I, II, and III separated by diagonal septa; all three cells in contact. Primary appendage free, bent towards the perithecium, consisting of 1–2 superposed cells and 1–2 terminal slender antheridia. Perithecium with four cells in each vertical row of outer wall cells; apex bearing 1–2 slender ligula-like outgrowths.

Remarks

The genus consists of four species, of which one in Europe. The most recently described species is *D. euborelliae* (Sugiyama & Majewski 1985a). All occurring on earwigs (Dermaptera) (see Santamaria 2003).

Fig. 52. A–**B**. *Diphymyces niger* (T.Majewski) I.I.Tav. Mature thalli. Some cells are labelled in B, as I, II, III and VI, as well as the stout, tooth-like prominence, on the perithecial tip (arrow). – **C**–**G**. *Dipodomyces phloeocharidis* T.Majewski. **C**. Mature thallus showing cells I, II, III, the primary septum (a), and the main axis of the primary appendage consisting of three superposed cells (*). **D**. Mature thallus. **E**. Reduced male thallus with apparently two functional antheridia. **F**–**G**. Immature thalli showing the original spore apex as a spinous process (sx) and trichogyne (tr). – **H**–**I**. *Distolomyces forficulae* (T.Majewski) I.I.Tav. Mature thalli. Scale bars: A–D, F–H = 50 µm; E, I = 25 µm. Photographs from slides ZMUC C-F-123826 (A), ZMUC C-F-124075 (B), ZMUC C-F-122514 (C–G), ZMUC C-F-124076 (H–I).

Distolomyces forficulae (T.Majewski) I.I.Tav.
MB#105280
Fig. 52H–I

Mycologia Memoirs 9: 207 (Tavares 1985). – **Basionym**: *Hesperomyces forficulae* T.Majewski, *Acta Mycologica* 10(2): 270 (Majewski 1974) [MB#315184]. – **Type**: "On *Forficula auricularia* L. (Dermaptera, Forficulidae): Warszawa–Marymont, in a small garden near the Vistula, 6.8.1973 leg. T.Majewski (TM. 1334 – holotype)"; KRAM. [Poland]

Diagnostic features

Receptacle with two dark spots, one on cell III and the other between cells I and II. Cell III flattened, bulging outwards. Appendage slanted between the basal and 2nd cells; consisting of three superposed cells, the humped, dark, as well as elongate basal cell, and the almost hyaline 2nd cell which is separated with a strongly oblique septum from the terminal flask-shaped and spinose antheridium. Perithecial apex bearing two ligula-like, strongly divergent, geniculate outgrowths. [Detailed descriptions: Majewski 1994b; Santamaria 2003; De Kesel & Gerstmans 2012]

Distribution and hosts

Only known on *Forficula auricularia* (Dermaptera, Forficulidae), typically growing on antennae. Reported from Poland, Spain, Portugal, Italy (Majewski 2008), Belgium and the Netherlands (De Kesel & Gerstmans 2012).

Collections examined from Denmark

On *Forficula auricularia* Linnaeus, 1758 (Dermaptera Forficulidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 3 Aug. 2019; *JP 1490*; JP det.; ZMUC C-F-124076. – **Nordvestsjælland (NWZ)** • Eriksminde syd for Korshage; 55°57.744′ N, 11°46.504′ E; PH70; 27 Oct. 2019; *JP 1534*; JP det.; ZMUC C-F-124293. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 3 Aug. 2019; *JP 1491*; JP det.; ZMUC C-F-124077.

Remarks

First record from Denmark. Probably overlooked, it may be a less rare species than can be deduced from the paucity or low amount of records.

Genus ***Hesperomyces*** Thaxt.
MB#2310

Proceedings of the American Academy of Arts and Sciences 25: 264 (Thaxter 1891). – Type species: *H. virescens* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cells I and II separated by an oblique septum. Cell III in contact with cell I and to a certain extent with cell VI. Primary appendage free, consisting of several superposed cells, each (except for the basal cell) giving rise to 1–2 lateral antheridia, where the uppermost bears a dorsal spinous process (the original spore apex, sx). Perithecium with four cells in each vertical row of outer wall cells; the perithecial tip bears a complex of subapical and apical lobes. Trichogyne two-celled, consisting of a basal cell bearing one apically papillate cell.

Remarks

The genus consists of ten species (Das *et al.* 2018), of which three in Europe, two in Denmark. The most recently described species is *H. halyziae* (Haelewaters & De Kesel 2020). This is perhaps one of the most studied and recorded genera in the laboulbenialean literature, especially concerning the mostly frequent species, *Hesperomyces virescens* Thaxt., well-studied both under SEM and light microscopy (Weir & Beakes 1996), one of the first Laboulbeniales to be sequenced (Weir & Blackwell 2001), and intensively reported and studied because of its presence on the invasive coccinellid beetle, the harlequin ladybird *Harmonia axyridis* (Garces & Williams 2004).

Key to the Danish species (partially following Santamaria – 2003–)

1. Perithecial tip with four lobes reaching approximately the same height. Lower lobes larger than upper lobes. On Col. Coccinellidae of the subfamily Scymninae ..... ***H. coccinelloides*** (Thaxt.) Thaxt.
– Upper lobes much longer and larger than minute lower lobes. On several genera of Col. Coccinellidae ..... ***H. virescens*** Thaxt.

Hesperomyces coccinelloides (Thaxt.) Thaxt.
MB#261211
Fig. 53A–B

Memoirs of the American Academy of Arts and Sciences 16: 110 (Thaxter 1931). – **Basionym**: *Stigmatomyces coccinelloides* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 52: 704 (Thaxter 1917) [MB#175707; as *S. coccinellidae*]. – **Type**: "On the elytra of minute species of Coccinellidae: No. 2560 (Type) …, Grenada (Brues)"; FH.

Diagnostic features

Thallus hyaline to pale yellowish. Primary appendage consisting of four superposed cells, where the 3rd and 4th bear one and two antheridia respectively. Perithecial tip with two broad lower lobes, two short and small upper lobes and two prominent lips surrounding the ostiole. [Detailed descriptions: Santamaria 2003; De Kesel 2011]

Distribution and hosts

Occurs on Col. Coccinellidae of the genus *Scymnus* Kugelann, 1794 and relatives like *Diomus* Mulsant, 1850 and *Stethorus* Weise, 1885 from **Europe**: Spain (Santamaria 1995b), Belgium (De Kesel 2011), Poland (Ceryngier 2013); **America**: Grenada (type), Jamaica (Thaxter 1917), USA (Seymour 1967), Panama, Trinidad & Tobago (Thaxter 1931), Brazil (Rossi & Bergonzo 2008), Ecuador (Proaño Castro & Rossi 2008); and **Asia**: Philippines (Thaxter 1931).

Collections examined from Denmark

On *Stethorus pusillus* (Herbst, 1797) (Col. Coccinellidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Sakskøbing, Tårsvej.; 54°50.433′ N, 11°39.106′ E; PF78; 20 Jun.–19 Oct. 2019; *P.N. Buhl 1578*; JP det.; ZMUC C-F-124339. – **Nordøstsjælland (NEZ)** • Brønshøj Kirkegård; 55°42.387′ N, 12°29.915′ E; UB47; 24 Jun. 2019; *JP 1482*; JP det.; ZMUC C-F-124067 • Hellerup; 55°44.024′ N, 12°33.014′ E; UB47; 2–4 Aug. 2019; *H. Enghoff 1486*; H. Enghoff det.; ZMUC C-F-124071 • Nørrebro i København N.; 55°42.332′ N, 12°33.228′ E; UB47; 18 Jun. 2019; *JP 1479*; JP det.; ZMUC C-F-124064 • Rødovre; 55°39.663′ N, 12°27.490′ E; UB37; 8 Jun. 2018; *JP 1138*; JP det.; ZMUC C-F-123662.

Remarks

First record from Denmark. This species is probably more frequent in Europe that the scarce number of records seems to indicate.

Hesperomyces virescens Thaxt.
MB#140369
Fig. 53C–D

Proceedings of the American Academy of Arts and Sciences 25: 264 (Thaxter 1891). – *Stigmatomyces virescens* Thaxt. (Thaxter 1894: 106) [MB#181575]. – **Type**: "On *Chilocorus bivulnerus*, California"; FH. [USA]

Hesperomyces hyperaspidis Thaxt. (Thaxter 1931: 111) [MB#267531]

Diagnostic features

Thallus bright yellow. Primary appendage consisting of (3–)4 superposed cells, where the 3rd and 4th bear one and two antheridia respectively. Perithecial tip with two very short and narrow lower lobes, two elongated upper lobes and two prominent lips surrounding the ostiole. [Detailed descriptions: Weir & Beakes 1996; Santamaria 2003; De Kesel 2011]

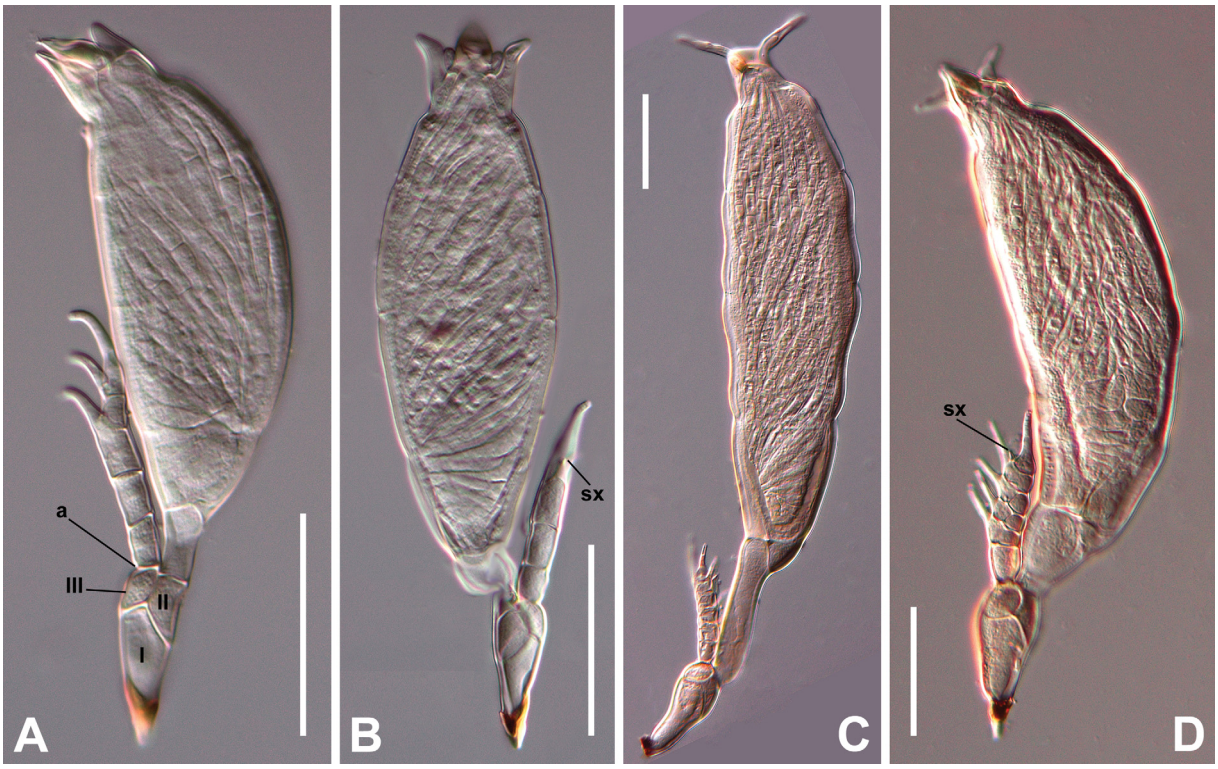

Fig. 53. *Hesperomyces* spp. **A**–**B**. *H. coccinelloides* (Thaxt.) Thaxt. Mature thalli showing labelled cells I, II, III, primary septum (a), and a spinous process from the original spore apex (sx). – **C**–**D**. *H. virescens* Thaxt. Mature thalli. In D, "sx" corresponds to the spiny original spore apex. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123662 (A–B), ZMUC C-F-124113 (C), ZMUC C-F-124109 (D).

Distribution and hosts

A very common and widespread species. Reported on no less than 30 species and 20 genera of ladybird species (Col. Coccinellidae) from the five continents (Haelewaters *et al.* 2017). Also reported from Denmark (see Table 1).

Collections examined from Denmark

On *Adalia bipunctata* (Linnaeus, 1758) (Col. Coccinellidae)

DENMARK – **Nordøstsjælland (NEZ)** • Blågårds Plads, Nørrebro; 55°41.183′ N, 12°33.424′ E; UB47; 8 Nov. 2007; *T. Steenberg Dry0047*; T. Steenberg det.; ZMUC C-F-124113 • Grøndalsparken, Vanløse; 55°41.351′ N, 12°30.518′ E; UB47; May 2011; *T. Steenberg Dry0043*; T. Steenberg det.; ZMUC C-F-124109 • Grønningen, København K.; 55°41.385′ N, 12°35.435′ E; UB47; 15 Jan. 2008; *T. Steenberg Dry0044*; T. Steenberg det.; ZMUC C-F-124110 • Kongens Have, København K.; 55°41.107′ N, 12°34.766′ E; UB47; 10 Nov. 2007; *T. Steenberg Dry0045*; T. Steenberg det.; ZMUC C-F-124111 • Thorvaldsensvej, Frederiksberg; 55°40.857′ N, 12°32.540′ E; UB47; 26 May 2009; *T. Steenberg Dry0046*; T. Steenberg det.; ZMUC C-F-124112.

Remarks

All the Danish records of this species come from specimens kept in dry museum collections. Perhaps a collective species including at least other seven undescribed taxa which have been revealed by sequencing thalli from multiple host species (Haelewaters *et al.* 2018a; Haelewaters & De Kesel 2020). According to Haelewaters & De Kesel (2020), the Danish samples collected on *Adalia* Mulsant, 1850 fall into the named *Adalia*-clade and should belong to some yet undescribed species separate from *H. virescens*, a species what is suggested by Haelewaters *et al.* (2018a) to be restricted to fungi found on *Chilocorus* Leach, 1815, as originally described.

Genus ***Rhadinomyces*** Thaxt.

MB#4687

Proceedings of the American Academy of Arts and Sciences 28: 179 (Thaxter 1893). – Type species: *R. pallidus* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Primary appendage free, consisting of several superposed cells bearing lateral sterile branches. Clustered antheridia on branchlets arising from corner cells on cell III and lower cells of appendage axis. Perithecium with four cells in each vertical row of outer wall cells.

Remarks

The genus consists of two or three species depending on whether *Rhadinomyces cristatus* Thaxt. is regarded as a synonym of *R. pallidus*; the other species is *Rhadinomyces gracilis* (Thaxt.) I.I.Tav. from Argentina and Uruguay (Tavares 1985). The segregation of this genus from *Corethromyces* has been widely debated. According to the literature *Rhadinomyces* is distinguished from *Corethromyces* because in the former some antheridial branchlets arise from corner cells of axial cells in the appendage. A thorough revision of the genus *Corethromyces* and allied genera is highly desirable, but this will require the help of molecular techniques.

Rhadinomyces pallidus Thaxt.
MB#193503
Figs 54, 105C

Proceedings of the American Academy of Arts and Sciences 28: 180 (Thaxter 1893). – *Corethromyces pallidus* (Thaxt.) Thaxt. (Thaxter 1912a: 180) [MB#433859] (nec *Corethromyces pallidus* Speg. (1917: 493) [MB#516952], nomen praeoccupum changed to *C. stereocephali* Thaxt. (1931: 218) [MB#278848]). – **Type**: [Not designated] [Ind. loc.] "On *Lathrobium punctulatum* Lee. and *L. angulare* Lee, Massachusetts. On *L. fulvipenne* Grav., Germany"; FH.

Rhadinomyces cristatus Thaxt. (Thaxter 1893: 180) [MB#193337]. – *Corethromyces cristatus* (Thaxt.) Thaxt. (Thaxter 1912a: 180) [MB#433857]

Diagnostic features

Cell II bearing 1–2(–3) perithecia or their initials, often on opposite sides. Above the cell II, 1–2 ± elongated cells bear upper corner cells in one side or on opposite sides giving rise to short branchlets bearing series of flask-shaped antheridia (Fig. 54F). Higher on the axis a similar cell forms the base of the appendage which consists of few to many variably elongated simple branches. [Detailed descriptions: Thaxter 1896; Majewski & Sugiyama 1985; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Known from several countries in Europe, USA, and Japan (Santamaria *et al.* 1991; Majewski 2008). Recent records are from Latvia (De Kesel & Krastina De Kesel 2006, as *R. cristatus*), Belgium (De Kesel & Gerstmans 2011, as *R. cristatus*), Sweden (Huggert 2010, as *R. pallidus*). Grows on *Lathrobium* and related genera, as *Tetartopeus* Czwalina, 1888 (Col. Staphylinidae Paederinae).

Collections examined from Denmark

On *Lathrobium brunnipes* (Fabricius, 1792) (Col. Staphylinidae Paederinae)

DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 752*; JP det.; ZMUC C-F-123246 • Hald Ege; 56°24.287′ N, 9°20.550′ E; NH25; 19 Oct. 2013; *JP 798*; JP det.; ZMUC C-F-123293 • Kjellerup; 56°17.282′ N, 9°26.197′ E; NH23; 16 Oct. 2014; *JP 321*; JP det.; ZMUC C-F-122799 • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015; *JP & H. Liljehult 512*; JP det.; ZMUC C-F-122995. – **Fyn (F)** • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; *JP 1068*; JP det.; ZMUC C-F-123585. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 7 May 2017; *JP 648*; JP det.; ZMUC C-F-123137 • ibid.; 4 Jun. 2018; *JP 1132*; JP det.; ZMUC C-F-123655. – **Nordøstsjælland (NEZ)** • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1217*; JP det.; ZMUC C-F-123744 • Gurre Vang; 56°1.470′ N, 12°29.486′ E; UC41; 14 Apr. 2017; *JP 271*; JP det.; ZMUC C-F-122750 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 670*; JP det.; ZMUC C-F-123159 • Mølleå ved Farum Lillevang; 55°49.093′ N, 12°18.496′ E; UB38; 24 Feb. 2018; *JP 990*; JP det.; ZMUC C-F-123497 • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 29 Apr. 2017; *JP 401*; JP det.; ZMUC C-F-122884 • Risby; 55°41.112′ N, 12°19.625′ E; UB37; 21 Mar. 2019; *J. Søgaard Hansen 1462*; JP det.; ZMUC C-F-124013 • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; 18 Nov. 2018; *JP 1243*; JP det.; ZMUC C-F-123770 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 785*; JP det.; ZMUC C-F-123280 • ibid.; 23 Mar. 2017; *JP 468*; JP det.; ZMUC C-F-122952. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 558*; JP det.; ZMUC C-F-123044. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 847*; JP det.; ZMUC C-F-123342 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1

Fig. 54. *Rhadinomyces pallidus* Thaxt. **A**. Mature thallus from type slide kept in FH; cell II is labelled. **B**–**E**, **G**–**I**. Mature thalli showing variability. **F**. Branch with antheridia in detail. Scale bars: A–E, G–I = 50 µm; F = 25 µm. Photographs from slides FH4591 (A) (type), ZMUC C-F-123008 (B, H–I), ZMUC C-F-122788 (C, E–F), ZMUC C-F-123585 (D), ZMUC C-F-122952 (G).

May 2013; *JP 762*; JP det.; ZMUC C-F-123256. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Jun. 2019; *JP 1472*; JP det.; ZMUC C-F-124052 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1408*; JP det.; ZMUC C-F-123954 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1380*; JP det.; ZMUC C-F-123921 • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 22 Jul. 2013; *H. Enghoff 309*; JP det.; ZMUC C-F-122788 • ibid.; 1–15 Aug. 2013; *JP 524*; JP det.; ZMUC C-F-123008 • Villa Gallina i Hesede Skov; 55°16.335′ N, 11°56.850′ E; PG82; 8 Mar. 2015; *JP 478*; JP det.; ZMUC C-F-122962. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1261*; JP det.; ZMUC C-F-123789.

On *Lathrobium fulvipenne* (Gravenhorst, 1806) (Col. Staphylinidae Paederinae)

DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1300*; JP det.; ZMUC C-F-123834.

On *Lathrobium geminum* Kraatz, 1857 (Col. Staphylinidae Paederinae)

DENMARK – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 557*; JP det.; ZMUC C-F-123043. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1262*; JP det.; ZMUC C-F-123790.

On *Tetartopeus quadratus* (Paykull, 1789) (Col. Staphylinidae Paederinae)

DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 18 Jan. 2015; *JP 449*; JP det.; ZMUC C-F-122934. – **Nordøstsjælland (NEZ)** • Damhusmosen; 55°41.119′ N, 12°28.169′ E; UB47; 26 Apr. 1896; *F. de Tengnagel Dry0124*; F. de Tengnagel det.; ZMUC C-F-124191 • Nærum; 55°48.976′ N, 12°32.253′ E; UB48; 2 May 1946; *Johs. Petersen Dry0122*; Johs. Petersen det.; ZMUC C-F-124189. – **Sydsjælland (SZ)** • Hulemose Sø; 55°0.214′ N, 11°58.466′ E; PF89; 29 Apr. 1917; *Chr. Engelhart Dry0123*; Chr. Engelhart det.; ZMUC C-F-124190.

On *Tetartopeus terminatus* (Gravenhorst, 1802) (Col. Staphylinidae Paederinae)

DENMARK – **Nordøstsjælland (NEZ)** • Boserup; 55°39.746′ N, 12°2.173′ E; UB17; 19 Sep. 1935; *Johs. Andersen Dry0118*; Johs. Andersen; ZMUC C-F-124185 • Frederiksdal; 55°46.873′ N, 12°26.858′ E; UB48; May? 1850; *leg. unknown Dry0121*; det. unknown; ZMUC C-F-124188. – **Sydsjælland (SZ)** • Munkeskov ved Bjerrede; 55°23.115′ N, 12°0.768′ E; UB14; 13 Sep. 1954; *U. Kornerup Dry0120*; U. Kornerup det.; ZMUC C-F-124187.

Other material examined

Type of *Rhadinomyces pallidus*

UNITED STATES • "*Rhadinomyces pallidus*, slide from FH, #4591, barcode 00313731, **type**, on *Lathrobium* sp., from Kittery Point, Maine, York County (USA), 08-1892"; FH[00313731] [includes three mature thalli in fair condition. (Fig. 54A)]

Remarks

First record from Denmark. This may be regarded as a variable species with roughly defined characters or as a collective species including several, not yet established species. The position of the primary septum has not been described. Two to three cells may be found above cell II; these form the thallial axis and the base of the appendage. The lowermost of these cells seems to be reasonably accepted as cell III but when a second cell is present above, with corner cells and branchlets bearing antheridia, a new difficulty appears, viz., identifying this new cell as the result of a cell III division, or as corresponding to the proper basal cell of the primary appendage (Majewski 1994b).

Thaxter (1896: 305–307) seemed not to be very convinced about the segregation of *R. pallidus* from *R. cristatus* and even about the separation of the genus *Rhadinomyces* from *Corethromyces*. The

characteristics distinguishing *R. pallidus* and *R. cristatus* are undeniably confusing. Some authors have considered them conspecific (Siemaszko & Siemaszko 1932; Balazuc 1973b) but others, as Majewski & Sugiyama (1985) distinguished *R. pallidus* from *R. cristatus* because in the former all parts of the thallus are distinctly shorter and paler, and because the antheridial branchlets arise only on the anterior side of the receptacle. Majewski (1994b) followed this criterion, and although he seemed to agree with the uncertainty concerning distinguishing both taxa he concluded that both species definitely differ by means of features displayed in his key, i.e.,: (1) *R. cristatus* – perithecia (including initials) typically on opposite sides of cell II; distal cells of receptacle and basal cells of appendage form corner cells on opposite sides; cell VI much shorter than the combination of cell III and basal cell of appendage; (2) *R. pallidus* – perithecia formed on one side of the thallus, posterior side of receptacle and appendage being sterile; cell VI about of the same length or longer than cell III and basal of appendage taken together.

Aware of the confusion, we decided to request the loan of the type slides from FH (see above under other material examined). According to the curatorial services, only one slide associated with the genus *Rhadinomyces* exists, labelled as the type for *Rhadinomyces pallidus*, whereas there are no clues about *R. cristatus*. The thalli in the borrowed slide are in fair condition and consist of three thalli (Fig. 54A). Unfortunately, its study does not help us to clarify the status of these two species.

Supported by the study of the very abundant material collected from Denmark, we conclude that it is impossible to separate the two species only with the available morphological characters. The variability is great and the limits between different forms become blurred. We challenge the reader to distinguish the two species with the images that we have included in Fig. 54.

Genus ***Rossiomyces*** R.K.Benj.
MB#28566

Aliso 19: 132 (Benjamin 2001). – Type species: *R. falcatus* (T.Majewski) R.K.Benj. (by monotypy)

Brief description

Monoecious. Receptacle three-celled. Primary appendage free, consisting of three superposed cells, where the median and upper cells give rise to antheridia, with a spinous process on the upper cell (Fig. 55B, sx). Perithecium with five cells in each vertical row of outer wall cells; showing apical conspicuous prominences.

Remarks

Monotypic. Benjamin (2001) reviewed and narrowed the limits of the genus *Autophagomyces*, erecting the new genus *Rossiomyces* based on *Autophagomyces falcatus* T.Majewski, with a combination of the following seven characteristics: (1) the structure of primary appendage (see brief description above), (2) the spinous process formed by the original spore, (3) cells I and II separated by a strongly oblique septum, (4) cells III and II separated by a strongly oblique septum, the first in contact with cell I, (5) the simple or bifurcate trichogyne, (6) the small remnant of trichogyne, and (7) the five tiered perithecial outer wall. Waiting for the discovery of additional species, it is currently difficult to delimit specific characters from generic ones.

Rossiomyces falcatus (T.Majewski) R.K.Benj.
MB#484468
Fig. 55A–B

Aliso 19: 133 (Benjamin 2001). – **Basionym**: *Autophagomyces falcatus* T.Majewski, *Acta Mycologica* 9(2): 229 (Majewski 1973c) [MB#309403]. – **Type**: "On *Cryptophagus pilosus* Gyll. (Col. Cryptophagidae): Kurzeszyn Nowy, Rawa Mazowiecka county, in a cellar, … leg. T. Majewski… 11.7.1972 (TM…. 1044 – holotype)"; KRAM. [Poland]

Diagnostic features

See genus description. [Detailed description: Majewski 1994b]

Distribution and hosts

Described from Poland, it has been collected in Finland (Huldén 1983), United Kingdom (Weir & Beakes 1993), USA, Italy (Benjamin 2001), and Sweden (Huggert 2010). Occurs on *Cryptophagus* spp. (Col. Cryptophagidae).

Collections examined from Denmark

On *Cryptophagus distinguendus* Sturm, 1845 (Col. Cryptophagidae)
DENMARK – **Nordvestsjælland (NWZ)** • Sonnerup skov; 55°56.525′ N, 11°33.988′ E; PH60; 1 Apr. 2017; *JP 253*; JP det.; ZMUC C-F-122733.

Remarks

First record from Denmark. This species has been reported in neighbouring countries, therefore its presence in Denmark is not surprising.

Genus ***Sphaleromyces*** Thaxt.
MB#5130

Proceedings of the American Academy of Arts and Sciences 29: 95 (Thaxter 1894). – Type species: *S. lathrobii* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cells II and III separated by a vertical or oblique septum. Primary appendage free, consisting of several superposed cells bearing on the inner side short lateral branches with intercalary and terminal antheridia; a spinous process directed outwards is found on the preapical region. Perithecium with five cells in each vertical row of outer wall cells.

Remarks

This genus consists of four or five species, depending on whether *Sphaleromyces montevideensis* (Speg.) I.I.Tav. (Tavares 1985) belongs here. Only *S. lathrobii* is known from Europe. No new species have been added after Thaxter's descriptions. Distinctiveness of this genus from *Corethromyces* will remain debatable until the whole set of similar genera (e.g., *Diphymyces*, *Rhadinomyces*, *Stichomyces*, etc.) may be studied and compared on the basis of modern techniques.

Sphaleromyces lathrobii Thaxt.
MB#212018
Fig. 55C–D

Proceedings of the American Academy of Arts and Sciences 29: 95 (Thaxter 1894). – **Type**: [Not designated] [Ind. loc.] "On *Lathrobium nitidulum* Lee. and *L. punctulatum* Lee. Kittery Point, Maine"; FH. [USA]

Corethromyces lathrobii (Thaxt.) Thaxt. (Thaxter 1912a: 180) [MB#433858]

Diagnostic features

Cells I and II elongate and overlapping, separated by an oblique septum. Cell III almost longer than cell II and sometimes contacting with cell I, slightly protruding dorsally below the primary septum (Fig. 55C, arrow). Appendage consisting of several superposed cells separated by strongly diagonal septa, giving rise to short branchlets including antheridia pointing to the perithecium. [Detailed description: Majewski 1994b]

Distribution and hosts

Usually on Col. Staphylinidae Paederinae of the genus *Lathrobium*, but also reported on *Philonthus* (Balazuc 1990). Recorded from USA (type), Poland, United Kingdom, France, Spain (Majewski 2008), and Sweden (Huggert 2010).

Collections examined from Denmark

On *Tetartopeus terminatus* (Gravenhorst, 1802) (Col. Staphylinidae Paederinae)
DENMARK – **Nordøstsjælland (NEZ)** • Sortemose; 55°48.061′ N, 12°20.120′ E; UB38; 16 Feb. 1949; *A. West Dry0119*; A. West det.; ZMUC C-F-124186.

Remarks

First record from Denmark. The Danish material consists of a single thallus, which was found among thalli of the common *Rhadinomyces pallidus*. As the Danish thallus is not in great condition, we include an image of a thallus from Spain (Fig. 55D) from material published in Santamaria (1995b), for comparison.

Genus ***Stichomyces*** Thaxt.
MB#5233

Proceedings of the American Academy of Arts and Sciences 37: 37 (Thaxter 1901b). – Type species: *C. conosomatis* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cell II and occasionally cell III giving rise to perithecia. Primary appendage free, forming a main axis like a prolongation of the receptacle; consisting of several superposed cells bearing lateral fertile or sterile branches borne on upper, opposite corner cells. Antheridia flask-shaped, solitary or clustered on branches. Perithecium with four cells in each vertical row of outer wall cells.

Remarks

The genus consists of three species: *S. capensis* Thaxt., *S. sumatrae* Thaxt., and the generitypus *S. conosomatis*, which is the only European species. This genus belongs to a group of genera closely related to *Corethromyces*, and revision is required to verify its distinctiveness. *Stichomyces* was isolated because cell III is sterile or gives rise to a perithecium, seldom to antheridial branchlets which are more

abundant on nearby cells of the appendage above. In *Rhadinomyces*, cell III bears antheridial branchlets which are less often formed on following cells of the appendage above. In *Corethromyces*, antheridial branchlets do not arise from corner cells as in *Stichomyces* and *Rhadinomyces*. As can be understood, the characteristics do not seem very substantial.

Stichomyces conosomatis Thaxt.
MB#200264
Fig. 55E–G

Proceedings of the American Academy of Arts and Sciences 37: 38 (Thaxter 1901b, as *conosomae*). – **Type**: "USA, Massachusetts, Belmont/Waltham, Waverley neighborhood, October 1901, R. Thaxter, on *Sepedophilus littoreus* (L., 1758), slide FH 00313505"; FH. [lectotype designated by Haelewaters *et al.* 2015b: 471]

Stichomyces europaeus T.Majewski (Majewski 1973a: 121) [MB#324091]

Diagnostic features

Cell II giving rise to one or two perithecia on opposite sides, usually from the same axial cell. Cell III giving rise to perithecia, to antheridial or to sterile branchlets. The appendage as a continuation of the receptacle forms a median axis in symmetrical thalli (Fig. 55E). [Detailed descriptions: Thaxter 1908; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Exclusively associated with beetles of the genus *Sepedophilus* (= *Conosoma* Kraatz, 1857) (Col. Staphylinidae Tachyporinae). Recently it has been recorded on *Speonemadus* Jeannel, 1922 (Col. Leiodidae) from Portugal by Reboleira *et al.* (2017), a rare case of host shift (sensu Rossi 2011). This species occurs in **Europe** (Spain, United Kingdom, France, Belgium, Italy, Poland, Greece), Northern **Africa** (Algeria), Eastern **Asia** (Japan) and North **America** (USA) (Majewski 2008). Also in Sweden (Huggert 2010), the Netherlands (Haelewaters & De Kesel 2010), Ecuador (Bernardi *et al.* 2014), Panama (Haelewaters *et al.* 2017), Portugal (Reboleira *et al.* 2017), Bulgaria (Rossi *et al.* 2019a), and Slovakia (Rossi *et al.* 2019b).

Collections examined from Denmark

On *Sepedophilus immaculatus* (Stephens, 1832) (Col. Staphylinidae Tachyporinae)
DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 673*; JP det.; ZMUC C-F-123162.

On S*epedophilus nigripennis* (Stephens, 1832) (Col. Staphylinidae Tachyporinae)
DENMARK – **Fyn (F)** • Ristinge; 54°49.793′ N, 10°38.242′ E; PF07; 7 Jun. 1940; *Christiani Dry0184*; Christiani det.; ZMUC C-F-124249.

On *Sepedophilus pedicularius* (Gravenhorst, 1802) (Col. Staphylinidae Tachyporinae)
DENMARK – **Fyn (F)** • Åløkke; 55°20.398′ N, 10°43.115′ E; PG03; Sep. 1896; *N.P. Jørgensen Dry0181*; N.P. Jørgensen det.; ZMUC C-F-124246. – **Nordøstsjælland (NEZ)** • Hillerød; 55°55.716′ N, 12°18.312′ E; UC30; 6 Apr. 1882; *Schiødte Dry0182*; Schiødte det.; ZMUC C-F-124247 • Løjesø; 55°49.922′ N, 12°28.867′ E; UB49; 28 Mar. 1954; *Johs. Petersen Dry0183*; Johs. Petersen det.; ZMUC C-F-124248. – **Nordvestsjælland (NWZ)** • Sonnerup Skov; 55°56.643′ N, 11°34.213′ E; PH60; 1 Apr. 2017; *JP 249*; JP det.; ZMUC C-F-122729.

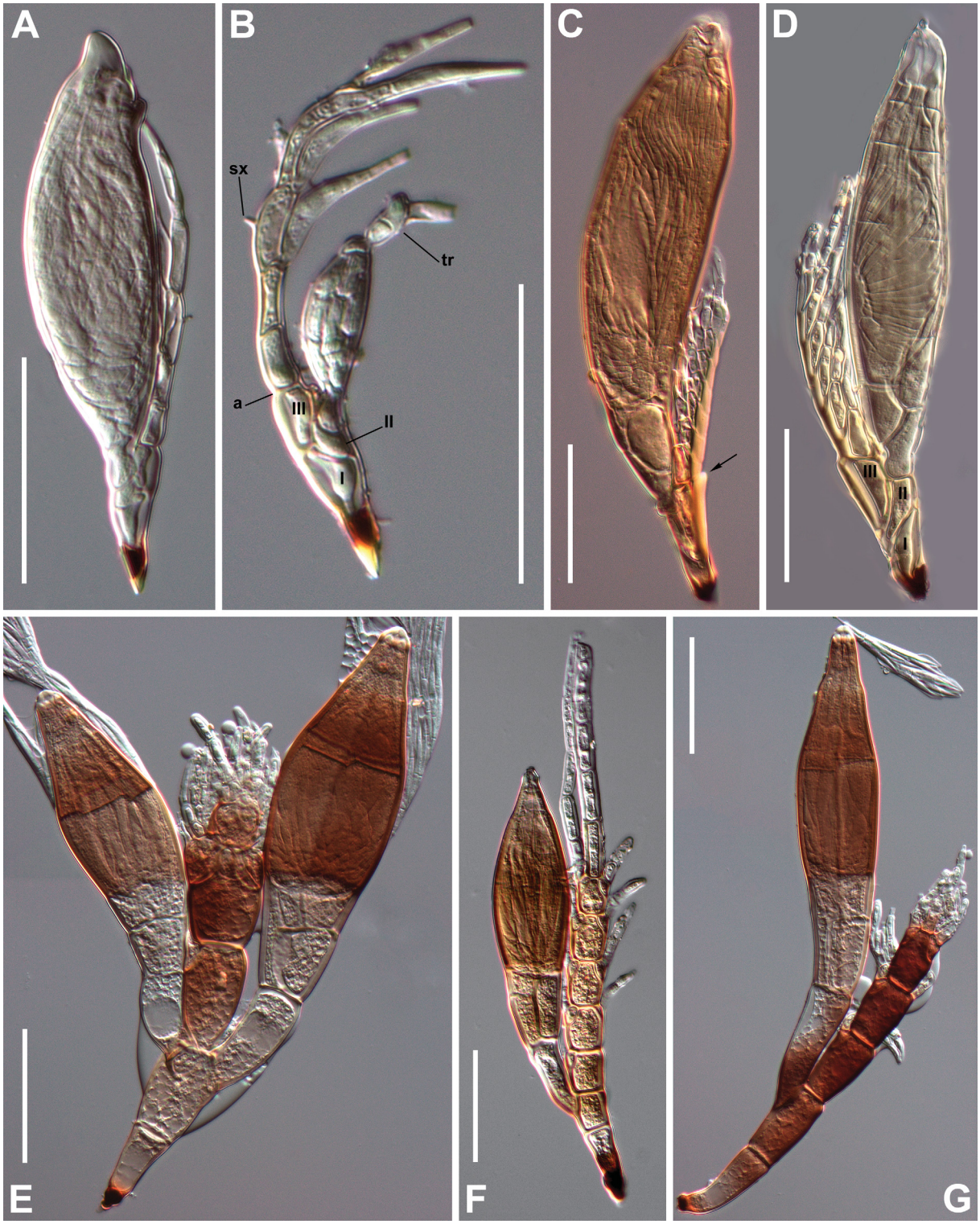

Fig. 55. A–**B**. *Rossiomyces falcatus* (T.Majewski) R.K.Benj. **A**. Mature thallus. **B**. Immature thallus showing labelled cells I, II, III, primary septum (a), trichogyne (tr), and spinous process from the original spore apex (sx). – **C**–**D**. *Sphaleromyces lathrobii* Thaxt. **C**. Mature thallus showing protrusion of cell III (arrow). **D**. Mature thallus from Spain showing labelled cells I, II and III. – **E**–**G**. *Stichomyces conosomatis* Thaxt. Mature thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122733 (A–B), ZMUC C-F-124186 (C), BCB-SS1543a (D), ZMUC C-F-122729 (E, G), ZMUC C-F-122630 (F).

On *Sepedophilus testaceus* (Fabricius, 1793) (Col. Staphylinidae Tachyporinae)

DENMARK – **Bornholm (B)** • Raghammer Odde; 55°1.193′ N, 14 55.777′ E; VA99; 13 Sep. 2016; *JP 120*; JP det.; ZMUC C-F-122597. – **Nordøstjylland (NEJ)** • Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 19 May 2013; *JP 315*; JP det.; ZMUC C-F-122794. – **Nordøstsjælland (NEZ)** • Bognæs Storskov; 55°41.242′ N, 12°1.678′ E; UB17; 1 Aug. 2013; *JP 364*; JP det.; ZMUC C-F-122847 • Brøndby; 55°39.245′ N, 12°24.778′ E; UB37; 10 May 2014; *JP 150*; JP det.; ZMUC C-F-122630 • Klinten ved Selsø; 55°44.158′ N, 11°59.634′ E; PG88; 11 Mar. 2007; *JP 519*; JP det.; ZMUC C-F-123002.

Remarks

First record from Denmark. This species is extremely variable in number of perithecia, length and branching of appendages, and pigmentation. It may represent a collective species; thus further studies are needed to distinguish probably undescribed taxa.

Genus ***Stigmatomyces*** H.Karst.
MB#5253

Chemismus der Pflanzenzelle. Eine morphologisch-chemische Untersuchung der Hefe: 78 (Karsten 1869). – Type species: *S. baeri* (Knoch) Peyrit.

Appendicularia Peck, *Annual Report on the New York State Museum of Natural History* 38: 95 (Peck 1885) [MB#288]
Appendiculina Berl., *Malpighia* 3: 59 (Berlese 1889) [MB#290]
Peckifungus Kuntze, *Revisio Generum Plantarum* 2: 864 (Kuntze 1891) [MB#3783]
Fanniomyces T.Majewski, *Acta Mycologica* 8 (2): 229 (Majewski 1972b) [MB#1973]

Brief description

Monoecious. Receptacle three-celled (Fig. 56A). Cell III (within this genus sometimes known as "appendage stalk cell") laterally adnate to cell VI (Fig. 56B). Primary appendage free, consisting of a basal cell (Fig. 56A, bc a) supporting a series of superposed cells bearing sidewise paired or solitary antheridia with corresponding supporting cells, alternatively bearing short ramified branchlets including terminal solitary flask-shaped antheridia (formerly species included in the genus *Fanniomyces*, Fig. 56A–D); sometimes basal and apical cells show variations of this arrangement. Perithecium with four cells in each vertical row of outer wall cells.

Remarks

This is a large genus consisting of 156 species, of which 49 in Europe, 14 in Denmark. The most recently described species are *S. ferrugineus* (Rossi & Leonardi 2020) and *S. scaptodrosophilae* (Rossi & Christian 2020). Nowadays, the genus *Stigmatomyces* only comprises species living on Diptera. The primary appendage design displays a great uniformity (except for the species included in the disputed genus *Fanniomyces*) and is a main characteristic to separating species.

According to Haelewaters *et al.* (2020), based on SSU-LSU ribosomal DNA two-locus studies, the genus *Stigmatomyces* is paraphyletic, including four clades: (I) two species formerly in *Fanniomyces* (*F. burdigalensis* and *F. ceratophorus*); (II) three species, viz. *S. gregarius*, *S. scaptomyzae* and *S. entomophilus*, the latter being the type of the previously described genus *Appendiculina*; (III) species included at present in the genus *Gloeandromyces*, and a clade (IV) including the remaining five analyzed species of *Stigmatomyces*. Based on this study, *Fanniomyces* and *Appendiculina* are reinstated for the species included in clades I and II, respectively. In that work, 14 species of *Stigmatomyces* have been sequenced, a number which is recognized by the authors themselves to be too low to pretend a

phylogenetic reconstruction of the genus. Although the taxa formerly included in *Fanniomyces* show distinctive morphological characteristics in the appendage structure, Weir & Rossi (1995) considered these of minor importance and synonymized the genus. The three species placed in the genus *Appendiculina* reinstated by Haelewaters *et al.* (2020) do not show any distinctive morphological characteristic that separate them from the species of *Stigmatomyces* included in clade IV. Also, because the number of the analysed species is very limited, because the distances in the phylogenetic tree are small, and because the split is not supported by morphological differences we prefer to treat the genus *Stigmatomyces* in a broad sense.

Key to the Danish species

1. Appendage branched (the cells forming the appendage axis give rise to short branchlets bearing antheridia). Former genus *Fanniomyces*..... ***S. burdigalensis*** (Balazuc) A.Weir & W.Rossi
– Appendage unbranched (compact series of superposed cells bearing lateral antheridia with respective supporting cells). *Stigmatomyces* s. str. 2

2. Perithecial apex showing a lip which extends into a pointed projection; w_3 and w_4 inflated by constrictions of septa w_3-w_4 and w_2-w_3. On *Hydrellia* Robineau-Desvoidy, 1830 (Diptera Ephydridae). ..... ***S. hydrelliae*** Thaxt.
– Perithecial tip different. On other hosts 3

3. Antheridia directed outwards. On Diptera Drosophilidae 4
– Antheridia directed inwards. On other Diptera..... 6

4. Venter of perithecium distally enlarged; perithecium with an arcuate neck. On *Scaptomyza* Hardy, 1850 and *Parascaptomyza* Duda, 1924 (Diptera Drosophilidae)..... ***S. scaptomyzae*** Thaxt.
– Venter of perithecium broadest in the middle; perithecium with an almost straight neck. On *Drosophila* Fallén, 1823 (Diptera Drosophilidae)..... 5

5. Appendage consisting of a basal cell supporting five superposed cells. On *Drosophila* subgenus *Drosophila* Sturtevant, 1939..... ***S. entomophilus*** (Peck) Thaxt.
– Appendage consisting of a basal cell supporting four superposed cells. On *Drosophila* subgenus *Sophophora* Sturtevant, 1939 ..... ***S. majewskii*** H.L.Dainat, Manier & Balazuc

6. Appendage consisting of a ± darkened and usually flattened basal cell supporting a series of several obliquely located, outwards bulging cells, bearing elongated antheridia on the inner side. Cell VI as long or longer than cell III. Mostly on Diptera Sphaeroceridae 7
– Appendage consisting of cells which are longer than broad, with straight outer margins, separated by horizontal septa. Cell VI shorter than cell III. On other Diptera 11

7. Venter of perithecium with ± distinct protuberances below the neck..... 8
– Venter of perithecium without such protuberances 9

8. Appendage consisting of a slightly darkened basal cell and a series of 3–9 superposed cells. Cell VII not protruding. On Diptera Sphaeroceridae belonging to the genera *Leptocera* Olivier, 1813, *Spelobia* Spuler, 1924, *Apteromyia* Vimmer, 1929, and *Limosina* Macquart, 1835..... ***S. divergatus*** Thaxt.
– Appendage consisting of a darkened basal cell and a series of 5–6 superposed cells. Cell VII protruding below the perithecium. On *Pullimosina* Roháček, 1983 (Diptera Sphaeroceridae) ....***S. platensis*** Speg.

9. Perithecial stalk cell (VI), secondary stalk cell (VII) and basal cells (m, n, n') forming a well distinguished peduncle, longer than the appendage ..... ***S. limosinae*** Thaxt.
– Perithecial stalk cell (VI), secondary stalk cell (VII) and basal cells (m, n, n') not forming a peduncle; taken together much shorter than the appendage..... 10

10. Appendage hyaline, contrasting with the dark, flattened basal cell; consisting of 5–6 cells which are much longer than wide, giving rise to broad antheridia with their large supporting cells. Distal part of appendage directed backwards. On *Thoracochaeta* Duda, 1918 (Diptera Sphaeroceridae) ..... ***S. thoracochaetae*** Santam. sp. nov.
– Appendage ± brownish pigmented, consisting of up to 12–13 almost strongly flattened cells, giving rise to antheridia bearing very elongated necks. Distal part of appendage oriented normally. On other genera of Diptera Sphaeroceridae..... ***S. crassicollis*** Thaxt.

11. Perithecial outer wall cells arranged spirally and forming conspicuous ridges on the venter..... 12
– Perithecial outer wall cells arranged vertically, not forming ridges 13

12. Appendage consisting of a darkened basal cell giving rise to a series of five cells. On *Geomyza* Fallén, 1810 (Diptera Opomyzidae) ..... ***S. geomyzae*** W.Rossi & Cesari
– Appendage consisting of a hyaline basal cell giving rise to a series of three cells. On *Scatella* Robineau-Desvoidy, 1830 (Diptera Ephydridae) ..... ***S. purpureus*** Thaxt.

13. Appendage consisting of a small basal cell giving rise to a series of three cells, the lower cell much longer than the others. Perithecium with eight round prominences, four at w_1-w_2 and four at w_2-w_3 septa. On Diptera Chloropidae..... ***S. constrictus*** Thaxt.
– Appendage consisting of a basal cell giving rise to a series of four similar cells. Perithecium with four distal prominences on the venter. On Diptera Ephydridae.... ***S. ephydrae*** L.Mercier & R.Poiss.

Stigmatomyces burdigalensis (Balazuc) A.Weir & W.Rossi
MB#414204
Fig. 56A–D

Mycological Research 99: 843 (Weir & Rossi 1995). – **Basionym**: *Fanniomyces burdigalensis* Balazuc, *Revue de Mycologie* 43 (4): 402 (Balazuc 1979) [MB#314066]. – **Type**: "Parasitus Sphaerocerae (Apterinae) pedestris (Meigen) (Diptera, Cyclorhapha, Drosophiloidea, Sphaeroceridae) in Aquitania. Typus in auctoris musaeo. [Deux exemplaires sur le sommet de la tête d'un *Sphaerocera pedestris* (Meigen) (Diptères Cyclorhaphes Drosophiloidea Sphaeroceridae) des marais de Parempuyre (Gironde), à 10 Km au nord de Bordeaux, 6 au 15-IV-1978, G. Tempere leg.]"; PC. [France]

Fanniomyces copromyzae Huldén (Huldén 1983: 50) [MB#107967]

Diagnostic features

Axis of the appendage long, consisting of a dark basal cell and five superposed, sympodial arranged cells, each giving rise to short branchlets bearing flask-shaped antheridia (Fig. 56C). Perithecial neck well-distinguished, with slightly undulate margins and a conical tip (Fig. 56D). [Detailed description: De Kesel & Hanssens 2007]

Distribution and hosts

Infects flies of the genera *Sphaerocera* Latreille, 1804, *Crumomyia* Macquart, 1835, and *Copromyza* Duda, 1923 (Diptera Sphaeroceridae). Recorded from France (type), Finland (type of *Fanniomyces copromyzae*,

Huldén 1983), United Kingdom (Weir & Rossi 1995), Belgium (De Kesel & Hanssens 2007), Czech Republic (Rossi *et al.* 2010), and Portugal (Goldmann & Weir 2018).

Collections examined from Denmark

On *Copromyza stercoraria* (Meigen, 1830) (Diptera Sphaeroceridae)
DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 1188*; W. Gritsch det.; ZMUC C-F-123712. – **Lolland, Falster, Møn (LFM)** • Hydeskov; 54°46.344′ N, 11°42.799′ E; PF77; 21 Aug. 1964; *N. M. Andersen Dry0003*; V. Michelsen det.; ZMUC C-F-124016. – **Nordøstjylland (NEJ)** • Knarmod i Tofte Skov; 56°51.824′ N, 10°15.470′ E; NJ70; 8–22 Aug. 2013; *I. Aggerholm 1187*; W. Gritsch det.; ZMUC C-F-123711 • ibid.; 19 Sep.–2 Oct. 2013; *I. Aggerholm 1186*; W. Gritsch det.; ZMUC C-F-123710 • Uggerby Plantage; 57°35.000′ N, 10°5.000′ E; NJ68; 25 Jul. 1990; *T. Munk Dry0002*; V. Michelsen det.; ZMUC C-F-124015. – **Nordøstsjælland (NEZ)** • Pinseskoven; 55°35.839′ N, 12°33.250′ E; UB46; 6–20 May 2017; *W. Gritsch 1185*; W. Gritsch det.; ZMUC C-F-123709.

On *Crumomyia fimetarii* (Meigen, 1830) (Diptera Sphaeroceridae)
DENMARK – **Nordøstsjælland (NEZ)** • Pinseskoven; 55°35.839′ N, 12°33.250′ E; UB46; 7–23 May 2016; *W. Gritsch 1183*; W. Gritsch det.; ZMUC C-F-123707.

On *Crumomyia glabrifrons* (Meigen, 1830) (Diptera Sphaeroceridae)
DENMARK – **Østjylland (EJ)** • Kolding; 55°28.892′ N, 9°26.998′ E; NG24; 16 Aug. 1981; *E. Frandsen Dry0001*; V. Michelsen det.; ZMUC C-F-124014.

On *Crumomyia pedestris* (Meigen, 1830) (Diptera Sphaeroceridae)
DENMARK – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 1184*; W. Gritsch det.; ZMUC C-F-123708.

Remarks

A record of this fungus from Denmark has appeared in a web page (Ahlburg 2011), with photographs of a *Crumomyia notabilis* (Collin, 1902) infested with the fungus which was identified by Dr Walter Rossi (Univ. L'Aquila, Italy).

Stigmatomyces constrictus Thaxt.
MB#189362
Fig. 56E–G

Proceedings of the American Academy of Arts and Sciences 36: 401 (Thaxter 1901a). – **Type**: "On the legs and abdomen of a small fly. Ralum, New Pomerania. Berlin Museum, No. 1294"; FH. [Papua New Guinea]

Stigmatomyces elachipterae Thaxt. (Thaxter 1905: 323) [MB#191996]

Diagnostic features

Basal cell of appendage small, supporting a lower elongate cell bearing three antheridia, and two additional cells with two and three antheridia from bottom to top cell respectively. Perithecium with a venter distally producing four rounded prominences, and four more prominences on the transition between tiers w_2 and w_3. [Detailed description: Weir & Rossi 1995]

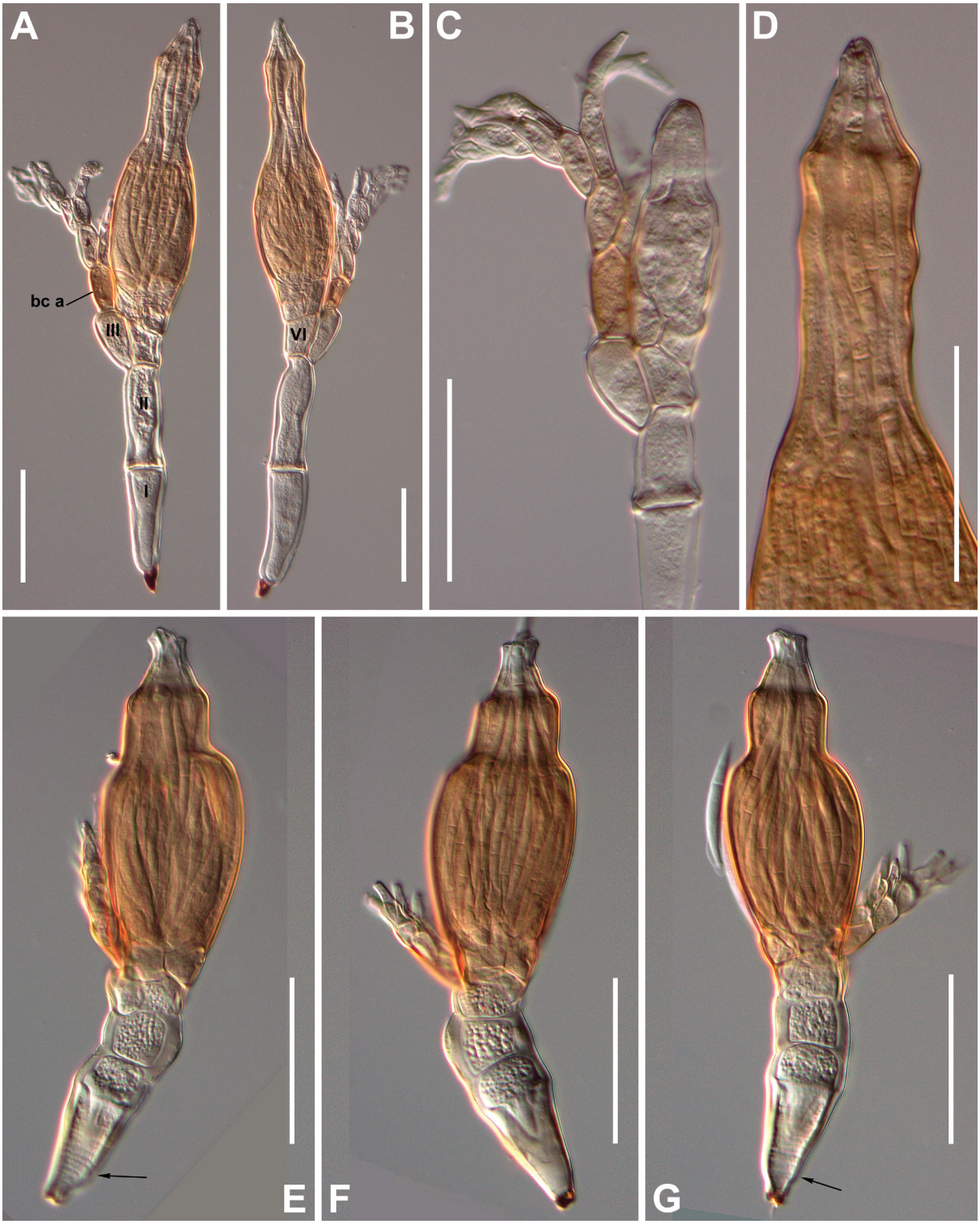

Fig. 56. *Stigmatomyces* spp. **A**–**D**. *S. burdigalensis* (Balazuc) A.Weir & W.Rossi. **A**–**B**. Mature thalli showing labelled cells I, II, III, VI, and basal cell of primary appendage (bc a). **C**. Primary appendage in detail from an immature thallus. **D**. Perithecial apex in detail showing slightly undulate margins and a conical tip. – **E**–**G**. *S. constrictus* Thaxt. Mature thalli. Surface of basal cell I appears characteristically striated (arrows in E and G). Scale bars: 50 µm. Photographs from slides ZMUC C-F-123707 (A–D), ZMUC C-F-124084 (E–G).

Distribution and hosts

Occurs on several genera of Diptera Chloropidae from the five continents: Papua New Guinea (type), Panama, Cameroon, Grenada, Jamaica, Trinidad & Tobago (Thaxter 1917), USA (Seymour 1967), Italy (Rossi 1993), United Kingdom (Weir & Rossi 1995), Bolivia (Rossi 1998), Brazil (Bergonzo *et al.* 2004), Uganda, Portugal, Sierra Leone, Taiwan, Germany, Yemen, Greece, Cuba (Rossi *et al.* 2013), and Slovenia (Rossi & Christian 2020).

Collections examined from Denmark

On *Elachiptera brevipennis* (Meigen, 1830) (Diptera Chloropidae)
DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.421′ N, 12°6.435′ E; UA19; 19 Aug. 2019; *JP 1497*; JP det.; ZMUC C-F-124084.

Remarks

First record from Denmark. Its presence in Denmark is not surprising according to the cosmopolitan distribution of the species. The surface of basal cell (I) appears characteristically striated (Fig. 56E–G, arrows).

Stigmatomyces crassicollis Thaxt.
MB#189218
Fig. 57A–F

Proceedings of the American Academy of Arts and Sciences 52: 661 (Thaxter 1917). – **Type**: "On the abdomen and legs of species of *Limosina*. No. 1863 (Type) …, Balaclava"; FH. [Jamaica]

Stigmatomyces longicollis Thaxt. (Thaxter 1917: 660) [MB#183955]
Stigmatomyces papuanus var. *leiostoma* Maire (Maire 1920: 137) [MB#621908]
Stigmatomyces hackmanii Huldén (Huldén 1983: 66) [MB#108566]

Diagnostic features

Basal cell of appendage slightly darkened, supporting a series of up to 12–13 flattened, oblique, outwards bulging cells, each bearing elongated antheridia on the inner side, except the distal cells which may be sterile. Perithecium with an oval venter and a well-distinguished, very elongate neck (about three times the length of the venter) which distally tapers to a distinct, slightly asymmetrical, pointed tip with four small lips. [Detailed descriptions: Thaxter 1931; Majewski 1994b; Weir & Rossi 1995; De Kesel & Hanssens 2007]

Distribution and hosts

Occurs on *Leptocera* (Diptera Sphaeroceridae) in a broad sense (including names like *Limosina*, *Spelobia*, *Opalimosina* Roháček, 1983, *Opacifrons* Duda, 1918, *Kimosina* Roháček, 1983, *Rachispoda* Lioy, 1864, *Pseudocollinella* Duda, 1924, *Terrilimosina* Roháček, 1983, *Hackmanina* Roháček, 1983); also on *Limnophora* Robineau-Desvoidy, 1830 (Diptera Muscidae) from Germany (Rossi *et al.* 2013). Known from **Europe** (Poland, Italy, Spain, United Kingdom), Jamaica, Bolivia, Algeria and New Zealand (Majewski 2008). Reported later from Belgium (De Kesel & Hanssens 2007), Slovakia (Rossi *et al.* 2010), Costa Rica, Germany and Portugal (Rossi *et al.* 2013).

Collections examined from Denmark

On *Leptocera fontinalis* (Fallen, 1826) (Diptera Sphaeroceridae)
DENMARK – **Nordøstsjælland (NEZ)** • Brønshøj; 55°42.234′ N, 12°30.135′ E; UB47; 30 Aug. 2019; *JP 1509*; V. Michelsen det.; ZMUC C-F-124097 • Kongelunden; 55°34.369′ N, 12°34.189′ E; UB46; 31 Mar. 2009; *W. Gritsch Dry0004*; W. Gritsch det.; ZMUC C-F-124017.

On *Spelobia* cf. *luteilabris* (Rondani, 1880) (Diptera Sphaeroceridae)
DENMARK – **Nordøstsjælland (NEZ)** • Svenskeholm; 55°36.123′ N, 12°31.715′ E; UB46; 9–14 May 2018; *W. Gritsch 1205*; W. Gritsch det.; ZMUC C-F-123732.

On *Spelobia luteilabris* (Rondani, 1880) (Diptera Sphaeroceridae)
DENMARK – **Nordøstsjælland (NEZ)** • Bagsværd (Skovsøen 15); 55°45.526′ N, 12°25.121′ E; UB38; 28 Feb. 1959; *L. Lyneborg Dry0005*; J. Rohacek det.; ZMUC C-F-124018.

On *Spelobia rufilabris* (Stenhammer, 1855) (Diptera Sphaeroceridae)
DENMARK – **Nordøstjylland (NEJ)** • Nordmarken, Læsø; 57°18.919′ N, 11°4.819′ E; PJ25; 11 Jul. 1969; *Zool. Mus. Exp. Dry0006*; V. Michelsen det.; ZMUC C-F-124019.

Remarks

First record from Denmark. Highly variable, especially as a function of growing on different parts of the host body, and perhaps a collective species. *Stigmatomyces hackmanii* was accepted as a separate species by Majewski (1994b) according to differences in the arrangement and shape of perithecial basal cells and cell III, although these supposedly differential characteristics were not depicted in his illustrations.

Stigmatomyces divergatus Thaxt.
MB#263386
Figs 57G–K, 106B

Memoirs of the American Academy of Arts and Sciences 16: 122 (Thaxter 1931). – **Type**: "On the superior tip of the abdomen of *Leptocera* sp., No. 3479, Fort de Kock, Sumatra"; FH.

Stigmatomyces chthonicus Huldén (Huldén 1983: 65) [MB#108564]
Stigmatomyces subterraneus Huldén (Huldén 1983: 68) [MB#108570]

Diagnostic features

Basal cell of appendage slightly darker, supporting a series of 3–10 flattened, oblique, dorsally almost inflated cells, each giving rise to rather elongated antheridia on the inner margin. Perithecium with an oval venter, showing distal knobs below the neck (Fig. 57K) and a well-distinguished, slightly bent, gradually tapering neck ending in a distinct, asymmetrical tip which shows two protruding lips. [Detailed descriptions: Majewski 1994b – as *S. chthonicus* and *S. subterraneus* –; De Kesel & Hanssens 2007]

Distribution and hosts

Reported from Indonesia (type), USA (Rossi *et al.* 2013), and some European countries like Finland (Huldén 1983, as *S. chthonicus* and *S. subterraneus*), Poland (Majewski 1990a, 1990b as *S. subterraneus* and *S. chthonicus*, respectively), Spain (Santamaria & Rossi 1993), Belgium (De Kesel & Hanssens 2007), and Portugal (Rossi *et al.* 2013). Occurs on *Leptocera*, *Spelobia*, *Apteromyia*, and *Limosina* (Diptera Sphaeroceridae).

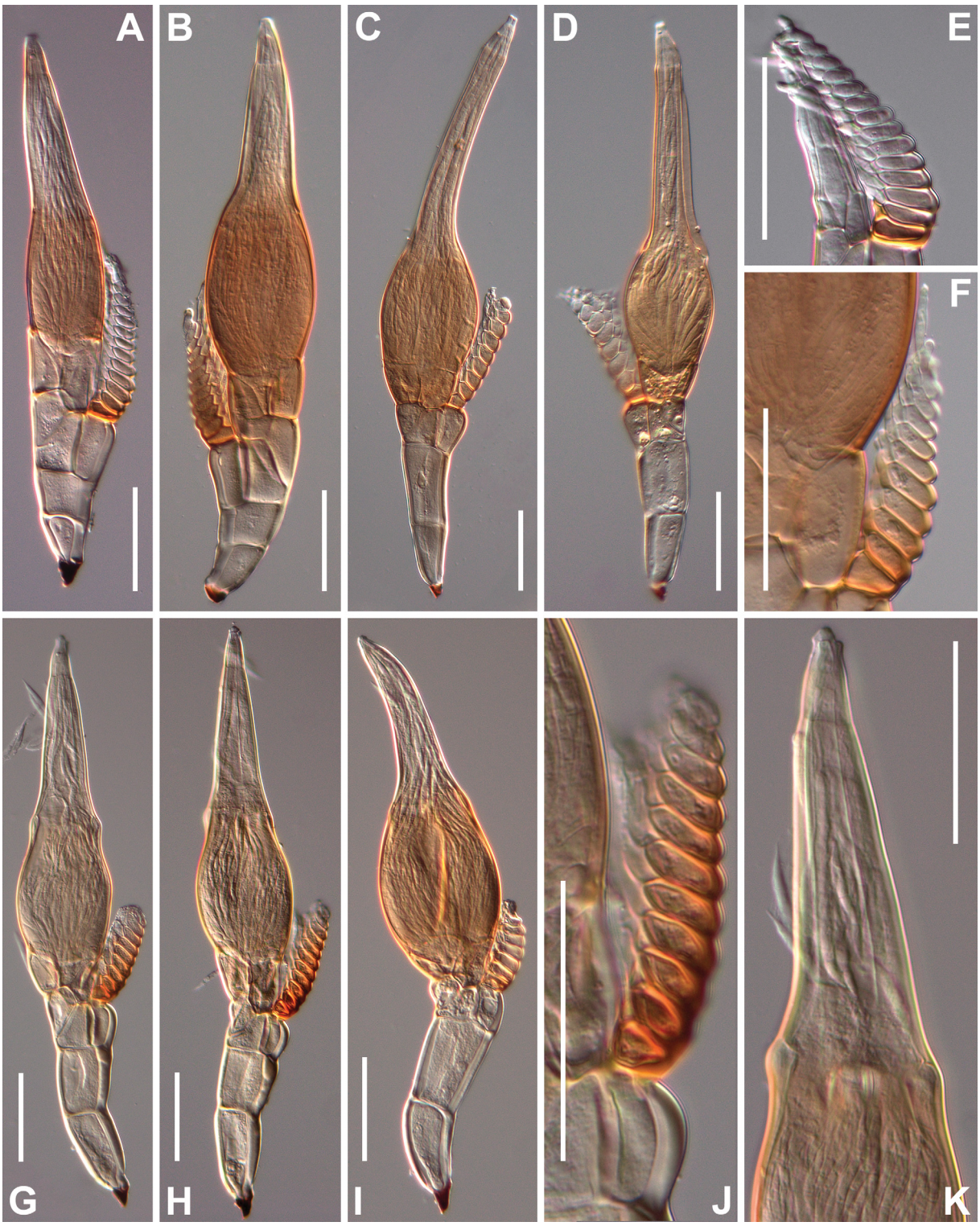

Fig. 57. *Stigmatomyces* spp. **A**–**F**. *S. crassicollis* Thaxt. **A**–**D**. Mature thalli, from *Leptocera fontinalis* (A–B), from *Spelobia luteilabris* (C), and from *Spelobia rufilabris* (D). **E**–**F**. Primary appendages in detail. – **G**–**K**. *S. divergatus* Thaxt. **G**–**I**. Mature thalli. **J**. Primary appendage in detail. **K**. Perithecial tip in detail. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124097 (A, E), ZMUC C-F-124017 (B, F), ZMUC C-F-124018 (C), ZMUC C-F-124019 (D), ZMUC C-F-123720 (G–H, J–K), ZMUC C-F-123717 (I).

Collections examined from Denmark

On *Spelobia clunipes* (Meigen, 1830) (Diptera Sphaeroceridae)

DENMARK – **Nordøstsjælland (NEZ)** • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 14 Apr. 2013; *JP 1191*; W. Gritsch det.; ZMUC C-F-123715. – **Sydsjælland (SZ)** • Gammel Dyrehave ved Edelesminde; 55°16.930′ N, 11°58.348′ E; PG83; 27 Nov. 2016; *JP 1192*; W. Gritsch det.; ZMUC C-F-123716 • Haslev; 55°19.669′ N, 11°58.206′ E; PG83; 19 Jun. 2016; *JP 1190*; W. Gritsch det.; ZMUC C-F-123714.

On *Spelobia luteilabris* (Rondani, 1880) (Diptera Sphaeroceridae)

DENMARK – **Fyn (F)** • Skovsgårds Mølle; 54°50.339′ N, 10°44.594′ E; PF17; 5 Oct. 2016; *JP 1195*; W. Gritsch det.; ZMUC C-F-123719.

On *Spelobia palmata* (Richards, 1927)/*talparum* (Richards, 1927) (Diptera Sphaeroceridae)

DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 1194*; W. Gritsch det.; ZMUC C-F-123718. – **Sydsjælland (SZ)** • Gammel Dyrehave ved Edelesminde; 55°16.930′ N, 11°58.348′ E; PG83; 27 Nov. 2016; *JP 1193*; W. Gritsch det.; ZMUC C-F-123717.

On *Spelobia* sp. (Diptera Sphaeroceridae)

DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 16 Feb. 2018; *JP 1196*; W. Gritsch det.; ZMUC C-F-123720.

Remarks

First record from Denmark. This species may be difficult to distinguish from *S. crassicollis* in the absence of the four knobs on the perithecial venter as in *S. divergatus.*

Stigmatomyces entomophilus (Peck) Thaxt.
MB#180765
Fig. 58A–C

Proceedings of the American Academy of Arts and Sciences 25: 8 (Thaxter 1890). – **Basionym**: *Appendicularia entomophila* Peck, Report of the botanist. *Annual Report on the New York State Museum of Natural History* 38: 96 (Peck 1885) [MB#431382]. – *Appendiculina entomophila* (Peck) Berlese (Berlese 1889: 96) [MB#178031]. – *Peckifungus entomophilus* (Peck) Kuntze (Kuntze 1891: 864) [MB#431921]. – **Type**: "On various parts of the body of *Drosophila nigricornis* Loew (Drosophilidae); Nyack, New York, USA, 19 Mar. 1884 (J.L. Zabriskie), in coll. FH (Syntypes 5942–5948)"; FH. [According to Weir & Rossi 1995: 844]

Stigmatomyces drosophilae Thaxt. (Thaxter 1931: 133) [MB#263532]

Diagnostic features

Basal cell of appendage small, distally darker, supporting a series of five cells, the lower flattened and dark, each of the five cells bearing paired antheridia on their outer side, except the upper cell which gives rise to three antheridia, the distal of which is spinose (Fig. 58C, sx). Perithecium with an oval venter tinged with brown, and a well-distinguished, very elongated neck which tapers distally to a distinct, asymmetrical tip, showing two protruding lips. [Detailed descriptions: Thaxter 1896; Weir & Rossi 1995]

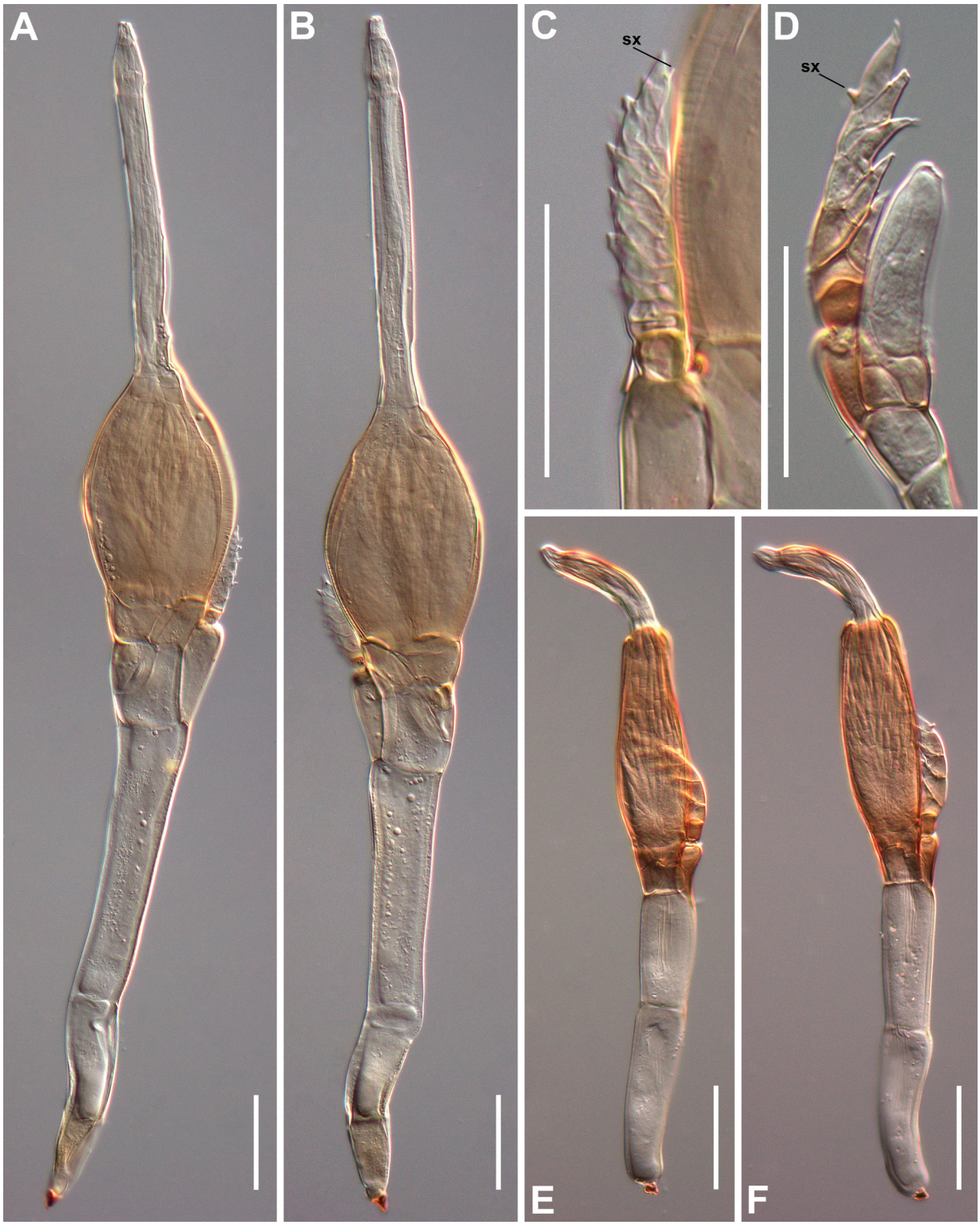

Fig. 58. *Stigmatomyces* spp. **A**–**C**. *S. entomophilus* (Peck) Thaxt. **A**–**B**. Mature thalli. **C**. Primary appendage in detail showing spinous process from the original spore apex (sx). – **D**–**F**. *S. ephydrae* L.Mercier & R.Poiss. **D**. Primary appendage in detail showing spinous process from the original spore apex (sx). **E**–**F**. Mature thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124020 (A–C), ZMUC C-F-124262 (D–F).

Distribution and hosts

On species of *Drosophila* in the subgenus *Drosophila* like *Drosophila nigricornis* Sturtevant, 1921, *D. funebris* and *D. confusa* Staeger, 1844 (Diptera Drosophilidae). Described from USA, it has been also found in Austria (Gercke 1886), France (Picard 1913), United Kingdom (Blair 1947), Bolivia (Rossi 1998), Czech Republic (Rossi & Máca 2006), and the Netherlands (Haelewaters *et al.* 2018b).

Collections examined from Denmark

On *Drosophila funebris* (Fabricius, 1787) (Diptera Drosophilidae)

DENMARK – **Nordøstsjælland (NEZ)** • Fredensborg; 55°58.535′ N, 12°24.317′ E; UC30; ca 1870; *Stæger Dry0007*; det. unknown; ZMUC C-F-124020.

Remarks

First record from Denmark. Records from Gabon and South Africa (Santamaria *et al.* 1991) require confirmation according to Weir & Rossi (1995). Records on *Drosophila* subgenus *Sophophora* as *Drosophila obscura* and *D. subobscura* Collin, 1936 correspond to *S. majewskii*. *Stigmatomyces entomophilus* and *S. majewskii* differ by the number of cells forming the axis of the appendage (including the basal cell), six in the former and five in the latter, and also because *S. entomophilus* is distinctly more elongate than *S. majewskii*.

Stigmatomyces ephydrae L.Mercier & R.Poiss.
MB#531320
Fig. 58D–F

Bulletin de la Société Zoologique de France 52: 226 (Mercier & Poisson 1927). – **Type**: [Type lost ?!] "Au cours de l'été dernier, chassant les Diptères dans les marais de Colleville-sur-Orne, en bordure de la côte du Calvados, nous avons capturé de nombreux exemplaires d'*Ephydra riparia* Fall., Diptère extrêmement commun …". [Mercier & Poisson 1927: 227, fig. 1] [France]

Stigmatomyces bottnicus Huldén (Huldén 1983: 64) [MB#108563]
Stigmatomyces setacerae Huldén (Huldén 1983: 68) [MB#108569]

Diagnostic features

Basal cell of appendage dark, slightly elongate, supporting a series of four superposed cells, each bearing one antheridium on the inner side, except for the upper cell which gives rise two antheridia, where the distal one bears a dorsal spinous process (Fig. 58D, sx). Perithecium with four rounded distal swellings and an abruptly distinguished, narrow, bent neck. [Detailed description: Thaxter 1931; Weir & Rossi 1995]

Distribution and hosts

Occurs on Diptera Ephydridae of the genera *Ephydra* Fallén, 1810, *Setacera* Cresson, 1930 and probably *Glenanthe* Haliday, 1839 (Rossi *et al.* 2013). Reported from France (type), Russia, Finland (Huldén 1983), Italy (Rossi 1993), United Kingdom (Weir & Rossi 1995), New Zealand (Hughes *et al.* 2004), Brazil (Bergonzo *et al.* 2004), China (Shen & Ye 2006), Canada, Kyrgyzstan, USA, and Portugal (Rossi *et al.* 2013).

Collections examined from Denmark

On *Ephydra riparia* Fallén, 1813 (Diptera Ephydridae)

DENMARK – **Nordøstsjælland (NEZ)** • Jersie Strand; 55°30.992′ N, 12°13.142′ E; UB25; 31 Aug. 2019; *JP 1510*; V. Michelsen det.; ZMUC C-F-124262.

Remarks

First record from Denmark. Its presence in Denmark is not surprising according to its records in neighbouring countries.

Stigmatomyces geomyzae W.Rossi & Cesari
MB#113381
Fig. 59A–F

Giornale Botanico Italiano 113 (5–6): 384 (Rossi & Cesari Rossi 1980). – **Type**: "Sullo scutello e tra le zampe di un esemplare di *Geomyza tripunctata* Fall. (Opomyzidae) catturato in località Colli del Forno, nel comune di Montelibretti (Roma). *Holotypus in herbario Instituti Botanici apud Universitatem Studiorum Romae, n. 933*"; RO.

Diagnostic features

Basal cell of appendage darkened (Fig. 59E, bc a), supporting a series of five ± isodiametric cells, each bearing solitary antheridia on the inner side, except the upper cell which gives rise to two antheridia, the distal of which is spinose (Fig. 59E, sx). Perithecium with an oval venter, and a well-distinguished, short neck which tapers distally to an asymmetrical tip, showing four lips arranged as: one protuberant in the back, two identical on the sides, and one short in the front (Fig. 59C–D). Perithecial outer wall cells arranged spirally and forming conspicuous ridges on the venter (Fig. 59F). [Detailed description: Weir & Rossi 1995]

Distribution and hosts

Reported from Italy (type), Spain (Santamaria & Rossi 1993), United Kingdom (Weir & Rossi 1995), and Portugal (Rossi *et al.* 2013). Specific on species of *Geomyza* (Diptera Opomyzidae).

Collections examined from Denmark

On *Geomyza balachowskyi* Mesnil, 1934 (Diptera Opomyzidae)

DENMARK – **Nordøstjylland (NEJ)** • Nordmarken, Læsø; 57°18.919′ N, 11°4.819′ E; PJ25; 11 Jul. 1969; *Zool. Mus. Exp. Dry0011*; J.W.A. v. Zuijlen det.; ZMUC C-F-124024.

On *Geomyza tripunctata* Fallén, 1823 (Diptera Opomyzidae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Møns Klint, Syd; 54°56.985′ N, 12°32.270′ E; UA49; 19 Aug. 2019; *JP 1494*; V. Michelsen det.; ZMUC C-F-124080. – **Nordøstjylland (NEJ)** • Nordmarken, Læsø; 57°18.919′ N, 11°4.819′ E; PJ25; 15 Jul. 1969; *Zool. Mus. Exp. Dry0010*; J.W.A. v. Zuijlen det.; ZMUC C-F-124023. – **Nordøstsjælland (NEZ)** • Pinseskoven; 55°35.839′ N, 12°33.250′ E; UB46; 6–20 May 2017; *W. Gritsch 1179*; W. Gritsch det.; ZMUC C-F-123703.

Remarks

First record from Denmark. It is probably a much more common species than the absence of records seems to indicate.

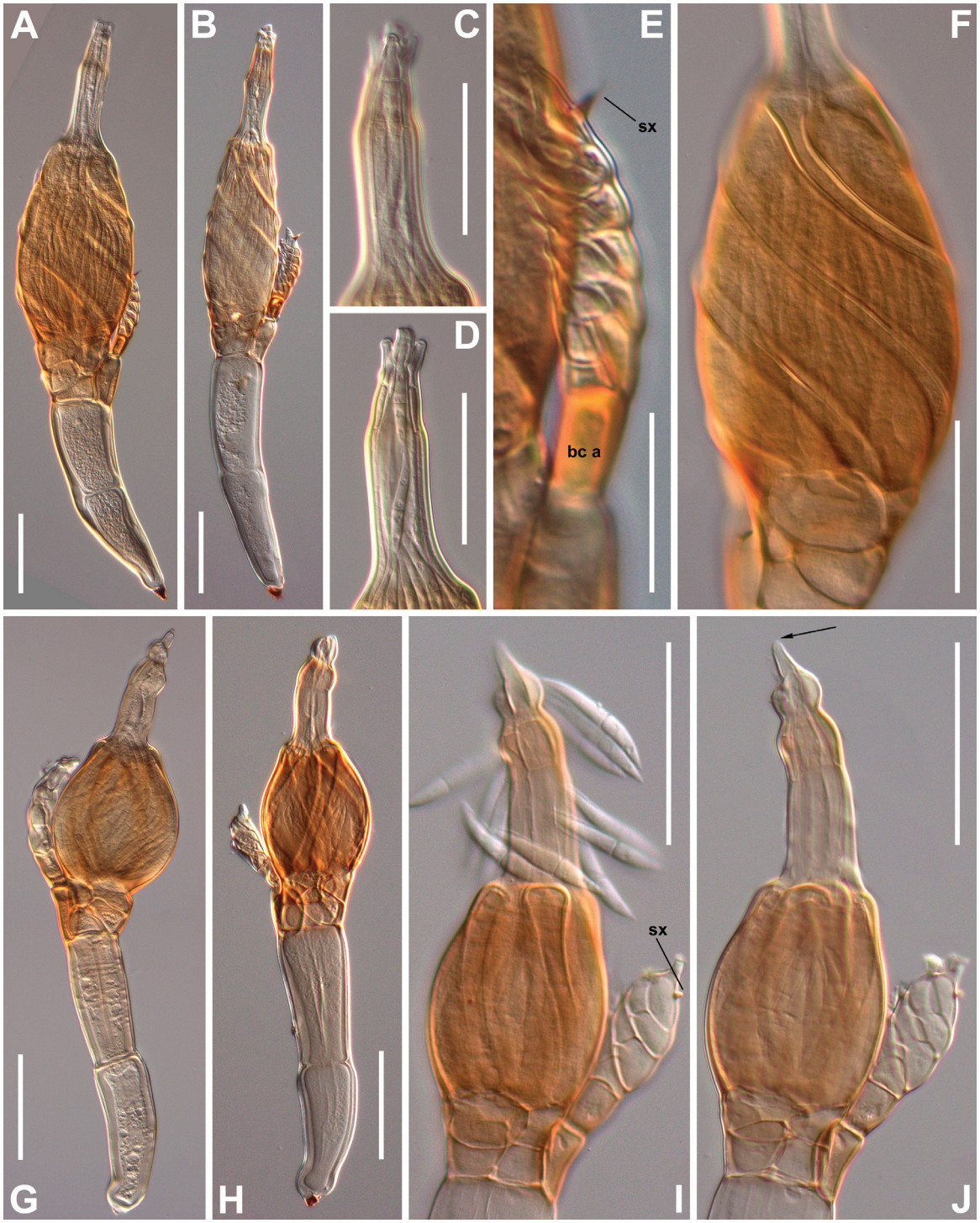

Fig. 59. *Stigmatomyces* spp. **A**–**F**. *S. geomyzae* W.Rossi & Cesari. **A**–**B**. Mature thalli. **C**–**D**. Perithecial tip in detail. **E**. Primary appendage in detail with labelled spinous process from the original spore apex (sx) and appendage basal cell (bc a). **F**. Perithecial outer wall cells in detail, arranged spirally and forming conspicuous ridges. – **G**–**J**. *S. hydrelliae* Thaxt. **G**–**H**. Mature thalli. **I**–**J**. Perithecium and appendage in detail at two different focus levels, showing spinous process from the original spore apex (sx) and pointed projection on the perithecial apex. Scale bars: A–D, F–J = 50 µm; E = 25 µm. Photographs from slides ZMUC C-F-123703 (A, C–F), ZMUC C-F-124024 (B), ZMUC C-F-123721 (G), ZMUC C-F-124032 (H–J).

Stigmatomyces hydrelliae Thaxt.
MB#193297
Fig. 59G–J

Proceedings of the American Academy of Arts and Sciences 36: 404 (Thaxter 1901a). – **Type**: "On the superior surface of the abdomen, sometimes on the legs of *Hydrellia* sp. Kittery Point, Maine"; FH. [USA]

Diagnostic features

Basal cell of appendage supporting a series of three ± isodiametric cells, each bearing solitary antheridia on the inner or outer side, except the upper cell which gives rise to two antheridia, the distal of which is spinose (Fig. 59I, sx). Perithecium with an oval venter and a well-distinguished short neck, which tapers distally into an asymmetrical and rounded, constricted near the tip, showing a lip which extends into a pointed projection (Fig. 59J, arrow). Perithecial outer wall cells arranged helically, forming conspicuous ribs and protuberances on the distal region of the venter (Fig. 59I). [Detailed descriptions: Thaxter 1908; Dainat 1971; Majewski 1994b; Weir & Rossi 1995]

Distribution and hosts

This is a common species reported from **Europe**: Portugal, Spain, France, United Kingdom, Italy, Denmark, Poland, Finland and Russia, as well as from the USA and New Zealand (Majewski 2008). The thalli from New Zealand (Hughes *et al.* 2004) may belong to a separate species. Recently reported from the Netherlands (Haelewaters & De Kesel 2020). On species of the genus *Hydrellia* (Diptera Ephydridae).

Collections examined from Denmark

On *Hydrellia griseola* (Fallén, 1813) (Diptera Ephydridae)

DENMARK – **Bornholm (B)** • Almindingen; 55°7.448′ N, 14°56.114′ E; VB90; *H.J. Hansen Dry0015*; ZMUC C-F-124029 • Snogebæk; 55°1.512′ N, 15°6.887′ E; WA09; 18 Jun. 1964; *L. Lyneborg et al. Dry0013*; T. Zatwarnicki det.; ZMUC C-F-124027 • Sose; 55°2.801′ N, 14°50.531′ E; VB90; 20 Jun. 1965; *O. Martin et al. Dry0014*; T. Zatwarnicki det.; ZMUC C-F-124028. – **Nordøstjylland (NEJ)** • Klitplantagen, Læsø; 57°17.795′ N, 11°2.022′ E; PJ25; 12 Jul. 1969; *Zool. Mus. Exp. Dry0019*; ZMUC C-F-124033 • Nordmarken, Læsø; 57°18.919′ N, 11°4.819′ E; PJ25; 16 Jul. 1969; *Zool. Mus. Exp. Dry0016*; ZMUC C-F-124030 • ibid.; 24 Jul. 1969; *Zool. Mus. Exp. Dry0017*; ZMUC C-F-124031 • ibid.; 27 Jul. 1969; *Zool. Mus. Exp. Dry0018*; ZMUC C-F-124032. – **Nordøstsjælland (NEZ)** • København; 55°41.332′ N, 12°33.762′ E; UB47; 23 Sep. 1905; *W. Lundbeck Dry0020*; ZMUC C-F-124034. – **Sydsjælland (SZ)** • Knudsskov; 55°3.534′ N, 11°44.251′ E; PG70; 14 Oct. 2013; *JP 1197*; W. Gritsch det.; ZMUC C-F-123721.

Remarks

Majewski (2008) reported the presence of this species from Denmark on *Hydrellia griseola* and *H. maura* Meigen, 1838 (see Table 1).

Stigmatomyces limosinae Thaxt.
MB#189647
Fig. 60A

Proceedings of the American Academy of Arts and Sciences 36: 406 (Thaxter 1901a). – **Type**: [Not designated] [Ind. loc.] "On *Limosina fontinalis* Fallen. Kittery Point, Maine, vicinity of Cambridge, Mass., Berkeley, California"; FH. [USA]

Stigmatomyces pedunculatus T.Majewski (Majewski 1972b: 231) [MB#324131]

Diagnostic features

Basal cell of appendage dark, supporting a series of up to 12 flattened, oblique, outwardly bulging cells, each bearing elongated antheridia on the inner side, except the upper cell which gives rise to an additional antheridium. Perithecium with an oval venter, and a well-distinguished, elongated neck (about two times the length of the venter) which tapers distally into a distinct, slightly asymmetrical, pointed tip, showing four small lips. Perithecial stalk cell (VI), secondary stalk cell (VII) and basal cells (m, n, n') forming a well distinguished peduncle [Detailed descriptions: Thaxter 1908; Majewski 1994b; Weir & Rossi 1995; De Kesel & Hanssens 2007]

Distribution and hosts

Described on *Limosina*, found also on *Leptocera*, *Rachispoda*, and *Spelobia* (Diptera Sphaeroceridae). Reported from USA, Mexico, Jamaica, New Zealand and **Europe** (Italy, Portugal, Poland, United Kingdom) (Majewski 2008; the record from Spain is a mistake). Also from Belgium (De Kesel & Hanssens 2007), Czech Republic (Rossi *et al.* 2010), the Netherlands (Haelewaters *et al.* 2012), Kenia, Sierra Leone, and Canada (Rossi & Leonardi 2018).

Collections examined from Denmark

On *Spelobia palmata* (Richards, 1927)/*talparum* (Richards, 1927) (Diptera Sphaeroceridae)
DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 1194*; W. Gritsch det.; ZMUC C-F-123718.

Remarks

First record from Denmark. This species is particularly similar to *S. crassicollis* from which it may be separated by the long-stalked perithecium.

Stigmatomyces majewskii H.L.Dainat, Manier & Balazuc
MB#324129
Fig. 60B–E

Bulletin de la Société Mycologique de France 90 (3): 171 (Dainat *et al.* 1974). – **Type**: [Not designated] [In ??] "Hôtes: *Drosophila obscura* Fallèn, *D. subobscura* Collin... Clapiers (Hérault), lisières vignes et pinèdes toute l'année. Penzé (Finistère): 27.7.1961. Cazaux (Gironde) 8.7.1961. Type Cl 10.70 coll. H. Dainat". [France]

Diagnostic features

Basal cell of appendage small, distally darker, supporting a series of four cells, the lower flattened, dark and sterile, the others bearing paired antheridia on their outer side, except for the upper cell which gives rise to three antheridia, the distalmost of which is spinose (Fig. 60D, sx). Perithecium with an oval, brownish venter, and a well-distinguished, very elongated neck, which tapers distally into a distinct, asymmetrical tip which shows two protruding lips (Fig. 60E).

Distribution and hosts

Reported from France (type), Czech Republic (Rossi *et al.* 2010), the Netherlands (Haelewaters & De Kesel 2010), Portugal, Zimbabwe, Taiwan, Germany and United Kingdom (Rossi *et al.* 2013). According to Rossi *et al.* (2010) the record of *S. majewskii* on *Scaptodrosophila* Duda, 1923 from Austria is erroneous. Grows on species of the genus *Drosophila* subgenus *Sophophora* (Diptera Drosophilidae).

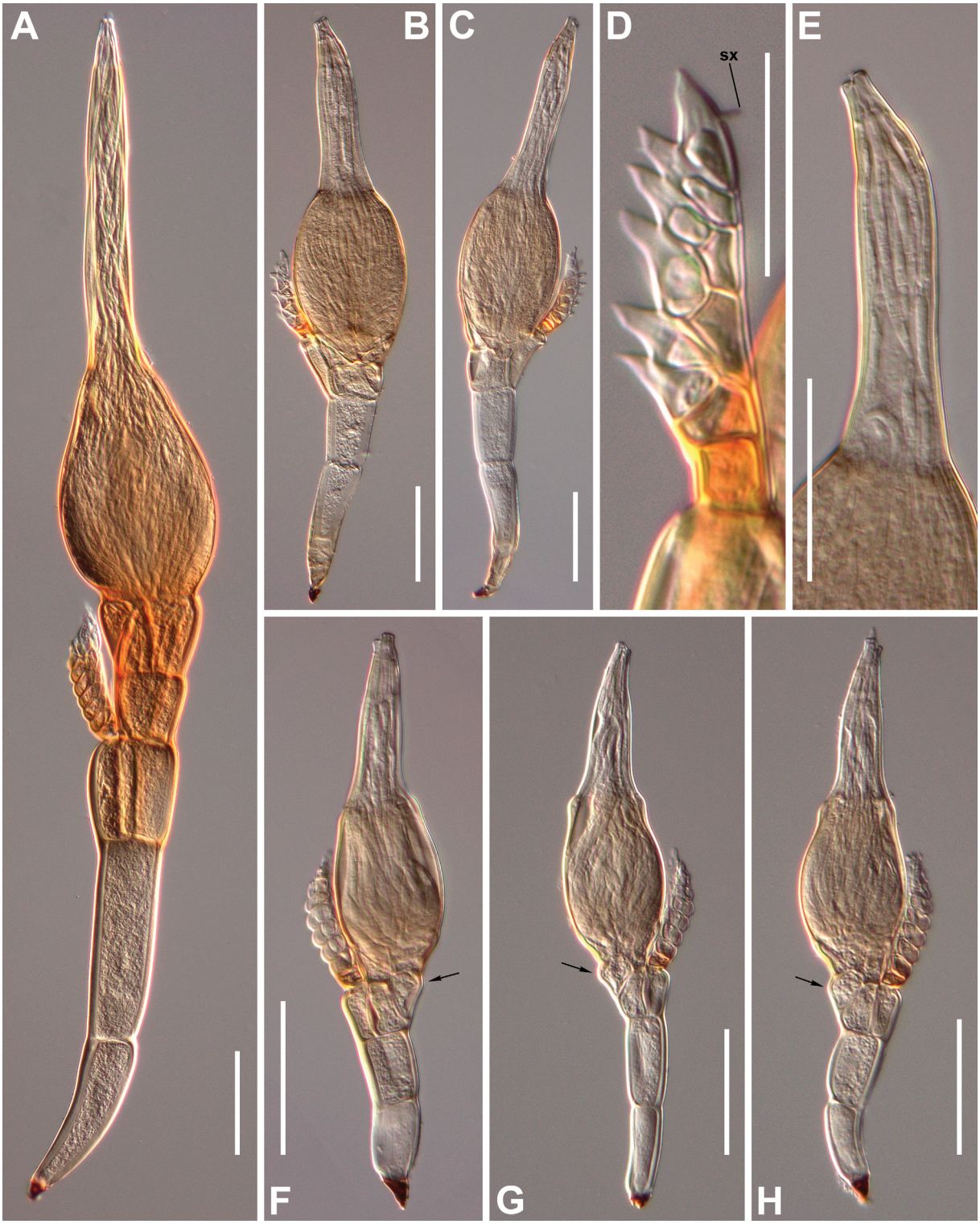

Fig. 60. *Stigmatomyces* spp. **A**. *S. limosinae* Thaxt. Mature thallus. – **B**–**E**. *S. majewskii* H.L.Dainat, Manier & Balazuc. **B**–**C**. Mature thalli. **D**. Primary appendage in detail with labelled spinous process from the original spore apex (sx). **E**. Perithecial tip in detail. – **F**–**H**. *S. platensis* Speg. Mature thalli showing protrusion of cell VII (arrows). Scale bars: A–C, E–H = 50 µm; D = 25 µm. Photographs from slides ZMUC C-F-123718 (A), ZMUC C-F-123705 (B, D–E), ZMUC C-F-123731 (C), ZMUC C-F-123713 (F–H).

Collections examined from Denmark

On *Drosophila* cf. *bifasciata* Pomini, 1940 (Diptera Drosophilidae)

DENMARK – **Nordøstsjælland (NEZ)** • Pinseskoven; 55°35.839′ N, 12°33.250′ E; UB46; 8–24 Jun. 2017; *W. Gritsch 1180*; W. Gritsch det.; ZMUC C-F-123704.

On *Drosophila obscura* Fallén, 1823 (Diptera Drosophilidae)

DENMARK – **Nordøstsjælland (NEZ)** • Gentofte; 55°44.005′ N, 12°33.020′ E; UB47; 27–28 Jun. 2018; *H. Enghoff 1182*; V. Michelsen det.; ZMUC C-F-123706 • Pinseskoven; 55°35.839′ N, 12°33.250′ E; UB46; 8–24 Jun. 2017; *W. Gritsch 1181*; W. Gritsch det.; ZMUC C-F-123705 • ibid.; 11–26 Jun. 2018; *W. Gritsch 1204*; W. Gritsch det.; ZMUC C-F-123731.

Remarks

First record from Denmark. See under *S. entomophilus* for comparison and additional remarks.

Stigmatomyces platensis Speg.
MB#188602
Fig. 60F–H

Anales del Museo Nacional de Historia Natural de Buenos Aires 29: 676 (Spegazzini 1917). – **Type**: "Sobre la superficie inferior de las alas y sobre el dorso del abdomen de una pequeña mosca, *Limosina*, en La Plata, Febr. y May. 1916"; LPS. [Argentina]

Stigmatomyces affinis Thaxt. (Thaxter 1918a: 732) [MB#160021]

Diagnostic features

Basal cell of appendage flattened, darker, supporting a series of 5–6 ± flattened, oblique, outwardly bulging cells, each bearing pairs of rather elongated antheridia on the inner side. Perithecium with an oval venter, with distal knobs and a well-distinguished, gradually tapering neck, which terminates in a distinct, asymmetrical tip showing two protuberant lips. Cell VII protruding below the perithecium (Fig. 60F–H, arrows) because the septum which separates this cell from cell n′ is noticeably constricted. [Detailed descriptions: Majewski 1994b; De Kesel & Hanssens 2007]

Distribution and hosts

Known in **Europe** from Poland (Majewski 1990a), Belgium (De Kesel & Hanssens 2007), Czech Republic, Italy (Rossi *et al.* 2010), and Portugal (Rossi *et al.* 2013); in **America** from Argentina (type); in **Africa** from Cameroon (Thaxter 1931); and in **Asia** from Indonesia (Thaxter 1931). Described on *Limosina*, reported also on "borborid flies", and on *Pullimosina* (Diptera Sphaeroceridae). Now, the name *S. platensis* should be exclusively retained for species living on flies of the genus *Pullimosina* (Rossi *et al.* 2010). The fungus recorded by De Kesel & Hanssens (2007) on *Paralimosina* Papp, 1973 from Belgium may belong to a different species (Rossi *et al.* 2010).

Collections examined from Denmark

On *Pullimosina vulgesta* Roháček, 2001 (Diptera; Sphaeroceridae)

DENMARK – **Østjylland (EJ)** • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 1189*; W. Gritsch det.; ZMUC C-F-123713.

Remarks

First record from Denmark. This species is particularly similar to *S. divergatus* from which it differs by minor characteristics, such as the protruding cell VII and its preference for flies of the genus *Pullimosina*.

Stigmatomyces purpureus Thaxt.
MB#191132
Fig. 61A–B

Proceedings of the American Academy of Arts and Sciences 36: 404 (Thaxter 1901a). – **Type**: [Not designated] [Ind. loc.] "On all parts of *Scatella stagnalis* Fallen. Kittery Point, Maine, and vicinity of Cambridge, Mass., September"; FH. [USA]

Stigmatomyces scatellae S.W.T.Batra. (Batra 1963: 986) [MB#339711]

Diagnostic features

Thallus hyaline. Basal cell of appendage supporting a series of three cells, each bearing solitary antheridia on the inner side, except for the uppermost cell which gives rise two antheridia, where the distal one bears a dorsal spinous process. Perithecium with an oval venter, and a well-distinguished, short neck, which tapers distally into an asymmetrical tip, showing two distinct projections (Fig. 61A, arrows). Perithecial

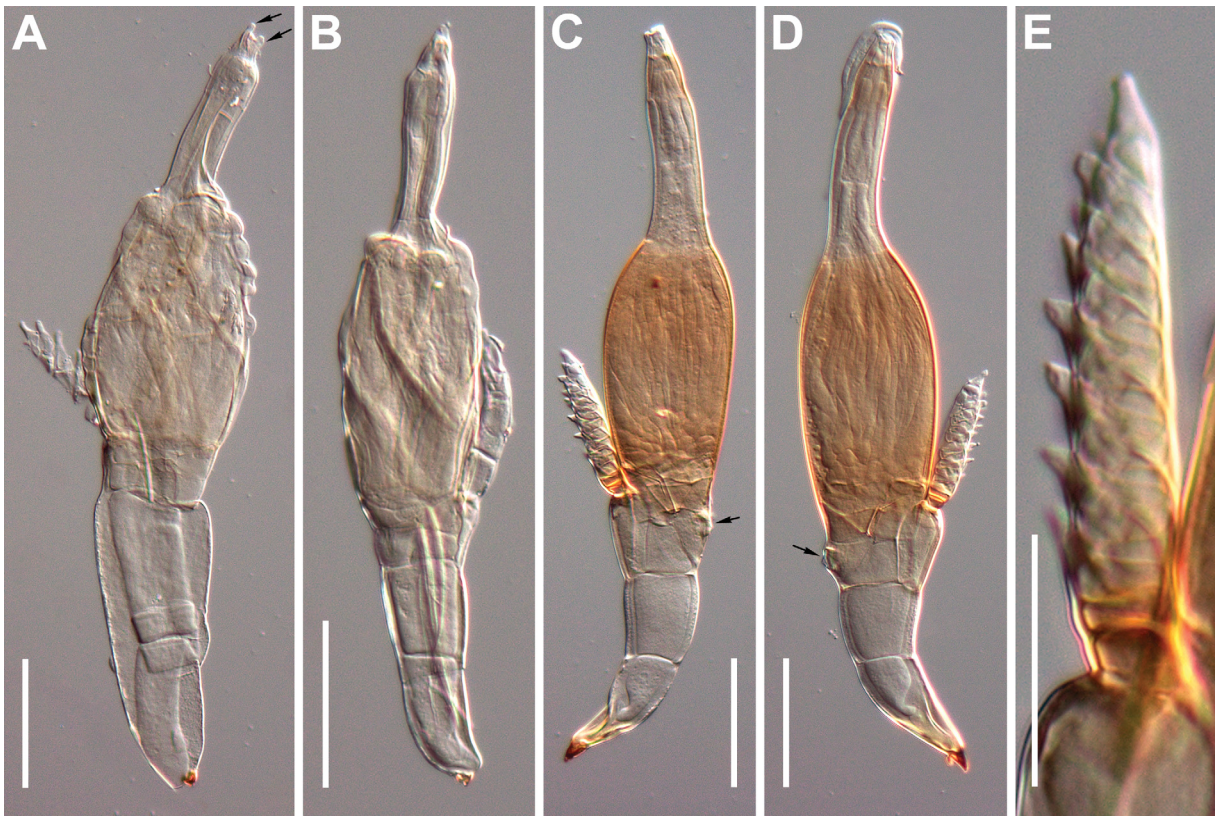

Fig. 61. *Stigmatomyces* spp. **A**–**B**. *S. purpureus* Thaxt. Mature thalli. In A, arrows point to the two projections of the perithecial apex. – **C**–**E**. *S. scaptomyzae* Thaxt. **C**–**D**. Mature thalli showing protrusion of cell VII (arrows). **E**. Primary appendage in detail. Scale bars: A–D = 50 µm; E = 25 µm. Photographs from slides ZMUC C-F-124025 (A), ZMUC C-F-124026 (B), ZMUC C-F-124021 (C–E).

outer wall cells arranged spirally and forming conspicuous ridges and corrugations. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Weir & Rossi 1995, 1997]

Distribution and hosts

Found on five continents: **Europe** (Spain, France, United Kingdom, Italy, Poland and Finland), **America** (USA), **Asia** (India), **Africa** (Algeria) and **Oceania** (New Zealand) (Majewski 2008). Recently reported also from Canada, Portugal (Rossi *et al.* 2013) and Turkey (Rossi 2016). It is common on flies of the genus *Scatella* (Diptera Ephydridae).

Collections examined from Denmark

On *Scatella stagnalis* (Fallen, 1813) (Diptera; Ephydridae)

DENMARK – **Østjylland (EJ)** • Gjerlev; 56°35.242′ N, 10°7.898′ E; NH67; Jul. 1882; *H.J. Hansen Dry0012*; V. Michelsen det.; ZMUC C-F-124025, C-F-124026.

Remarks

First record from Denmark. Although the Danish material is in rather poor condition, it is perfectly identifiable by the two projections from the perithecial apex and the spiral ridges on the venter of the perithecium.

Stigmatomyces scaptomyzae Thaxt.
MB#179870
Fig. 61C–E

Proceedings of the American Academy of Arts and Sciences 36: 400 (Thaxter 1901a). – **Type**: [Not designated] [Ind. loc.] "On the abdomen and legs of *Scaptomyza graminum* Fallen. Kittery Point, Maine, vicinity of Cambridge, Mass., Berkeley, California"; FH. [USA]

Diagnostic features

Basal cell of appendage dark, supporting a series of 5–6 cells, the lower flattened, darkened and sterile, the others bearing paired antheridia on their outer side, except for the upper cell which gives rise to three antheridia, the distal of which is spinose (Fig. 61E). Cell VII showing an outer enlargement of the wall which forms a sort of protrusion (Fig. 61C–D, arrows). Perithecium with a somewhat cylindrical, and enlarged distally venter, and a well-distinguished, arcuate neck, which tapers distally into a distinct, slightly asymmetrical tip. [Detailed descriptions: Thaxter 1908; Majewski 1994b]

Distribution and hosts

This species is known from **America** (USA, Venezuela), **Africa** (Burundi), **Asia** (Turkey) and **Europe** (Portugal, Spain, France, Italy, Austria, Czech Republic, Slovakia, Poland and Finland) (Majewski 2008). Subsequently reported from Afghanistan, Montenegro, Canada, Romania, and Germany (Rossi & Máca 2006). Occurs on species of the genera *Scaptomyza* and *Parascaptomyza* (Diptera Drosophilidae) (Rossi *et al.* 2019b).

Collections examined from Denmark

On *Scaptomyza pallida* (Zetterstedt, 1857) (Diptera; Drosophilidae)

DENMARK – **Nordøstjylland (NEJ)** • Læsø (Laboratorie have); 57°14.827′ N, 11°2.736′ E; PJ25; 10 Oct. 1970; *Zool. Mus. Exp. Dry0008*; G. Bächli det.; ZMUC C-F-124021 • Sjælland Northeast; without coordinates; ca 1900; *R.W. Schlick Dry0009*; G. Bächli det.; ZMUC C-F-124022.

Remarks

First record from Denmark. The presence of this species in Denmark is not surprising since it is very common and widely distributed. In Rossi *et al.* (2019b) it is written that *Scaptomyza graminum* and *S. pallida* "… were confused with each other for a long time and it seems possible that *S. pallida* is the 'true' host of *Stigmatomyces scaptomyzae*, while the 'true' *Scaptomyza graminum* is parasitized only by *Stigmatomyces venetus*".

Stigmatomyces thoracochaetae Santam. sp. nov.
MB#840610
Fig. 62

Diagnosis

Similar to *S. crassicollis*, but differing by overall paler colour, brown wall thickenings below cell II and under perithecium, appendage axis with fewer rounded cells which are longer than broad, as well as by the distal area of appendage axis being curved backwards.

Etymology

The species epithet is derived from the name of the host insect (*Thoracochaeta*).

Type material

Holotype

DENMARK – **Nordvestsjælland (NWZ)** • On *Thoracochaeta brachystoma* (Stenhammer, 1855) (Diptera Sphaeroceridae); Bjerge Sydstrand; 55°34.046′ N, 11°9.459′ E; PG35; 24 Oct. 2018; *JP 1207*; V. Michelsen det.; ZMUC C-F-123733.

Description

Habitus slender. Thallus hyaline to pale yellowish, with slightly darker perithecial venter, and much darker basal cell of appendage. Basal cell of receptacle (I) obconical, about two times as long as broad, enlarged distally. Suprabasal cell of receptacle (II) almost cylindrical, longer than broad; bearing a brown wall thickening on the lower ventral side (Fig. 62A–B, D, H–J, arrows). Cell III outwards convex, about twice as long as broad, with its base at the same level as the II–VI septum.

Axis of appendage consisting of a dark, flattened basal cell above a constricted yet darker primary septum and five rounded, externally bulging, superimposed cells which are longer than broad, some of them slightly suffused with brown at their dorsal side. The lower four of these cells (including the basal) bearing one flask-shaped antheridium inwards, each with short, straight necks, and with squarish supporting cells. The two uppermost axial cells bear 1(–2) squarish cells supporting what seem to be sterile antheridia-like cells which are strongly backwards oriented (Fig. 62F, arrow).

Perithecial stalk cell (VI), secondary stalk cell (VII) and basal cells (m, n, n') showing brown thickenings on the walls (Fig. 62J, *). Perithecial venter rounded, almost spherical. Neck long and narrow, gradually tapering until septum w_2-w_3 which is marked by slight elevations, to the perithecial apex showing four lips, two of them ± protuberant (Fig. 62C). Preapical area slightly constricted.

Length from foot to tip of perithecium 220–303 µm. Perithecium (including basal cells) 151–170(–219) × 38–47 µm. Appendage length from primary septum to the apex 55–63(–80) µm. Ascospores length (including expanded sheath at basal area) 16–18 µm.

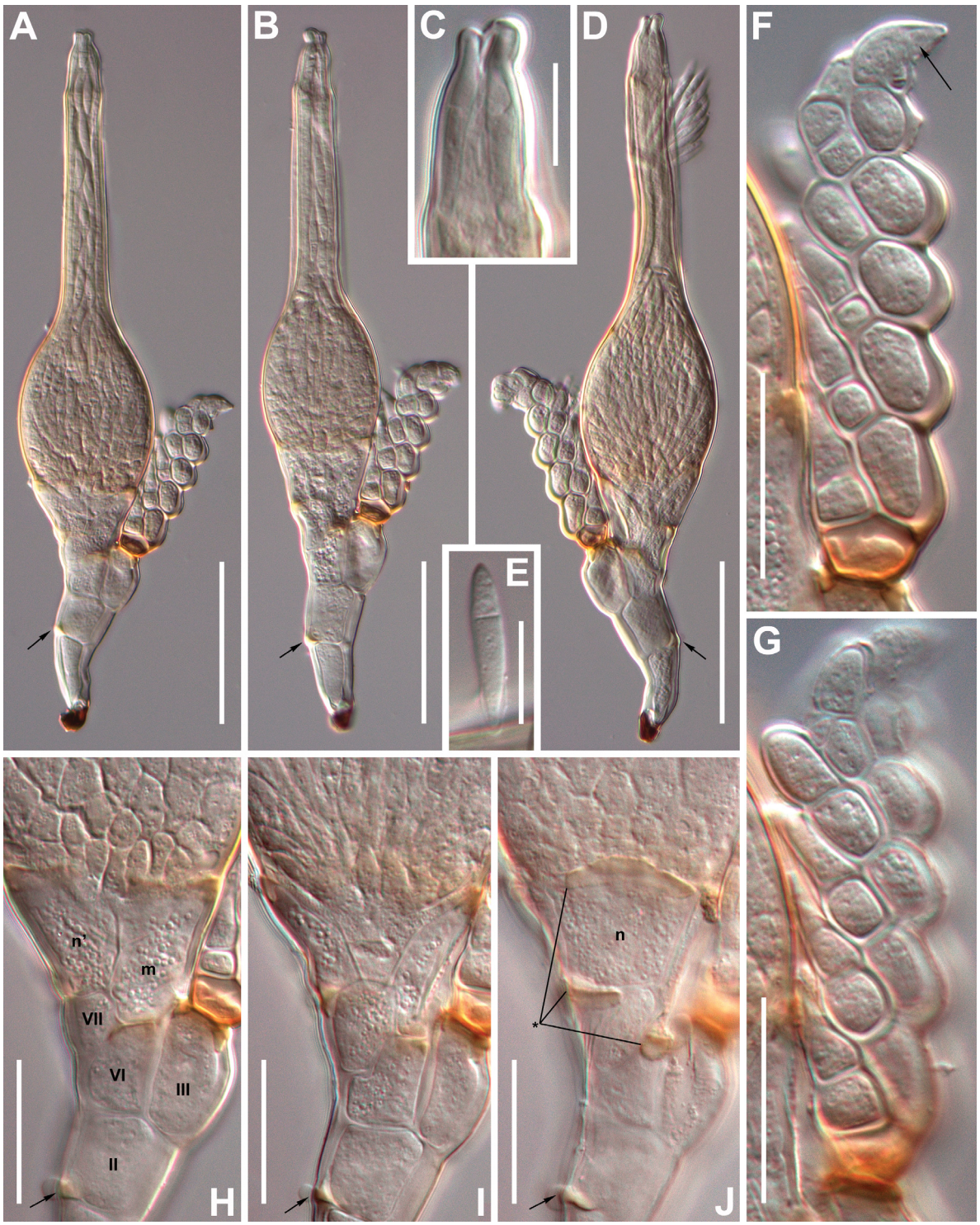

Fig. 62. *Stigmatomyces thoracochaetae* Santam. sp. nov. **A**–**B**, **D**. Mature thalli showing brown wall thickening on the lower ventral side of cell II (arrows). **C**. Perithecial apex in detail. **E**. Ascospore. **F**–**G**. Primary appendage in detail; in F the arrow points to uppermost axial antheridium-like cell which is oriented strongly backwards. **H**–**J**. Receptacle and lower area of perithecium in detail at three focusing levels, far (H), middle (I), near (J), showing cells II, III, VI, VII, m, n, n', thickening on the lower ventral side of cell II (arrows), and brown thickenings on the walls (*). Scale bars: A–B, D = 50 µm; C, E = 10 µm; F–J = 20 µm. Photographs from slide ZMUC C-F-123733 (holotype).

Thalli were found on the wings and sternites of the hosts. The hosts were sifted from moist, rotten seaweed on a sandy beach.

Remarks

This is the first species of a laboulbeniaceous fungus described on the genus *Thoracochaeta*. The species is particularly similar to *S. crassicollis* but may be separated from it by several characteristics like those mentioned in the diagnosis above, specially remarkable those related to the appendage arrangement.

Genus ***Tanmaurkiella*** Santam. gen. nov.
MB#840611

Diagnosis

Receptacle and primary appendage forming a common main axis without any evident transition between the receptacle and the primary appendage (i.e., the primary septum is not noticeable). Perithecium lateral, borne on a lower axial cell. Perithecial outer wall consisting of four vertical rows with four unequal cells each.

Etymology

Based on "Tanmaurk", a name which appears in runic scripture on the larger of the two Jelling stones, which are strongly identified with the creation of Denmark as a national state and the origin for the actual name of Denmark.

Type species

Tanmaurkiella pselaphi Santam.

Description

Receptacle and primary appendage forming a common, continuous, long axis. The exact position of the primary septum could not be determined, therefore cell III cannot be properly described. Perithecium lateral, usually arising from the second or third axial cell, and separated from them by a vertical septum; if any additional perithecium is formed it arises from cells above. Perithecial basal cells (m, n, n') and secondary perithecial stalk cell (VII) with well-distinguished walls at maturity. Perithecial outer wall consisting of four vertical rows, each with four cells of unequal height, the cells of each row progressively shorter towards the perithecial tip. Perithecial apex ornamented with lobes developed by tier w_4 cells (Fig. 63F–G). Antheridia unknown.

Remarks

This genus seems related with *Bordea* and *Cryptandromyces* according to certain morphological and ecological affinities. These genera, like *Tanmaurkiella*, infect Pselaphinae beetles (Col. Staphylinidae). *Bordea* and *Cryptandromyces* may be separated from *Tanmaurkiella* by one to several characteristics. Species of *Bordea* show a different appendage arrangement, with three superposed cells, including a distal antheridium; nevertheless, the perithecial apex of species in *Tanmaurkiella* remind those of *Bordea* by the presence of a crown-like structure. The genus *Cryptandromyces* includes species with three-celled receptacles and with perithecia where the outer wall shows five cells of subequal height in each vertical row of cells. Also, the new genus might be morphologically compared with some species of *Siemaszkoa*, like *S. ptenidii*, by the organization of the receptacle and appendage forming a continuous axis, with clearly lateral perithecia; nevertheless, this may be considered a homoplasy because remaining characteristics are very different, especially those dealing with the perithecium.

Key to the Danish species

1. Appendage flexuous, moniliform, with mostly inflated lower cells, separated by constricted septa ..... ***T. huggertii*** Santam. gen. et sp. nov.
– Appendage ± straight, apparently rigid, neither flexuous nor moniliform, with parallel margins, cells not inflated and septa not constricted..... ***T. pselaphi*** Santam. gen. et sp. nov.

Tanmaurkiella huggertii Santam. gen. et sp. nov.
MB#840612
Fig. 63

Diagnosis

Axis moniliform, flexuous, cells ± inflated, separated by constricted septa. Perithecium broadly ovoidal. Trichogyne stump reduced to a minute knob (Fig. 63D, ts).

Etymology

The species is named after Lars Huggert, a Swedish student of Laboulbeniales, because he was the first one who discovered it, although he did not describe it formally (Huggert 2010).

Type material

Holotype

DENMARK – **Østjylland (EJ)** • On *Pselaphus heisei* Herbst, 1792 (Col. Staphylinidae Pselaphinae); Serup Skov; 56°14.504′ N, 9°28.051′ E; NH23; 26 Mar. 2017; *JP 240*; JP det.; ZMUC C-F-122720.

Description

Thallus pale yellowish, shady in the perithecium. Basal cell of the receptacle (I) obconical, with a pointed hyaline beak at the base (Fig. 63A, arrow), two or more times as long as broad. Suprabasal cell of the receptacle (II) may be subdivided into three or more cells, where the perithecium develops from the second or third cell, or from any cell above if additional perithecia are formed (Fig. 63C); these cells originating from division of cell II are very variable in shape, broader than long or vice versa.

Appendage unbranched, very elongated, moniliform, flexuous, far exceeding the perithecial apex, starting with the cell bearing perithecium consisting of up to 20 superposed cells. Lower cells of appendage inflated, separated by constricted septa, very variable in length/width ratio; upper cells of appendage gradually longer and narrowing towards the distal area. Antheridia unknown.

Perithecial stalk cell (VI) small, rounded, flattened to isodiametric, separated from cell II that gave rise to it by a vertical septum. Perithecium broadly ovoidal, with an inflated venter and a short, nearly undistinguished neck. Perithecial basal cells flattened, occupying a narrow section below the venter. Perithecial tip rounded, showing four preapical protuberances which form a crown-like structure around the ostiolar area (Fig. 63F–G).

Length from foot to apex of perithecium 111–128 µm. Perithecium (including basal cells) 67–71 × 36–39 µm. Length from foot to appendage apex 235–283 µm.

Thalli were found on the elytra and dorsal tergites of the host. The host was sifted from mice-nests and moist moss and leaf litter in and around *Carex paniculata* L. tussocks at a sun-exposed spring.

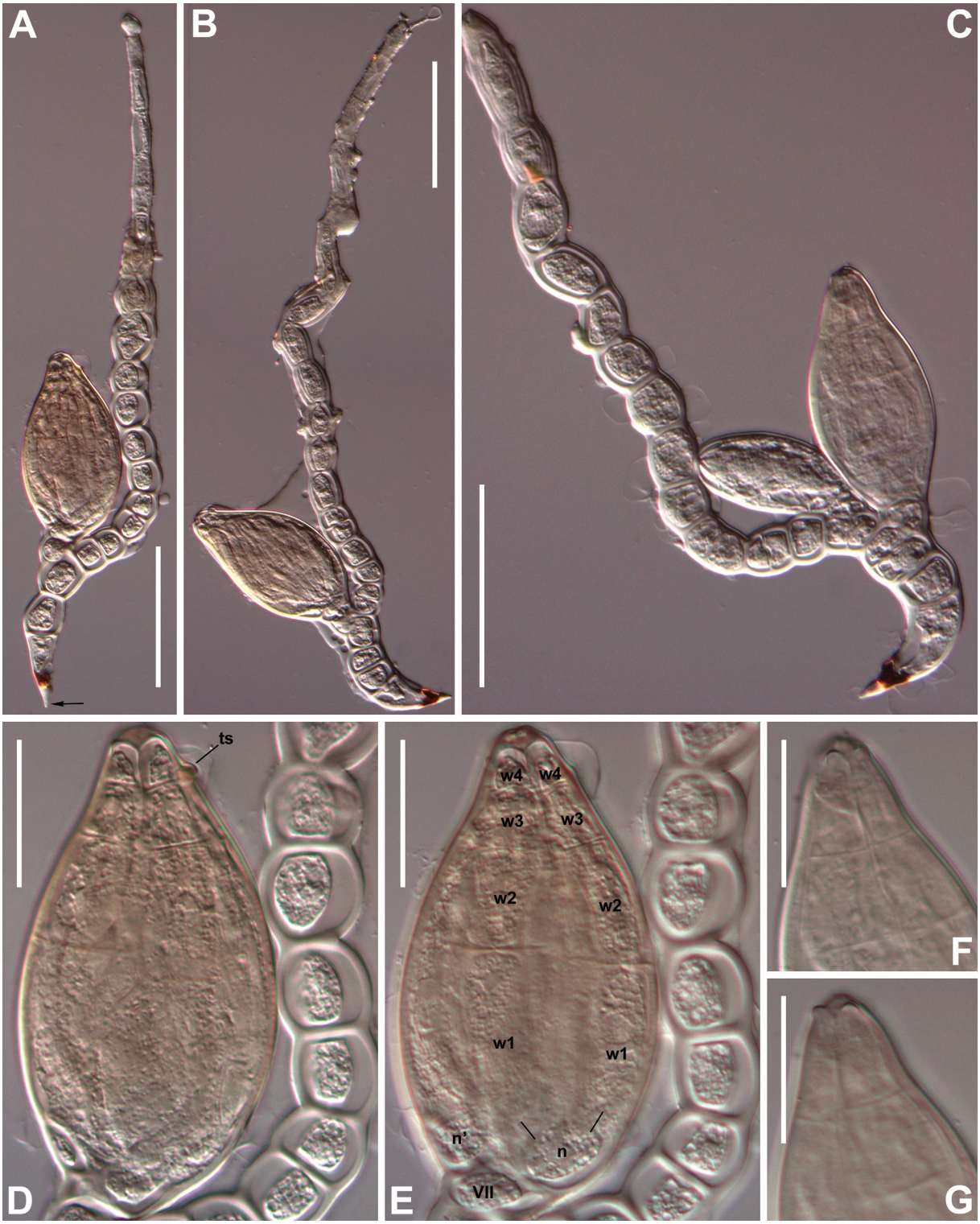

Fig. 63. *Tanmaurkiella huggertii* Santam. gen. et sp. nov. **A**–**B**. Mature thalli. In A, the pointed hyaline beak at the base of the foot is labelled (arrow). **C**. Mature thallus with a second young perithecium. **D**–**E**. Perithecium in detail, at two focus levels, near (D) and far (E), to show perithecial wall cells (w_n) developed from cell "n", cells n', VII and trichogyne scar (ts). **F**–**G**. Perithecial tip in detail at near (F) and far (G) focus to show the four preapical protuberances. Scale bars: A–C = 50 µm; D–G = 20 µm. Photographs from slide ZMUC C-F-122720 (holotype).

Remarks

This species is very similar to the other species of the genus but may be separated from it by the shape of the perithecium, the perithecial apex, the shape of the appendage cells (non inflated versus inflated), and the axis outline. Its presence in Sweden should be confirmed (see above under etymology).

Tanmaurkiella pselaphi Santam. gen. et sp. nov.
MB#840613
Fig. 64

Diagnosis

Axis with almost parallel margins, apparently rigid, cells not inflated. Perithecium narrowly fusiform. Trichogyne stump forming a horn-like protuberance (Fig. 64D–F, ts).

Etymology

The species epithet is derived from the name of the host insect (*Pselaphus*).

Type material

Holotype

DENMARK – **Nordøstsjælland (NEZ)** • On *Pselaphus heisei* Herbst, 1792 (Col. Staphylinidae Pselaphinae); Lejre; 55°36.245′ N, 11°58.315′ E; PG86; 10 May 1895; *Chr. Engelhart Dry0099*; Chr. Engelhart det.; ZMUC C-F-124165.

Description

Thallus hyaline, except for the slightly darkened perithecium. Basal cell of receptacle (I) obconical, with a blunt pale brown, rather undefined foot at base (Fig. 64F, fo), about 1.5 times as long as broad. Suprabasal cell of receptacle (II) sometimes subdivided, where the second, rarely the third cell (Fig. 64G, black line), gives rise to perithecium.

Appendage unbranched, very elongate, apparently rigid, with parallel margins, far exceeding the perithecial apex, starting from the cell bearing the perithecium consisting of up to 15 superposed cells. Lower cells of appendage cylindrical, not inflated, slightly variable in length/width ratio; upper cells of appendage gradually longer and narrowing towards the distal area. Antheridia unknown.

Perithecial stalk cell (VI) trapezoidal, slightly longer than broad, separated from cell II that gave rise to it by a strongly oblique to vertical septum. Perithecium narrowly fusiform, with a not very inflated venter and a short, nearly undistinguished neck. Perithecial tip rounded to flat, dome-shaped, showing four preapical protuberances which form a crown-like structure around the preostiolar area (Fig. 64A–E, H). Between tiers w_3 and w_4 a horn-like outgrowth represents a conspicuous trichogyne stump (Fig. 64D, F, ts).

Length from foot to apex of perithecium 79–88 µm. Perithecium (including basal cells) 48–57 × 13–19 µm. Maximum length from foot to appendage apex 163 µm.

Thalli were found on the elytra and tergites of the host. Nothing is known about the collecting circumstances of the host.

Remarks

The host is the same that of *Tanmaurkiella huggertii* gen. et sp. nov. although the two collections come from localities in different parts of Denmark and were obtained more than 100 years apart. The perithecial apex shows a distal dome-shaped area above the crown-like arranged protuberances that seem to be

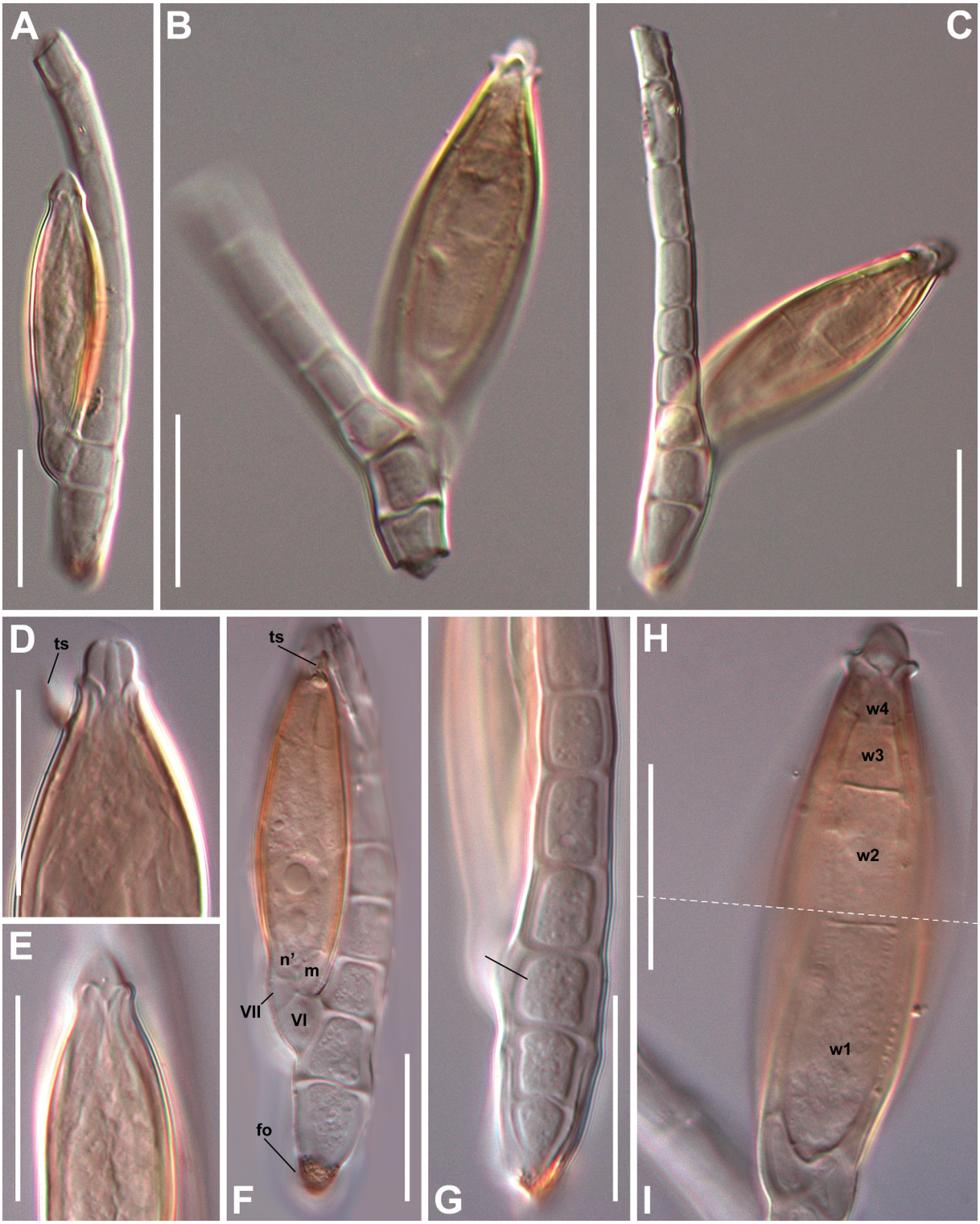

Fig. 64. *Tanmaurkiella pselaphi* Santam. gen. et sp. nov. **A**–**C**. Mature thalli. **D**. Perithecial tip in detail, showing trichogyne scar (ts) out of focus. **E**. Perithecial tip in detail. **F**. Mature thallus showing labelled VI, VII, m, and n′ cells, foot (fo), and trichogyne scar (ts). **G**. Third cell of the axis is labelled with a black line. **H**–**I**. Perithecium in detail with different focus level above and below the stippled line to have in focus outer wall cells (w_n). Scale bars: A–C = 25 µm; D–I = 20 µm. Photographs from slide ZMUC C-F-124165 (holotype).

acellular, i.e., without cytoplasmatic contents, similar to what occurs in the conical tip in species of *Acompsomyces* (Santamaria 1993c).

Genus ***Tavaresiella*** T.Majewski
MB#5359

Acta Mycologica 16: 147 (Majewski 1981). – Type species: *T. hebri* T.Majewski.

Brief description

Monoecious. Receptacle three-celled. Cells I and II separated by an oblique septum. Cells II and III laterally adnate. Primary appendage once ramified; the inner branch consisting of a series of superposed cells giving rise to lateral branchlets bearing antheridia; the outer branch simple and consisting of a small number of superposed cells. Perithecium with five cells in each vertical row of outer wall cells.

Remarks

The genus consists of four species, of which two in Europe, one in Denmark. After the original description with only the type species, Benjamin (1993) added three more: *T. majewskii* R.K.Benj. and *T. polhemi* R.K.Benj. from Indonesia, and *T. santamariae* R.K.Benj. from Indonesia, Madagascar, Spain, Poland and Turkey (Rossi 2016). Species of this genus are restricted to Hemiptera Hebridae of the genera *Hebrus* Curtis, 1831 and *Timasius* (Distant, 1909).

Tavaresiella hebri T.Majewski
MB#112656
Fig. 65A–B

Acta Mycologica 16: 148 (Majewski 1981). – **Type**: "On *Hebrus ruficeps* Thoms. (Heteroptera, Hebridae): Dlugie near Izbica Kujawska (Wloclawek voivodeship), muddy borders of shallow ditches at a meadow on the Northern end of Dlugie Lake, 22.5.1976, leg. T. Majewski (… 1590 – holotype …)"; KRAM–F. [Poland]

Diagnostic features

Cell I forming a thin, straight, externally darkened projection (Fig. 55A–B, arrows). Primary appendage consisting of a somewhat flattened basal cell giving rise to an inner antheridial branch and a simple outer branch. Inner branch formed by an elongated main cell (Fig. 55A–B, *) bearing on the outside a row of sessile antheridia or simple branchlets supporting antheridia. [Detailed descriptions: Benjamin 1993; Majewski 1994b]

Distribution and hosts

Confined to the true bug *Hebrus ruficeps* (Hemiptera Hebridae) from Poland (type), Spain (Santamaria 1993a), and Costa Rica (Goldmann & Weir 2018).

Collections examined from Denmark

On *Hebrus ruficeps* Thomson, 1871 (Heteroptera; Hebridae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Hjelm Kobbel; 54°54.863′ N, 12°14.918′ E; UA28; 28 Aug. 2019; *JP 1504*; JP det.; ZMUC C-F-124091. – **Sydsjælland (SZ)** • Bårse; 55°7.680′ N, 11°56.494′ E; PG81; 24 Aug. 2019; *JP 1503*; JP det.; ZMUC C-F-124090.

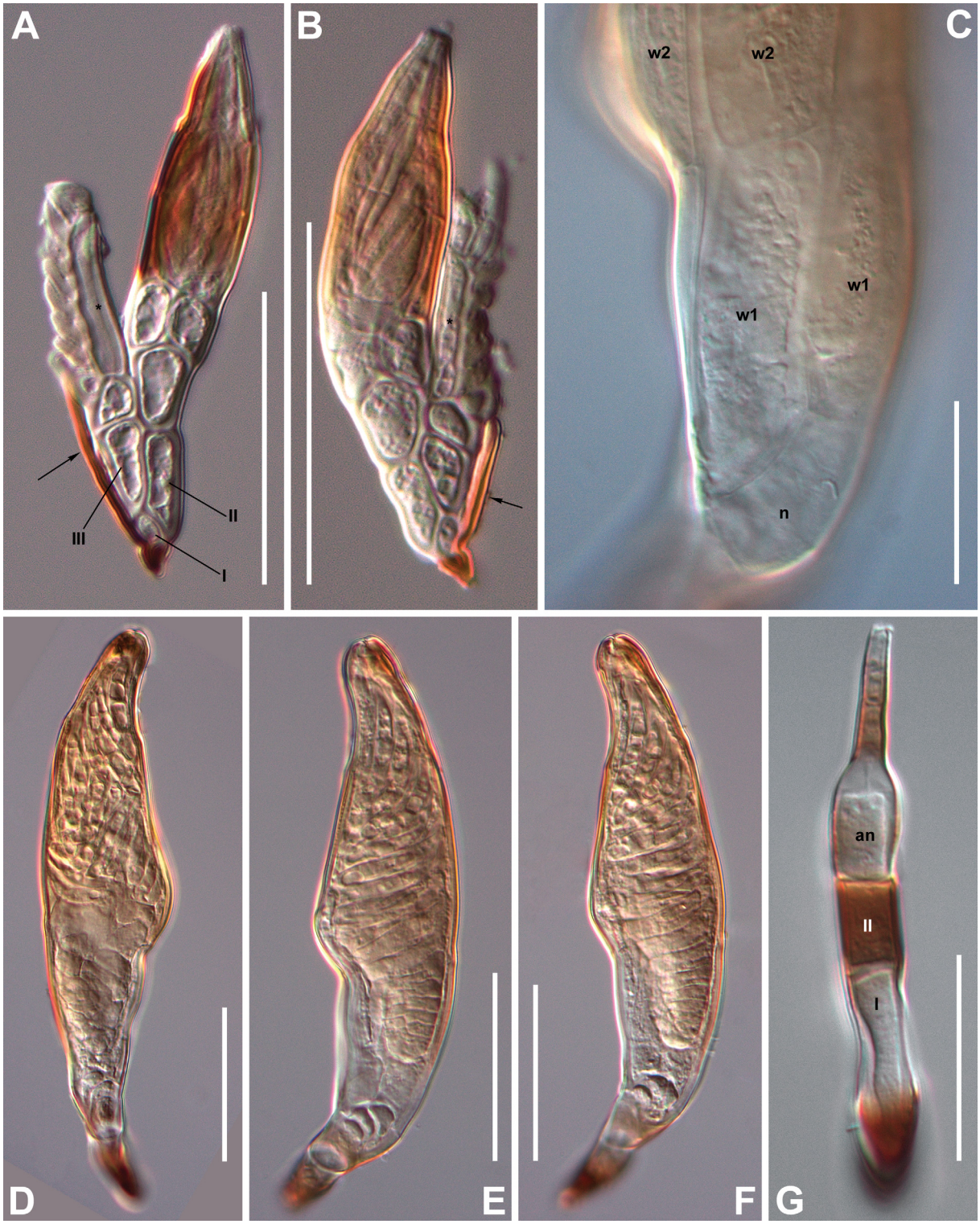

Fig. 65. A–**B**. *Tavaresiella hebri* T.Majewski. Two mature thalli with labelled I, II, III cells, elongated main cell of inner appendage branch (*), and darkened projection from cell I (arrows). – **C**–**G**. *Amorphomyces ventricosus* Santam. sp. nov. **C**. Lower area of perithecium in detail to focus on cells n and some of the wall cells (w_n). **D**–**F**. Female mature thalli. **G**. Male thallus with labelled cells I, II and antheridium (an). Scale bars: A–B, D–F = 50 µm; C, G = 25 µm. Photographs from slides ZMUC C-F-124090 (A–B), ZMUC C-F-123457 (D–G) (holotype).

Remarks

First record from Denmark. A second species of *Tavaresiella*, i.e., *T. santamariae*, was reported from Europe only on *Hebrus pusillus* (Fallén).

Genus ***Troglomyces*** S.Colla
MB#5614

Nuovo Giornale Botanico Italiano 39: 450 (Colla 1932). – Type species: *T. manfrediae* S.Colla.

Brief description

Monoecious or dioecious. Receptacle three-celled, with superposed cells I, II and III. Cell III very narrow and adnate to the perithecium. Perithecium with 5–6 outer wall cells in each vertical row. Perithecial apex bearing four ± conspicuous lobes.

Remarks

The genus consists of nine species, of which six in Europe, one in Denmark. The most recently described species is *T. twitteri* (Santamaria *et al.* 2020b). The original description of the genus was expanded twice to include new species (Enghoff & Santamaria 2015; Santamaria *et al.* 2020b).

Troglomyces triandrus Santam. & Enghoff
MB#810240

Organisms Diversity & Evolution 15: 253 (Enghoff & Santamaria 2015). – **Type**: "Holotype DENMARK: NE Zealand, Copenhagen, Gentofte, on the head of a female of *Archiboreoiulus pallidus* (Brade-Birks, 1920) (Diplopoda, Blaniulidae) collected in an old garden at Lyngbyvej, 1 June 1972, H. Enghoff leg. (slide C–F 92230)"; ZMUC C–F.

This species was described from Denmark and reported from several Danish localities, all in *Archiboreoiulus pallidus* by Enghoff & Santamaria (2015). Hosts, possible carriers of this species, are not among the material studied in this work.

Subtribe Amorphomycetinae (Thaxt.) I.I.Tav.

Genus ***Amorphomyces*** Thaxt.
MB#160

Proceedings of the American Academy of Arts and Sciences 28: 158 (Thaxter 1893). – Type species: *A. falagriae* Thaxt.

Brief description

Dioecious. Male thalli consisting of three superposed cells, the uppermost functioning as a single antheridium. Female thalli consisting of a two-celled receptacle, a perithecium and a two-celled primary appendage which usually is vestigial and concealed inside the perithecium or rarely free and distinguishable but very inconspicuous. Perithecium with 4–5 cells in each vertical row of outer wall cells.

Remarks

The genus consists of 11 species, of which four in Europe, one in Denmark. The most recently described species is *A. hernandoi* (Santamaria 2000). *Amorphomyces italicus* Speg. is the unique species of the genus where the primary appendage is visible outside the perithecium (Santamaria 2000).

Amorphomyces ventricosus Santam. sp. nov.
MB#840594
Fig. 65C–G

Diagnosis

Similar to *Amorphomyces falagriae* Thaxt., but the female thalli differ by the bulging on the perithecial margin involving second and, sometimes, also the first wall cells tiers, i.e., w_2 and part of the w_1 cell; and for straight male thalli.

Etymology

The species epithet means "inflated" and refers to the swelling of the perithecial margin.

Type material

Holotype

DENMARK – **Lolland, Falster, Møn (LFM) •** On *Myrmecocephalus concinnus* (Erichson, 1839) (Col. Staphylinidae Aleocharinae); Stensø ved Nakskov; 54°49.465′ N, 11°7.254′ E; PF37; 7 Jan. 2018; *JP 951*; JP det.; ZMUC C-F-123457.

Description

Male thalli consisting of a basal cell (I) about 2–3 times as long as broad, hyaline except for the dark brown lower foot; suprabasal cell (II) slightly longer as broad, about half as long as the basal cell, rectangular in section, uniformly darkish brown, separated by an almost horizontal septum from cell I; antheridium flask-shaped, symmetrical, with a venter variably tinged with brown, bearing an elongate, straight, ± brown efferent neck (Fig. 65G).

Female thalli yellowish brown except for the darkened foot and lower part of cell I; basal cell (I) as long as broad, enlarged distally, separated by an oblique septum from cells above; perithecium asymmetric, largely fusiform, slightly bent, with a smoothly curved margin on one side and with a conspicuous bulging of a w_2 cell above and also a slightly inflated w_1 cell on the opposite side; the perithecial tip slightly asymmetric, rounded, blunt, showing a centered apical ostiole.

Length of male thalli from foot to apex of antheridium 57–62 µm. Venter of antheridium 12–13 × 7–8 µm. Length of efferent neck 13–19 µm. Length of female thalli from foot to apex of perithecium 157–190 µm. Perithecium (length from septum above cell I × width at bulging) 144–167 × 39–41 µm.

Thalli were found on abdominal tergites of the host. The host was sifted from mouldy, warm fermenting wood chips.

Remarks

This species should be compared with *A. falagriae* but is easily distinguished from it by the swelling of the perithecium below the middle of the margin. The genus host of *A. ventricosus* sp. nov. is known as *Falagrioma* Casey, 1906 or *Falagria* Leach, 1819 in old literature, the latter is the host for *A. falagriae*. The new species is the only of the genus showing a bulging on the perithecium margin, only remotely

comparable with *A. biformis* Thaxt. which shows an unusual lateral finger-like extension. *Amorphomyces ventricosus* sp. nov. doesn't show a free primary appendage.

Genus ***Dioicomyces*** Thaxt.
MB#1592

Proceedings of the American Academy of Arts and Sciences 37: 33 (Thaxter 1901b). – Type species: *D. anthici* Thaxt.

Brief description

Dioecious. Male thalli consisting of four superposed cells, the uppermost functioning as a single antheridium. Female thalli consisting of a three-celled receptacle (Fig. 66A), a perithecium and a single celled primary appendage. Perithecium with 4–5(–6) cells in each vertical row of outer wall cells. Trichogyne reflexed, two-celled, the distal cell bearing terminal slender branchlets or papillae.

Remarks

The genus consists of 23 species, of which nine in Europe, two in Denmark. The most recently described species are *D. ladoi* and *D. leptalei* (Santamaria 2002). In this paper an extensive revision of the genus *Dioicomyces*, with numerous synonymies and typifications, is provided. For classification of species, male thalli are almost useless.

Key to the Danish species (partially following Santamaria 2002)

1. Female thalli bearing outgrowths on and near the perithecial tip. On *Myrmechixenus* Chevrolat, 1835 (Col. Tenebrionidae) ..... ***D. myrmecophilus*** T.Majewski
– Female thalli without outgrowths. On Col. Anthicidae ..... ***D. anthici*** Thaxt.

Dioicomyces anthici Thaxt.
MB#248070
Fig. 66A–E

Proceedings of the American Academy of Arts and Sciences 37: 33 (Thaxter 1901b). – **Type**: "USA: Fresh Pond, Cambridge (Mass.), on *Anthicus floralis*, Oct. 1900"; FH[FH–3488] [lectotype designed by Santamaria 2002: 619]

Dioicomyces formicillae Thaxt. (Thaxter 1912a: 169, as *D. formicellae*) [MB#149873]
Dioicomyces angularis Thaxt. (Thaxter 1912a: 171) [MB#236037]
Dioicomyces falcatus Speg. (Spegazzini 1917: 522) [MB#246417]
Dioicomyces infuscatus Speg. (Spegazzini 1917: 526) [MB#149845]
Dioicomyces pallidus Speg. (Spegazzini 1917: 527) [MB#240603]
Dioicomyces refractus Speg. (Spegazzini 1917: 528) [MB#240387]
Dioicomyces uncinatus Speg. (Spegazzini 1917: 532) [MB#240872]
Dioicomyces guatemalensis Thaxt. (Thaxter 1931: 64) [MB#266608]

Diagnostic features

Female thalli with conical or elongate-oblong primary appendage, having a ± pointed and inwardly curved apex. Perithecium ovoid, showing one strongly convex side whereas the opposite side is straight to slightly concave. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 2002; Santamaria 2003]

Distribution and hosts

Widespread and known from all continents except Oceania. Occurs on *Anthicus* Paykull, 1798 and allied genera (Col. Anthicidae) (Santamaria 2002; Majewski 2008; Bernardi *et al.* 2014). Also in Korea (Lee *et al.* 2011).

Collections examined from Denmark

On *Omonadus formicarius* (Goeze, 1777) (Col. Anthicidae)

DENMARK – **Østjylland (EJ)** • Høgdal; 56°6.449′ N, 9°36.941′ E; NH31; 28 Jan. 1990; *V. Mahler Dry0041*; V. Mahler det.; ZMUC C-F-124107. – **Nordøstsjælland (NEZ)** • Amager; 55°37.023′ N, 12°36.367′ E; 26 Sep. 1920; *V. Hansen Dry0037*; V. Hansen det.; ZMUC C-F-124103 • Jægerspris Nordskov; 55°54.438′ N, 11°58.702′ E; PH80; 19 Aug. 1965; *F. Bangsholt Dry0040*; F. Bangsholt det.; ZMUC C-F-124106 • Ledøje; 55°42.571′ N, 12°17.695′ E; UB37; 19 Aug. 2018; *JP 1172*; JP det.; ZMUC C-F-123697 • Østerlide; 55°49.832′ N, 12°29.432′ E; UB49; 25 Aug. 1945; *Johs. Petersen Dry0039*; Johs. Petersen; ZMUC C-F-124105 • Skærød; 56°0.673′ N, 12°9.646′ E; UC21; 14 Jan. 2018; *JP 957*; JP det.; ZMUC C-F-123463. – **Sydjylland (SJ)** • Havnen i Åbenrå; 55°2.479′ N, 9°25.429′ E; NF29; 27 Sep. 2009; *JP 62*; JP det.; ZMUC C-F-122537, C-F-122538, C-F-122539. – **Sydsjælland (SZ)** • Næstved; 55°13.968′ N, 11°45.755′ E; PG72; 10 Jul. 1922; *Høeg Dry0038*; Høeg det.; ZMUC C-F-124104.

Remarks

First record from Denmark. This is a very variable species, with numerous variations connected to one another through an inseparable mess of intermediate forms (Santamaria 2002). The absence of protuberances on the perithecial body and of outgrowths near or at the perithecial apex is a first clue to classify this perhaps collective species.

Dioicomyces myrmecophilus T.Majewski
MB#313129
Fig. 66F–I

Acta Mycologica 9 (1): 115 (Majewski 1973a). – **Type**: "On *Myrmecoxenus subterraneus* Chevrl. (Col., Colydiidae): Sadówka, Nowy Dwór Mazowiecki county, in anthill of *Formica rufa* at edge of wood, … 8.1.1972 (TM. … Nr 913 – holotype), leg. T. Majewski"; KRAM. [Poland] [Host genus is now *Myrmechixenus*, and belongs to Col. Tenebrionidae]

Diagnostic features

Female thalli with the perithecium showing an undistinguished neck and a broad, blunt, truncated apex which bears a finger-like, apically curved, sometimes uncinate outgrowth (Fig. 66G, arrow) and a blunt prominence near the perithecial tip (Fig. 66H, arrow). [Detailed descriptions: Majewski 1994b; Santamaria 2002]

Distribution and hosts

Only known from Poland where the species was described on *Myrmechixenus subterraneus* (Col. Tenebrionidae) a beetle that occurs in nests of *Formica* Linnaeus, 1758 ants.

Collections examined from Denmark

On *Myrmechixenus subterraneus* Chevrolat, 1835 (Col. Tenebrionidae)

DENMARK – **Østjylland (EJ)** • Ørnsø; 56°9.446′ N, 9°31.488′ E; NH32; 27 Sep. 1931; *Johs. Andersen Dry0042*; Johs. Andersen det.; ZMUC C-F-124108. – **Nordøstsjælland (NEZ)** • Grib Skov syd for Store Gribsø; 55°58.486′ N, 12°18.521′ E; UC30; 20 Jul. 2013; *JP 124*; JP det.; ZMUC C-F-122601.

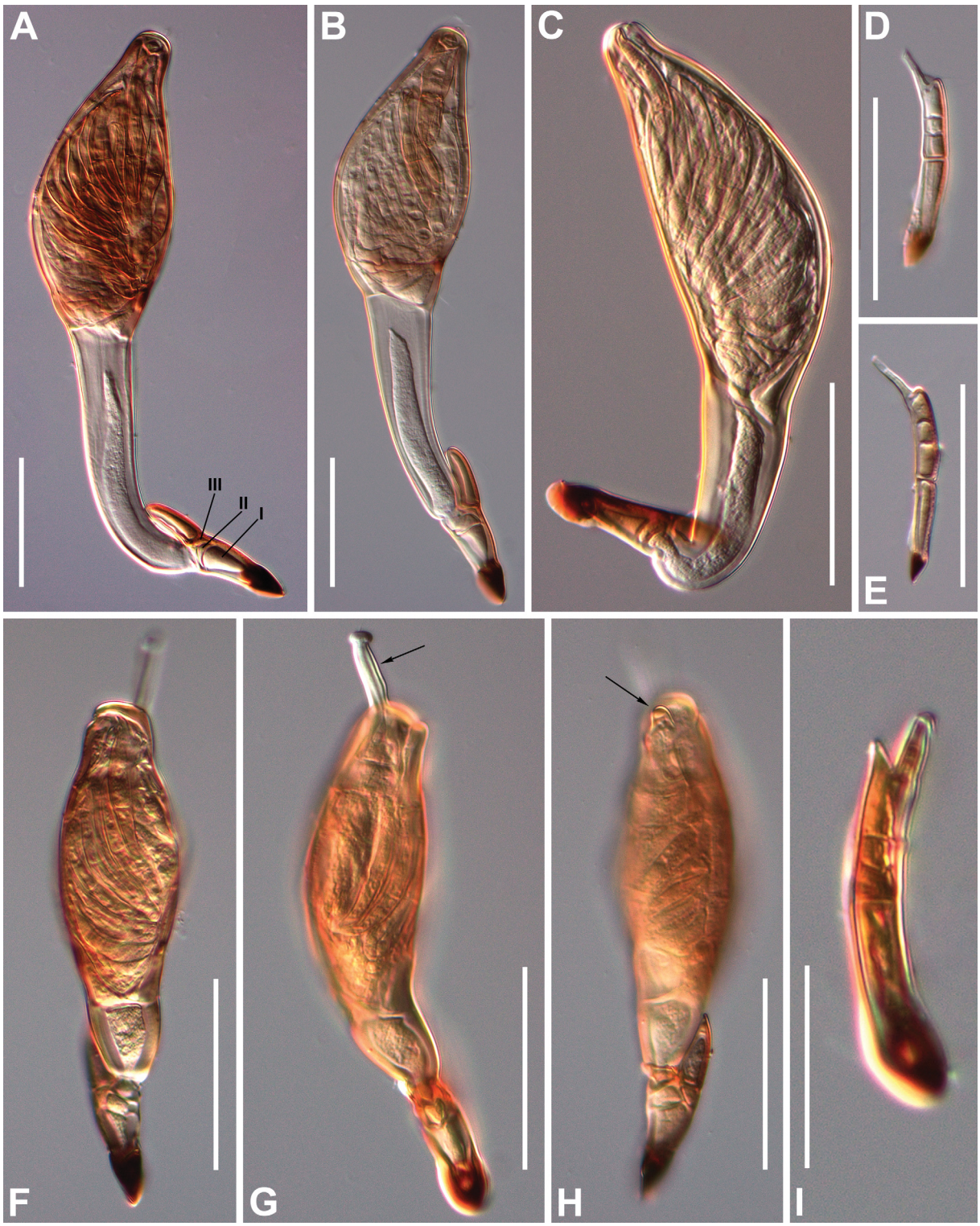

Fig. 66. *Dioicomyces* spp. **A**–**E**. *D. anthici* Thaxt. **A**–**C**. Mature female thalli. In A, cells I, II and III are labelled. **D**–**E**. Male thalli. – **F**–**I**. *D. myrmecophilus* T.Majewski. **F**–**H**. Mature female thalli showing a finger-like perithecial outgrowth in G (arrow), and a blunt prominence near the perithecial tip in H (arrow). **I**. Male thallus. Scale bars: A–H = 50 µm; I = 25 µm. Photographs from slides ZMUC C-F-123463 (A–B, D–E), ZMUC C-F-122537 (C), ZMUC C-F-122601 (F–I).

Remarks

First record from Denmark and second world record after its description. This well-distinguished and characteristic species appears to be very rare in Denmark and elsewhere. Although the host is quite widespread and common in Denmark, the fungus is probably overlooked, especially when considering the host's habitat preference.

Subfamily Peyritschielloideae (Thaxt.) I.I.Tav.
Tribe Peyritschielleae Thaxt.
Subtribe Peyritschiellinae s. str.

Genus ***Peyritschiella*** Thaxt.
MB#3856

Proceedings of the American Academy of Arts and Sciences 25: 8 (Thaxter 1890). – Type species: *P. curvata* Thaxt.

Dichomyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 28: 183 (Thaxter 1893) [MB#1516]
Rheophila Cépède & F.Picard, *Compte rendu, Association Française pour l'Avancement des Sciences, 36 session, Reims* 2: 783 (Cépède & Picard 1907) [MB#4695]

Brief description

Monoecious. Receptacle laminate, multiseriate, consisting of a basal cell (I) and three superposed tiers of horizontally arranged cells which support compound flask-shaped antheridia, perithecia and unicellular appendages (Fig. 68E). Each tier of cells consists of a median or axial cell (II', II", and II"') which divides laterally by longitudinal septa giving rise to a variable number of laterally arranged cells. The axial cell of the upper tier supports what should be the terminal cell (III) which bears the primary appendage above a darkened and constricted primary septum (Fig. 68E). In the lower tier, the axial cell is mostly flanked at both sides by cells which divide by longitudinal septa into a variable number of cells. Perithecium with four cells in each vertical row of outer wall cells and sometimes bearing on the apex short finger-like expansions termed auricles.

Remarks

The genus consists of 49 species, of which 15 in Europe, six in Denmark. The most recently described species is *P. heinemanniana* (De Kesel 1998).

Thalli of *Peyritschiella* are very characteristic by the flattened, leaf-like and multiseriate receptacle. The primary appendage and the primary septum follow the axial cell in the upper tier (see Fig. 58 of Santamaria 1989: 293, although the position of cell III seems misunderstood in that figure). In the lower tier, the first two contiguous cells may also be once divided by horizontal septa (e.g., *P. princeps*, Fig. 69A–C, labelled with arrows in C; Santamaria 1989: 293), although not all the species show this character, for example *P. oxyteli*. To our knowledge, this feature, which has not been mentioned by any other author, may be a remarkable morphological character to be taken into account.

The genus *Dichomyces* (Thaxter 1893) was separated early by differences in the symmetry of thalli, until Tavares (1985) decided with good judgment to unite them under the prioritary name of *Peyritschiella*. Symmetry or asymmetry of the receptacles are often altered by damage or by growth on unsuitable host body positions as, for example, the legs where fungi suffer the friction with environment. This genus is comparable to *Rickia* with whom it shares the subtribe Peyritschiellinae.

Key to the Danish species (partially following Majewski 1994b)

(Characters in the key are based on thalli in fair condition. In species of this genus any injury leads to strong variations in morphology)

1. Lower tier of cells laterally or entirely blackened, septa between cells obscured 2
– Lower tier of cells not blackened or septa between cells clearly visible 5

2. Perithecia usually with auricles 3
– Perithecia without auricles (see *P. hybrida* for explanation) 4

3. Thallus slender and short, up to 60 µm broad and up to 160 µm long, with two perithecia ..... ***P. furcifera*** (Thaxt.) I.I.Tav.
– Thallus bigger, up to 120 µm broad and up to 250 µm long, with four perithecia ..... ***P. vulgata*** (Thaxt.) I.I.Tav.

4. Thallus asymmetrical with only one perithecium on the upper tier, borne from one of the cells adnate to the axial cell ..... ***P. nigrescens*** Thaxt.
– Thallus symmetrical with 2–6 perithecia ..... ***P. hybrida*** (Thaxt.) I.I.Tav.

5. Thallus symmetrical, with median and upper tiers of cells of similar width; with two perithecia. On *Philonthus* and allied genera (Col. Staphylinidae Staphylinini) ..... ***P. princeps*** (Thaxt.) I.I.Tav.
– Thallus asymmetrical, with lower and middle tiers of cells primarily three-celled; with one brownish perithecium; appendages entirely tinged with brown. On *Oxytelus* and *Anotylus* Thomson, 1859 (Col. Staphylinidae Oxytelini) ..... ***P. oxyteli*** (Cépède & F.Picard) Santam.

Peyritschiella furcifera (Thaxt.) I.I.Tav.
MB#105641
Fig. 67A–B

Mycologia Memoirs 9: 270 (Tavares 1985). – **Basionym**: *Dichomyces furcifer* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 28: 184 [MB#142988] (Thaxter 1893, as *furciferus*, [MB#375051]) [Note: MycoBank gives two registration numbers, one for *D. furciferus* and the other for *D. furcifer*]. – **Type**: "On abdomen of *Philonthus debilis* Grav., Massachusetts"; FH. [USA]

Diagnostic features

Thallus symmetrical, small, up to 160 µm long. Lower tier of cells blackened, almost entirely opaque except for the central area. Middle tier of cells blackened outwards; extending with laterally superposed cells forming strip-like expansions as far as the upper part of the receptacle, right below the base of perithecia. Perithecia two in number; bearing short auricles on the apices. [Detailed descriptions: Thaxter 1896; Sugiyama 1973; Santamaria 1989; Majewski 1994b]

Distribution and hosts

This species has a worldwide distribution, known from the five continents. **Europe**: Finland, Germany, the Netherlands, Poland, Spain, United Kingdom; **Africa**: Algeria, Canary Islands, Ethiopia; **America**: Argentina, Grenada, Guatemala, Mexico, Uruguay, USA, Venezuela; **Asia**: Japan, Korea, Sri Lanka, Sumatra, Taiwan; **Oceania**: Australia (Santamaria *et al.* 1991). Not included in Santamaria *et al.* (1991) are records from Hungary (Bánhegyi *et al.* 1985), France (Duverger 1995), India (Kaur & Mukerji 1996b), Russia (Markovskaja 2004), China (Shen & Ye 2006), Sweden (Huggert 2010), Ecuador (Bernardi *et al.* 2014), and Turkey (Rossi 2016). Occurs on Col. Staphylinidae of the genus *Philonthus* and allied like

Spatulonthus, but also on *Gabrius*, *Eulissus* Mannerheim, 1830, *Gabronthus*, *Cafius*, *Rabigus* Mulsant & Rey, 1876, and *Xantholinus*.

Collections examined from Denmark

On *Philonthus coprophilus* Jarrige, 1949 (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Høvblege; 54°57.826′ N, 12°30.574′ E; UB20; 6 Sep. 2019; *JP 1514*; JP det.; ZMUC C-F-124269.

On *Philonthus debilis* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 820*; JP det.; ZMUC C-F-123314. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1085*; JP det.; ZMUC C-F-123603.

On *Philonthus discoideus* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 142*; JP det.; ZMUC C-F-122619.

On *Philonthus rectangulus* Sharp, 1874 (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Bispebjerg; 55°43.063′ N, 12°31.288′ E; UB47; 3 Nov. 2019; *JP 1541*; JP det.; ZMUC C-F-124301.

On *Philonthus umbratilis* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Bispebjerg; 55°43.063′ N, 12°31.288′ E; UB47; 3 Nov. 2019; *JP 1540*; JP det.; ZMUC C-F-124300.

Remarks

First record from Denmark. Cosmopolitan as it is, its presence in Denmark is not surprising.

Peyritschiella hybrida (Thaxt.) I.I.Tav.
MB#105644
Fig. 67C–D

Mycologia Memoirs 9: 270 (Tavares 1985). – **Basionym**: *Dichomyces hybridus* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 35: 423 (Thaxter 1900) [MB#243880]. – **Type**: [Not designated] [Ind. loc.] "With both types of perithecia (the type form): on *Philonthus aeneipennis* Boh., Paris Museum, No. 203, Gulf of Oman, India; on *Philonthus* sp., British Museum, No. 366, Sylhet, Assam, India; *Philonthus* sp., Bengal, India, Berlin Museum, No. 825: *P. Lewisius* Shp., Japan, Sharp Coll., No. 1122; on *Philonthus* sp., British Museum, No. 368, Hong Kong, China"; FH.

Diagnostic features

Thallus symmetrical, up to 300 × 150 µm (length × width). Lower tier of cells blackened, almost entirely opaque except for the central area. Middle tier of cells blackened outwards; extending with laterally superposed cells forming strip-like expansions exceeding in length the upper part of the receptacle. Perithecia 2–6 in number; with the apices usually without auricles in Danish thalli. [Detailed descriptions: Thaxter 1908; Terada 1976; Santamaria 1989]

Distribution and hosts

A species with a wide distribution. Known from **Europe** (Finland, Spain, United Kingdom), **America** (Grenada, USA), **Asia** (China, India, Japan, Korea, Sri Lanka, Taiwan), Canary Islands and Madeira

(Santamaria *et al.* 1991). Recently recorded from Cambodia (Try *et al.* 2017), and Thailand (Rossi & Bernardi 2018). Found on *Philonthus* and *Spatulonthus* (Col. Staphylinidae Staphylininae).

Collections examined from Denmark

On *Philonthus discoideus* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Skærød; 56°0.673′ N, 12°9.646′ E; UC21; 14 Jan. 2018; *JP 958*; JP det.; ZMUC C-F-123464.

Remarks

First record from Denmark. This is not an easily recognizable species, it can only be identified with certainty when thalli show long lateral expansions of the first tier of cells in combination with a broad upper tier (Fig. 67C). Auriculate and not auriculate forms have been described, a detail that seems to be related with different growing locations of thalli on the host body (Try *et al.* 2017). The Danish material is very scarce and belongs to the non-auriculate form.

Peyritschiella nigrescens Thaxt.
MB#181067
Fig. 67E–G

Proceedings of the American Academy of Arts and Sciences 28 (10): 184 (Thaxter 1893). – *Dichomyces nigrescens* (Thaxt.) Scheloske (Scheloske 1969: 106) [Not registered in MycoBank]. – **Type**: "On leg of *Philonthus debilis* Grav., Massachusetts"; FH. [USA]

Dichomyces inaequalis Thaxt. (Thaxter 1894: 103) [MB#243210]

Diagnostic features

Thallus asymmetrical, small, up to 130 µm long. Lower tier of cells blackened, almost entirely opaque except for the central area. Middle tier of cells blackened outwards, extending with laterally superposed cells forming strips-like expansions as far as the upper part of the receptacle, right below the base of the perithecium. One perithecium for each thallus, on the upper tier, borne from one of the cells adnate to the axial cell in the center; auricles absent. [Detailed description: Thaxter 1896]

Distribution and hosts

Reported from **Europe** (Finland, France, Germany, Italy, United Kingdom, Russia), **America** (USA), and **Asia** (Taiwan) (Santamaria *et al.* 1991). Also in China (Shen & Ye 2006), and Thailand (Rossi & Bernardi 2018). Infects species of the genus *Philonthus* (Col. Staphylinidae Staphylininae).

Collections examined from Denmark

On *Philonthus debilis* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 820*; JP det.; ZMUC C-F-123314. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1085*; JP det.; ZMUC C-F-123603.

On *Philonthus discoideus* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 142*; JP det.; ZMUC C-F-122620.

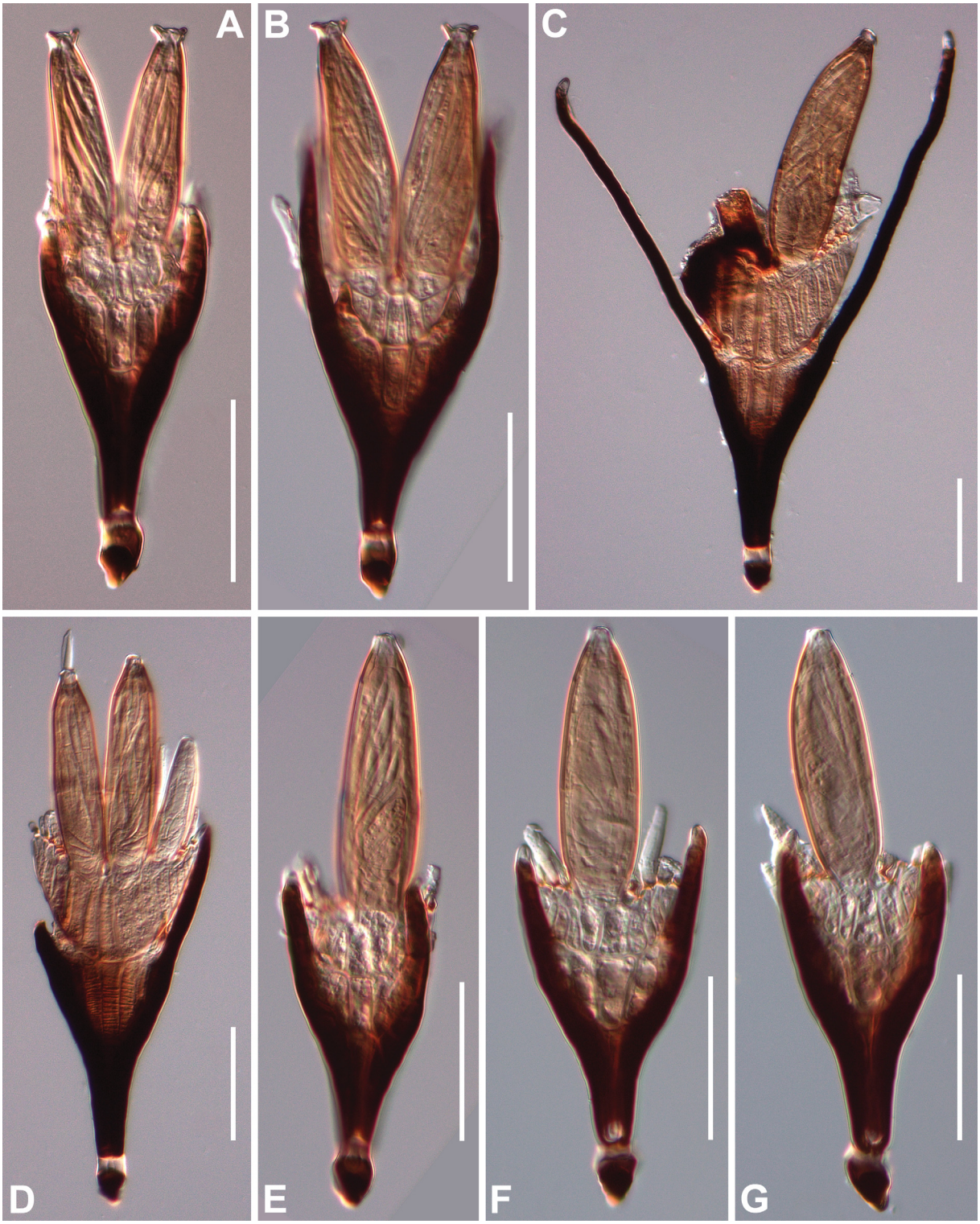

Fig. 67. *Peyritschiella* spp. **A**–**B**. *P. furcifera* (Thaxt.) I.I.Tav. Mature thalli. – **C**–**D**. *P. hybrida* (Thaxt.) I.I.Tav. Mature thalli. – **E**–**G**. *P. nigrescens* Thaxt. Mature thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122619 (A), ZMUC C-F-123314 (B), ZMUC C-F-123464 (C–D), ZMUC C-F-123314 (E), ZMUC C-F-123603 (F–G).

On *Philonthus quisquiliarius* (Gyllenhal, 1810) (Col. Staphylinidae Staphylininae)
DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1303*; JP det.; ZMUC C-F-123837.

Remarks

First record from Denmark. This species should be compared with *P. furcifera* by size but differs from that species by the off-centered solitary perithecium lacking apical auricles.

Peyritschiella oxyteli (Cépède & F.Picard) Santam. comb. nov.
MB#840614
Fig. 68A–E

Basionym: *Rheophila oxyteli* Cépède & F.Picard, *Compte Rendu, Association Française pour l'Avancement des Sciences* (part 2): 783 (Cépède & Picard 1907) [MB#432033]. – **Type**: DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; on *Anotylus rugosus* (Fabricius, 1775) (Col. Staphylinidae Oxytelinae); 12 Apr. 2016; *JP 2*; JP det.; **neotype**: ZMUC C-F-122472, **here designated**.

Diagnostic features

Thallus asymmetrical, of regular shape in comparison to *Peyritschiella protea*, yellowish-brown, with parallel margins when in good condition or growing in suitable locations. Lower and middle tiers of cells with three cells of similar size and shape. Typically, one brownish perithecium for each thallus on the upper tier, borne from one of the cells adnate to the median axial cell. Appendages entirely tinged with pale brown, distinctively darker than surrounding cells.

Distribution and hosts

Usually on *Oxytelus*, *Anotylus* and *Styloxys* Gozis, 1886 (Col. Staphylinidae Oxytelini), records on other rove beetles require confirmation. According to the list of hosts, *P. oxyteli* should be found from Europe, America, China (?) and Algeria (see below). Records on *Bledius* should be maintained in the "true" *Peyritschiella protea*.

The following is a complete list of the published records, but not necessarily pure *P. oxyteli*, arranged by genus hosts. The specimens should be verified one-by-one to see if they are true *P. protea* or *P. oxyteli*. On *Oxytelus*: United Kingdom (Thaxter 1900), France (Cépède & Picard 1907), USA (Thaxter 1908), Poland (Siemaszko & Siemaszko 1932), the Netherlands (Middelhoek 1943), Hungary (Bánhegyi 1944), Belgium (Collart 1945), Romania (Bánhegyi 1949), Germany (Scheloske 1969), Lithuania (Markovskaja 2000), Sweden (Huggert 2010). On *Anotylus*: Denmark (Rostrup 1935), Russia, Finland (Huldén 1983), Czech Republic, Austria, France, Germany, Romania, Sweden, United Kingdom, Ireland (Huldén 1985), Poland (Majewski 1994b), Lithuania (Markovskaja 2000), Latvia (De Kesel & Krastina De Kesel 2006), Belgium (De Kesel & Gerstmans 2011), the Netherlands (Haelewaters *et al.* 2012), USA (Haelewaters *et al.* 2015b), Armenia, Bulgaria (Rossi *et al.* 2019a). On *Styloxys*: France (Balazuc 1974f), Italy (Rossi 1975), Spain (Santamaria 1992b). On *Acrognathus* Erichson, 1839: Sweden (Huggert 2010). On *Planeustomus* Jacquelin du Val, 1857: Algeria (Maire 1920), Sweden (Huggert 2010). On *Manda* Blackwelder, 1952: Poland (Majewski 1994b). On *Philonthus*: Poland (Majewski 1994b), China? (Lee *et al.* 2006), Belgium (De Kesel & Gerstmans 2011). On *Phloeopora*?: Denmark (Høier 2009). On *Platydracus* Thomson, 1858: Panama (Haelewaters *et al.* 2017). De Kesel *et al.* (2020) reported *P. protea* on an undetermined staphylinid.

Fig. 68. *Peyritschiella* spp. **A**–**E**. *P. oxyteli* (Cépède & F.Picard) Santam. comb. nov. **A**–**D**. Mature thalli. **E**. Immature thallus with labelling of cells I, II', II"; II"', III, primary appendage (pa), and perithecium initial (per). – **F**–**G**. *P. protea* Thaxt. **F**. Mature thallus from *Bledius* in Spain. **G**. Mature thallus from type slide kept in FH. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122472 (A–C) (neotype), ZMUC C-F-122702 (D), ZMUC C-F-122809 (E), BCB-SS2016 (F), FH2590 (G) (lectotype).

Collections examined from Denmark

On *Anotylus rugifrons* (Hochhuth, 1849) (Col. Staphylinidae Oxytelinae)

DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 819*; JP det.; ZMUC C-F-123313.

On *Anotylus rugosus* (Fabricius, 1775) (Col. Staphylinidae Oxytelinae)

DENMARK – **Østjylland (EJ)** • Grejsdal syd for Hornstrup; 55°44.791′ N, 9°33.051′ E; NG37; 8 Mar. 2014; *JP 751*; JP det.; ZMUC C-F-123245 • Havnen i Randers; 56°27.687′ N, 10°3.546′ E; NH65; 19 May 2013; *JP 373*; JP det.; ZMUC C-F-122856 • Kjellerup; 56°17.282′ N, 9°26.197′ E; NH23; 22 Nov. 2013; *JP 111*; JP det.; ZMUC C-F-122588 • ibid.; 56°17.589′ N, 9°26.117′ E; NH23; 21 Oct. 2017; *JP 582*; JP det.; ZMUC C-F-123068 • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 17 Oct. 2014; *JP 196*; JP det.; ZMUC C-F-122675 • ibid.; 18 Jan. 2015; JP 452; JP det.; ZMUC C-F-122937 • Lindholm Hoved i Mossø; 56°2.772′ N, 9°42.809′ E; NH41; 18 Jan. 2015; *JP & H. Liljehult 513*; JP det.; ZMUC C-F-122996 • Ørnsø ved Silkeborg; 56°9.446′ N, 9°31.488′ E; NH32; 20 May 2013; *JP 381*; JP det.; ZMUC C-F-122864 • Serup Skov; 56°14.504′ N, 9°28.051′ E; NH23; 26 Mar. 2017; *JP 242*; JP det.; ZMUC C-F-122722 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 987*; JP det.; ZMUC C-F-123494 • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; 10 Nov. 2018; *JP 1229*; JP det.; ZMUC C-F-123756 • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 534*; JP det.; ZMUC C-F-123018. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 688*; JP det.; ZMUC C-F-123176 • Rishave; 55°33.475′ N, 10°24.013′ E; NG85; 19 Apr. 2018; JP 1067; JP det.; ZMUC C-F-123584. – **Lolland, Falster, Møn (LFM)** • Hobyskov; 54°44.069′ N, 11°15.296′ E; PF46; 7 Jan. 2018; *JP 955*; JP det.; ZMUC C-F-123461 • Næsby Strand; 54°44.625′ N, 11°4.539′ E; PF36; 23 Feb. 2014; *JP 554*; JP det.; ZMUC C-F-123040 • Nyord; 55°2.885′ N, 12°12.380′ E; UB20; 27 Apr. 2013; *JP 842*; JP det.; ZMUC C-F-123337 • Stensø ved Nakskov; 54°49.465′ N, 11°7.254′ E; PF37; 25 Feb. 2017; *JP 237*; JP det.; ZMUC C-F-122717 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1332*; JP det.; ZMUC C-F-123871. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 728*; JP det.; ZMUC C-F-123221 • Færgelunden; 55°50.540′ N, 12°1.735′ E; UB19; 16 Nov. 2013; *JP 597*; JP det.; ZMUC C-F-123086 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 2*; JP det.; ZMUC C-F-122472 • ibid.; 19 Mar. 2017; *JP 671*; JP det.; ZMUC C-F-123160 • Ledøje; 55°42.601′ N, 12°17.977′ E; UB37; 18 Apr. 2018; *JP 1046*; JP det.; ZMUC C-F-123562 • Nord for Risø; 55°42.184′ N, 12°6.692′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 622*; JP det.; ZMUC C-F-123110 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; 12 Apr. 2018; *JP 1033*; JP det.; ZMUC C-F-123545 • Syd for Veddelev; 55°40.346′ N, 12°4.915′ E; UB17; 14 Dec. 2013; *R. Aagaard Jensen 336*; JP det.; ZMUC C-F-122815 • Tisvilde Hegn; 56°2.171′ N, 12°3.429′ E; UC11; 27 Jan. 2018; *JP 974*; JP det.; ZMUC C-F-123481 • Tokkekøb Hegn; 55°52.334′ N, 12°22.229′ E; UB39; 6 May 2013; *JP 331*; JP det.; ZMUC C-F-122809 • Ud for Kongelundsfortet; 55°33.724′ N, 12°33.731′ E; UB46; 15 Apr. 2018; *JP 1050*; JP det.; ZMUC C-F-123566. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 555*; JP det.; ZMUC C-F-123041 • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 221*; JP det.; ZMUC C-F-122702 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 764*; JP det.; ZMUC C-F-123258. – **Nordvestsjælland (NWZ)** • Bjerge Sydstrand; 55°33.493′ N, 11°9.730′ E; PG35; 1 May 2013; *JP 301*; JP det.; ZMUC C-F-122780 • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 890*; JP det.; ZMUC C-F-123388 • Flasken nord for Reersø; 55°31.965′ N, 11°9.831′ E; PG35; 26 Jan. 2014; *JP 604*; JP det.; ZMUC C-F-123093 • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 848*; JP det.; ZMUC C-F-123343 • ibid.; 55°39.469′ N, 11°23.147′ E; PG47; 21 Apr. 2018; *JP 1057*; JP det.; ZMUC C-F-123574 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 760*; JP det.; ZMUC C-F-123254 • Nordbredden af Tissø ved Halleby Å's udløb; 55°35.602′ N, 11°18.532′ E; PG46; 18 Feb. 2017; *JP 386*; JP det.; ZMUC C-F-122869 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 634*; JP det.; ZMUC C-F-123123. – **Sydjylland**

(SJ) • Brænøre Mose; 55°23.906′ N, 9°25.714′ E; NG23; 5 Aug. 2018; *JP 1164*; JP det.; ZMUC C-F-123689 • Mørksø Sydøst for Kliplev; 54°52.481′ N, 9°26.561′ E; NF28; 1 Nov. 2013; *JP 356*; JP det.; ZMUC C-F-122838 • Store Søgård Sø; 54°56.251′ N, 9°27.063′ E; NF28; 23 Apr. 2000; *H. Liljehult 327*; JP det.; ZMUC C-F-122805. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 494*; JP det.; ZMUC C-F-122978 • Enemærket ved Næsbyholm; 55°22.429′ N, 11°36.776′ E; PG63; 17 Nov. 2019; *JP 1559*; JP det.; ZMUC C-F-124320 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1010*; JP det.; ZMUC C-F-123517 • ibid.; 27 Apr. 2018; *JP 1084*; JP det.; ZMUC C-F-123602 • ibid.; 25 Apr. 2019; *JP 1450*; JP det.; ZMUC C-F-124000 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1409*; JP det.; ZMUC C-F-123955 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1377*; JP det.; ZMUC C-F-123918 • Præstø; 55°6.913′ N, 12°2.035′ E; UB11; 25 Apr. 2019; *JP 1434*; JP det.; ZMUC C-F-123981 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 970*; JP det.; ZMUC C-F-123477. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1259*; JP det.; ZMUC C-F-123787.

Other material examined

Lectotype of *Peyritschiella protea*

GERMANY • "*Peyritschiella protea*, slide from FH, #2590, barcode 00313501, **lectotype**, on legs of *Bledius tricornis* (Herbst, 1784), from Thuringia (Germany), ex British Museum coll."; FH[00313501] [the slide consists of ten thalli in poor condition (Fig. 68G)] [lectotype designated by Haelewaters *et al.* 2015b: 469]

Remarks

Peyritschiella protea was described by Thaxter (1900: 427 [MB#181317]) on *Bledius*, *Oxytelus* and *Acrognathus* from Europe. In his second monograph, Thaxter (1908: 260) wrote about *P. protea*: "The specimens from *Bledius bicornis* Germ. are regarded as the type forms, and both figures have been drawn from this material". In his description Thaxter mentioned the variability of this species but preferred not to split it. Nearly at the same time, Cépède & Picard (1907) described *Rheophila oxyteli* on *Oxytelus rugosus* from France with a too brief description and lacking any illustration. Shortly after, the same authors (Cépède & Picard 1908) synonymized their taxon with *P. protea* with almost no explanation. Later, Thaxter (1931) included *Rheophila oxyteli* among the synonyms of *P. protea* in agreement with the opinion of Cépède & Picard.

Nevertheless, although the synonymy at the genus level is beyond doubt, this is not true at the species level. After studying the abundant material on *Oxytelus* and *Anotylus* collected from Denmark, we have observed enough differences of these thalli with those that should be considered as the "true" *P. protea* (e.g., on *Bledius* from Spain, Fig. 68F; Santamaria 1989), and after examination of all the available material we detected enough characters to separate two species. To support this argument we decided to borrow the type material of *P. protea* from FH.

With the name *Peyritschiella oxyteli* comb. nov. we restore an old taxon preserving the specific epithet published by Cépède & Picard (1907) and a neotype is here designated because the entire Picard collection is thought to be lost (see Catalogue organization under the Material and methods section).

Peyritschiella protea and *P. oxyteli* comb. nov. can be easily distinguished by several characteristics. Representative thalli of *P. oxyteli* comb. nov. consist of a lower tier of cells including only three main, large, subequal cells; the middle tier consists of a large central, nearly rectangular cell, flanked by two cells, which later may divide to give rise to antheridia; the upper tier is variably broadened, although the central cell continues to be as large as those below which form the main axis of the thallus. The lower and middle tiers, less so the upper tier, show almost parallel margins. The upper tier supports one large,

ovoid, brown perithecium, flanked with short brownish appendages at both sides. The brown colour of perithecium and appendages contrasts with the remainder paler yellowish thallus. Moreover, perithecium and appendages are asymmetrically arranged on the upper tier. When over-mature, a second perithecium may appear laterally from the second tier of cells. Older and damaged thalli may develop additional perithecia and should be discarded to properly distinguish the species.

Thalli of *P. protea* show an irregular shape, with divergent margins, and a very variable number of cells for each tier. The lower tier consists of more than three cells. Also, the perithecia are very variable in position and number, without an evident pattern; the appendages which are abundant in the upper tier, but also present in the middle tier, are always pale, even paler than the receptacle itself.

Records without accompanying figures are difficult to assign to one or the other of these two species. Majewski (1994b: pl. 96, fig. 1) included a drawing of a thallus from *Manda* that may represent an undescribed species; the medium and small sized thalli represented by Majewski (1994b: pl. 96 figs 4–8) are typical *P. oxyteli* comb. nov. De Kesel *et al.* (2020: fig. 67a–c) illustrated typical thalli of *P. oxyteli* comb. nov., as *P. protea*, on *Anotylus rugosus* from Belgium.

Peyritschiella princeps (Thaxt.) I.I.Tav.
MB#105655
Fig. 69A–C

Mycologia Memoirs 9: 269 (Tavares 1985). – **Basionym**: *Dichomyces princeps* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 30: 479 (Thaxter 1895) [MB#146013]. – **Type**: "On *Philonthus sordidus* Grav. Massachusetts"; FH. [USA]

Diagnostic features

Thallus symmetrical, up to 350 µm long, with middle and upper tiers of cells of similar width. Uniformly yellowish-brown, sometimes slightly darkened at the margins of the lower tier of cells. Two perithecia for each thallus, on the upper tier; auricles absent. [Detailed descriptions: Thaxter 1896; Sugiyama 1972; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Peyritschiella princeps is known from **Europe** (Belgium, Finland, France, Germany, the Netherlands, Italy, Poland, Spain), **Africa** (Algeria, Sierra Leone), Madeira, **America** (Argentina, Mexico, Peru, USA), **Asia** (India, Korea), and Australia (Santamaria *et al.* 1991). Also from Czech Republic (Rossi & Máca 2006), Sweden (Huggert 2010), and Indonesia (Haelewaters & Yaakop 2014). It occurs on species of the genus *Philonthus* and related genera like *Spatulonthus*, *Quediomacrus* Sharp, 1884 and *Bisnius* (Col. Staphylinidae Staphylininae).

Collections examined from Denmark

On *Bisnius cephalotes* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Østjylland (EJ)** • Hampen Plantage; 56°1.561′ N, 9°22.546′ E; NH20; 6 Oct. 2019; *JP 1525*; JP det.; ZMUC C-F-124280 • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 18 Nov. 2017; *JP 821*; JP det.; ZMUC C-F-123315. – **Sydjylland (SJ)** • Havnen i Åbenrå; 55°2.479′ N, 9°25.429′ E; NF29; 27 Sep. 2009; *JP 60*; JP det.; ZMUC C-F-122535.

On *Bisnius parcus* (Sharp, 1874) (Col. Staphylinidae Staphylininae)
DENMARK – **Sydjylland (SJ)** • Havnen i Åbenrå; 55°2.479′ N, 9°25.429′ E; NF29; 27 Sep. 2009; *JP 61*; JP det.; ZMUC C-F-122536.

On *Bisnius sordidus* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Bispebjerg; 55°43.063′ N, 12°31.288′ E; UB47; 3 Nov. 2019; *JP 1542*; JP det.; ZMUC C-F-124302.

On *Bisnius subuliformis* (Gravenhorst, 1802) (Col. Staphylinidae Staphylininae)
DENMARK – **Sydjylland (SJ)** • Havnen i Åbenrå; 55°2.479′ N, 9°25.429′ E; NF29; 27 Sep. 2009; *JP 63*; JP det.; ZMUC C-F-122540.

On *Philonthus politus* (Linnaeus, 1758) (Col. Staphylinidae Staphylininae)
DENMARK – **Nordøstsjælland (NEZ)** • Husum; 55°42.851′ N, 12°29.061′ E; UB47; 6 Oct. 2018; *JP 1200*; JP det.; ZMUC C-F-123726.

Remarks

First record from Denmark. Only slightly variable regarding the darkening of the lower tier of cells, from totally pale (Fig. 69C) to darker (Fig. 69B), through intermediate forms (Fig. 69A).

Peyritschiella vulgata (Thaxt.) I.I.Tav.
MB#105659
Fig. 69D

Mycologia Memoirs 9: 271 (Tavares 1985). – **Basionym**: *Dichomyces vulgatus* Thaxt., *Proceedings of the American Academy of Arts and Sciences* 35: 424 (Thaxter 1900) [MB#145545]. – **Type**:

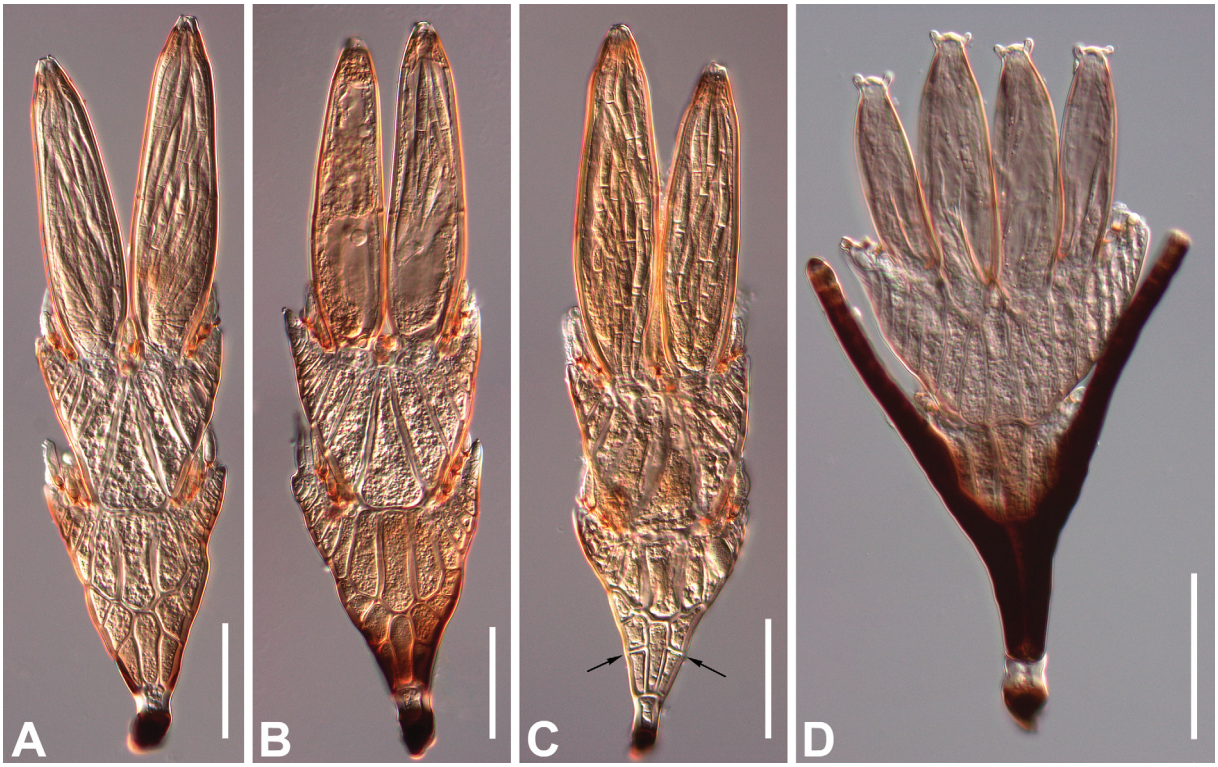

Fig. 69. *Peyritschiella* spp. **A**–**C**. *P. princeps* (Thaxt.) I.I.Tav. Mature thalli. In C arrows point to horizontal septa that divide the first two contiguous cells in the lower tier. – **D**. *P. vulgata* (Thaxt.) I.I.Tav. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-122535 (A–B), ZMUC C-F-122536 (C), ZMUC C-F-123973 (D).

[Not designated] [Ind. loc.] "On *Philonthus* spp. in many localities from Europe, America, Asia and Oceania"; FH.

Diagnostic features

Thallus symmetrical, up to 250 × 120 µm (length × width). Lower tier of cells blackened, almost entirely opaque except for the central area. Middle tier of cells blackened outwards; extending with laterally superposed cells forming strip-like expansions exceeding in length the upper part of the receptacle. Perithecia (2–)4 in number, with the apices bearing auricles. [Detailed descriptions: Thaxter 1908; Sugiyama 1973; Santamaria 1989; Majewski 1999]

Distribution and hosts

Grows on species of *Philonthus* and its allies (like *Spatulonthus*) (Col. Staphylinidae Staphylininae). Widespread and reported from the five continents. Santamaria *et al.* (1991) gather records from these countries in **Europe**: Austria, Finland, France, the Netherlands, Hungary, Italy, Spain, United Kingdom, Russia; **Africa**: Algeria, Cameroon, Ethiopia, Madeira, St Helena; **America**: Argentina, Chile, Grenada, Guatemala, Jamaica, Mexico, Nicaragua, Panama, Uruguay, USA; **Asia**: Arabia, Bali, China; and **Oceania**: Australia. Subsequent to that check-list, *P. vulgata* has been reported from Korea (Lee & Choi 1992b), India (Kaur & Mukerji 1996b), Poland (Majewski 1999), Slovakia, Czech Republic (Rossi *et al.* 2010), and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Philonthus quisquiliarius* (Gyllenhal, 1810) (Col. Staphylinidae Staphylininae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Gedser Odde; 54°33.687′ N, 11°57.806′ E; PF95; 21 Apr. 2019; *JP 1427*; JP det.; ZMUC C-F-123973.

Remarks

First record from Denmark. This species has been described as a variable species including atypical thalli lacking the lateral blackish strips formed from the middle tier and with perithecia where the apices lack auricles. All the Danish thalli studied belong to the typical form.

Genus ***Rickia*** Cavara
MB#4752

Malpighia 13: 182 (Cavara 1899). – Type species: *R. wasmannii* Cavara

Distichomyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 41: 308 (Thaxter 1905) [MB#1673]

Brief description

Monoecious. Receptacle laminate, flattened, multiseriate, consisting of three vertical rows of cells known as anterior (ventral), posterior (dorsal) and median (axial) series. Sometimes the median series is missing. Anterior and posterior series bear secondary one-celled appendages and flask-shaped antheridia. In most species, the perithecium seems to be borne from the anterior series. Perithecium with four cells in each vertical row of outer wall cells.

Remarks

Rickia is one of the largest genera in Laboulbeniales consisting of 156 species, of which 16 in Europe, five in Denmark. The most recently described species is *R. cifoneae* (Rossi & Bernardi 2018). For more details on the morphology of the genus *Rickia* see Santamaria *et al.* (2016).

Key to the Danish species (partially following Majewski 1994b and Santamaria *et al.* 2016)

1. Anterior series consisting of 2–5 cells 2
– Anterior series consisting of more than 16 cells. On *Scaphisoma* Leach, 1815 (Col. Staphylinidae Scaphidiinae) ..... ***R. peyerimhoffii*** Maire

2. Anterior series consisting of two cells. Uppermost cell of posterior series (p_6) forming a conspicuous free pedicel that serves of base for the primary appendage. On *Cylindroiulus* Verhoeff, 1894 (Diplopoda Julidae)..... ***R. laboulbenioides*** De Kesel
– Anterior series consisting of 3–5 cells. Other characters not as above 3

3. Antheridia numerous. Thallus more than 190 µm long. On *Unciger* Brandt, 1841 (Diplopoda Julidae). ..... ***R. uncigeri*** Scheloske
– One to a few antheridia. Thallus less than 190 µm long. On Col. Staphylinidae..... 4

4. Perithecium with a narrow and fairly long neck. Antheridia on both, anterior and posterior series. On *Proteinus* Latreille, 1796 (Col. Staphylinidae)..... ***R. proteini*** T.Majewski
– Perithecial neck not as above. One or two antheridia on the anterior series. On *Omalium* Gravenhorst, 1802 (Col. Staphylinidae)..... ***R. huggertii*** Balazuc

Rickia huggertii Balazuc
MB#113368
Fig. 70A–C

Bulletin du Muséum National d'Histoire Naturelle. Sér. 4, miscellanea. Paris. 2(2): 214 (Balazuc 1980, as *huggerti*). – **Type**: "Parasitus Homaliorum (Coleopt. Staphylinidae) in pluribus Europae regionibus. Typus in Galliae normanno litore lectus"; PC. [France]

Diagnostic features

Receptacle triseriate. Anterior series consisting of 3–4 cells, median series consisting of 9–10 cells, posterior series consisting of 9–10 cells. Only one (rarely two) antheridia on the upper cell of the anterior series (Fig. 70C, an). Perithecium as long as half of the total length of the thallus, almost surrounded by the median series of cells.

Distribution and hosts

Known from France (type), Italy, and Sweden (Balazuc 1980). Occurs on *Omalium* (= *Homalium* Ljungh, 1804) (Col. Staphylinidae Omalinae).

Collections examined from Denmark

On *Omalium riparium* Thomson, 1857 (Col. Staphylinidae Omalinae)

DENMARK – **Fyn (F)** • Flyvesandet ved Agernæs; 55°37.294′ N, 10°18.251′ E; NG86; 19 Apr. 2018; *JP 1044*; JP det.; ZMUC C-F-123560 • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 690*; JP det.; ZMUC C-F-123178 • Knudshoved; 55°18.212′ N, 10°49.828′ E; PG13; 11 Nov. 2018; *JP 1227*; JP det.; ZMUC C-F-123754. – **Lolland, Falster, Møn (LFM)** • Ulvshale; 55°2.305′ N, 12°17.042′ E; UB20; 2 May 2018; *JP 1103*; JP det.; ZMUC C-F-123621. – **Nordøstsjælland**

(NEZ) • Liseleje; 56°1.048′ N, 11°58.454′ E; PH81; 7 Oct. 2018; *JP 1202*; JP det.; ZMUC C-F-123729. – **Nordvestsjælland (NWZ)** • Bjerge Sydstrand; 55°33.493′ N, 11°9.730′ E; PG35; 1 May 2013; *JP 302*; JP det.; ZMUC C-F-122781 • Dybesø ved Rørvig; 55°58.117′ N, 11°45.004′ E; PH70; 17 May 2019; *JP 1464*; JP det.; ZMUC C-F-124044 • Stold Skydeterræn; 55°45.124′ N, 11°17.634′ E; PG48; 25 May 2014; *JP 379*; JP det.; ZMUC C-F-122862.

Remarks

First record from Denmark. The presence of this species in Denmark is not surprising given its existence in neighbouring Sweden. The study of immature thalli allows to determine that the perithecium is formed from the median series of cells (Fig. 70C, *). This characteristic is believed to be unusual (see the genus description) although thallus development has been studied for very few species of *Rickia.* A photo of this species is given here for the first time.

Rickia laboulbenioides De Kesel
MB#805476

Sterbeeckia 32: 6 (De Kesel *et al.* 2013). – **Type**: "Netherlands, Prov. Zeeland, Nieuwe Sluis (51°24′21,14″N – 3°30′19,08″E), on front legs of *Cylindroiulus latestriatus* (Julida, Blaniulidae) collected from litter of the high-tide mark, 25.iv.2013, leg. A. De Kesel, slides: De Kesel 5533b (HOLOTYPE, BR–MYCO 174750–53)"; BR.

Reported from Denmark on *Cylindroiulus* spp. by Santamaria *et al.* (2016), and on *C. punctatus* by Haelewaters *et al.* (2019a). Hosts, possible carriers of this species, are not mentioned among the material studied in this work.

New findings by H. Enghoff (pers. comm.) from Denmark

On *Cylindroiulus latestriatus* (Curtis, 1845)

DENMARK – **Nordøstjylland (NEJ)** • Kandestederne; 57°39.417′ N, 10°22.500 E; NJ89; 26 Oct. 2014; *I. B. Enghoff & H. Enghoff leg.*, H. Enghoff det.; NHMD 621783, ZMUC C-F 92231, C-F 92232, C-F 92233.

On *Cylindroiulus punctatus* (Leach, 1815)

DENMARK – **Sydjylland (SJ)** • Kollund Skov; 54°50.917′ N, 9°28.433′ E; NF38; 1 Jul. 1971, *K. Fog leg.*, H. Enghoff det.; NHMD 621784.

Rickia peyerimhoffii Maire
MB#181302
Fig. 70D

Bulletin Scientifique de la France et de la Belgique 49(3): 290 (Maire 1916c). – **Type**: [Not designated] [Ind. loc.] [Type lost?!] "Sur le prothorax de *Scaphisoma agaricinum* L. Algérie: bois d'Oum-el-Hallouf près Koléa, sur des Polypores lignicoles pourissants, 18/10 1910. Sur le prothorax de *Scaphosoma flavonotatum* Pic.: Algérie, bois de Farghen près Koléa, sous l'écorce d'un tronc mort de *Salix alba* L. couvert de *Polyporus adustus* Fa. pourrissants, spécimens immatures, janvier 1916".

Diagnostic features

Receptacle triseriate. Anterior series consisting of 16–20 cells, median series consisting of 13–16 cells, posterior series consisting of 16–21 cells. Thallus deeply darkened towards the 1–3 lower cells of the anterior and posterior series. Antheridia very abundant and interspersed among secondary appendages

on the posterior and anterior series. Perithecium immersed among the anterior and posterior series, protruding only by its ¼ of length; with two preostiolar black spots. [Detailed descriptions: Thaxter 1926; Siemaszko & Siemaszko 1932; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Grows exclusively on species of the genus *Scaphisoma* (Col. Staphylinidae, Scaphidiinae). This species has been recorded in **Europe** (Spain, United Kingdom, Italy, Germany, Czech Republic, Poland, Finland, Greece, Russia and Ukraine), as well as in Algeria (type) and Korea (Majewski 2008). Also in Hungary (Bánhegyi *et al.* 1985), France (Duverger 1995), Sweden (Huggert 2010), Bulgaria (Rossi *et al.* 2019a), and Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Scaphisoma agaricinum* (Linnaeus, 1758) (Col. Staphylinidae Scaphidiinae)
DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14°45.260′ E; VB81; 23 Jun. 2018; *JP 1152*; JP det.; ZMUC C-F-123676. – **Sydsjælland (SZ)** • Sorø, Kristiansminde; 55°25.115′ N, 11°35.209′ E; PG64; 27 Jun. 2013; *JP 390*; JP det.; ZMUC C-F-122873 • ibid.; 7–14 Aug. 2013; *JP 177*; JP det.; ZMUC C-F-122656.

On *Scaphisoma assimile* Erichson, 1845 (Col. Staphylinidae Scaphidiinae)
DENMARK – **Østjylland (EJ)** • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 982*; JP det.; ZMUC C-F-123489.

Remarks

First record from Denmark. This is an uncommon and well-distinguished species.

Rickia proteini T.Majewski
MB#103791
Fig. 70E

Acta Mycologica 19 (2): 191 (Majewski 1986a). – **Type**: "On *Proteinus brachypterus* F. (Col. Staphylinidae): Bieszczady Mts., Tarnica Mt. (Krosno voiv.), in *Fagetum*, on *Russula* sp., 1200 m above sea level, 21.8.1964, leg. Andrzej Szujecki (TM. 1682 – holotype)"; KRAM. [Poland]

Diagnostic features

Receptacle triseriate. Anterior series consisting of 3–5 cells, median series consisting of 6–8 cells, posterior series consisting of 7–9 cells. One to a few solitary antheridia on the anterior and posterior series, sometimes replaced by secondary appendages. Perithecium with a narrow and fairly long neck, almost surrounded by the median series of cells. [Detailed descriptions: Majewski 1994b; De Kesel *et al.* 2013]

Distribution and hosts

Known from Poland (type), Japan (Majewski 1988), France (Duverger 1995), Norway (Majewski 2008), and Belgium (De Kesel *et al.* 2013). Occurs on *Proteinus* (Col. Staphylinidae Proteininae).

Collections examined from Denmark

On *Proteinus laevigatus* Hochhuth, 1872 (Col. Staphylinidae Proteininae)
DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 12*; JP det.; ZMUC C-F-122485.

Fig. 70. *Rickia* spp. **A**–**C**. *R. huggertii* Balazuc. **A**–**B**. Mature thalli. **C**. Immature thallus showing the trichogyne scar (ts) and the antheridium (an). – **D**. *R. peyerimhoffii* Maire. Mature thallus. – **E**. *R. proteini* T.Majewski. Immature thallus at left and mature thallus on the right. Scale bars: A–B, D–E = 50 µm; C = 20 µm. Photographs from slides ZMUC C-F-122781 (A–B), ZMUC C-F-122862 (C), ZMUC C-F-122656 (D), ZMUC C-F-122485 (E).

Remarks

First record from Denmark. Rare and very scarce in Denmark (only the two thalli in Fig. 70E), but perfectly identifiable. A photo of this species is given here for the first time.

Rickia uncigeri Scheloske
MB#338612

Parasitologische Schriftenreihe 19: 147 (Scheloske 1969). – **Type**: [In ?] "An sich über den ganzen Körper verteilt, bevorzugt aber ventral auf dem Kopf und den vorderen Segmenten und Beinpaaren (also nahe den Geschlechts organen bei ♂ und ♀) von *Unciger foetidus* (Diplopoda: Julidae). Die Wirte wurden in einem Buchenwald bei Streitberg/Ebermannstadt erbeutet. Deutschland. Holotypus Abb. 45". [Germany]

Reported from Denmark on *Unciger foetidus* (Koch, 1838) by Santamaria *et al.* (2016) and Haelewaters *et al.* (2019a). Hosts, possible carriers of this species, are not among the material studied in this work.

New findings by H. Enghoff (pers. comm.) from Denmark

On *Unciger foetidus* (Koch, 1838)

DENMARK – **Fyn (F)** • Teglværksskov N of Nyborg; 55°20.267′ N, 10°48.167′ E; PG13; 14 Jul. 1971, *Entomologisk Fredningsudvalgs Expedition leg*., H. Enghoff det.; NHMD 621785. – **Nordøstsjælland (NEZ)** • Stenholtsvang, 55°57.439′ N, 12°21.204′ E; UC30; 28 Oct. 2017; *JP leg.*, H. Enghoff det.; NHMD 621786.

Tribe Dimorphomyceteae Thaxt.

Genus ***Dimeromyces*** Thaxt.
MB#1583

Memoirs of the American Academy of Arts and Sciences 12: 267 (Thaxter 1896). – Type species: *D. africanus* Thaxt.

Eudimeromyces Thaxt., *Proceedings of the American Academy of Arts and Sciences* 54: 215 (Thaxter 1918b) [MB#1923]

Jeanneliomyces Lepesme, *Mémoires du Muséum d'Histoire Naturelle* 19(1): 149 (Lepesme 1945) [MB#22460]

Brief description

Dioecious. Male thalli consisting of a receptacle with a few to many cells, compound antheridia and an unbranched primary appendage. Female thalli consisting of a vertical or horizontal row of cells, some of them giving rise to sterile secondary appendages, perithecia, and an unbranched primary appendage. Perithecium with an undetermined number of cells in each vertical row of outer wall cells, only the 2–3 upper cells being visible at the maturity. As perithecia mature, wall cells of stalk and basal cells degrade and vanish.

Remarks

This is one of the largest genera among Laboulbeniales consisting of 115 species (including the 112 mentioned by Reboleira *et al.* 2018, the two new species in Dogonniuck *et al.* 2019, and the new species described here), of which 13 in Europe, two in Denmark. The most recently described species are *D. capensis* and *D. streblidarum* (Dogonniuck *et al.* 2019). Species of *Dimeromyces* are known from

very diverse host groups, viz., Acarina, Isoptera, Orthoptera, Dermaptera, Thysanoptera, Coleoptera and Diptera. In spite of its cosmopolitan distribution, the major diversity of species is in tropical regions.

Key to the Danish species

1. Apical cell of primary appendage sharp-pointed. On *Longitarsus* Latreille, 1829 (Col. Chrysomelidae)..... ***D. oculatus*** Santam. sp. nov.
– Apical cell of primary appendage obtuse. On *Necrobia* Olivier, 1795 (Col. Cleridae)..... ..... ***D. corynetis*** Thaxt.

Dimeromyces corynetis Thaxt.
MB#569544
Fig. 71

Proceedings of the American Academy of Arts and Sciences 48: 157 (Thaxter 1912a, as *D. Corynitis*). – **Type**: "On the elytra of *Corynites ruficollis* Fabr., La Plata, No. 1459"; FH. [Argentina]

Diagnostic features

Male thalli consisting of 5–8 superposed cells separated by horizontal septa, bearing lateral flask-shaped compound antheridia, and an apical unbranched, unicellular, rounded primary appendage (Fig. 71D, pa). Female thalli consisting of 4–6 superposed cells separated by horizontal septa. The 2nd and/or 3rd cells bear a unicellular secondary appendage (Fig. 71A, arrow). The 3rd and/or 4th cells give rise to perithecia.

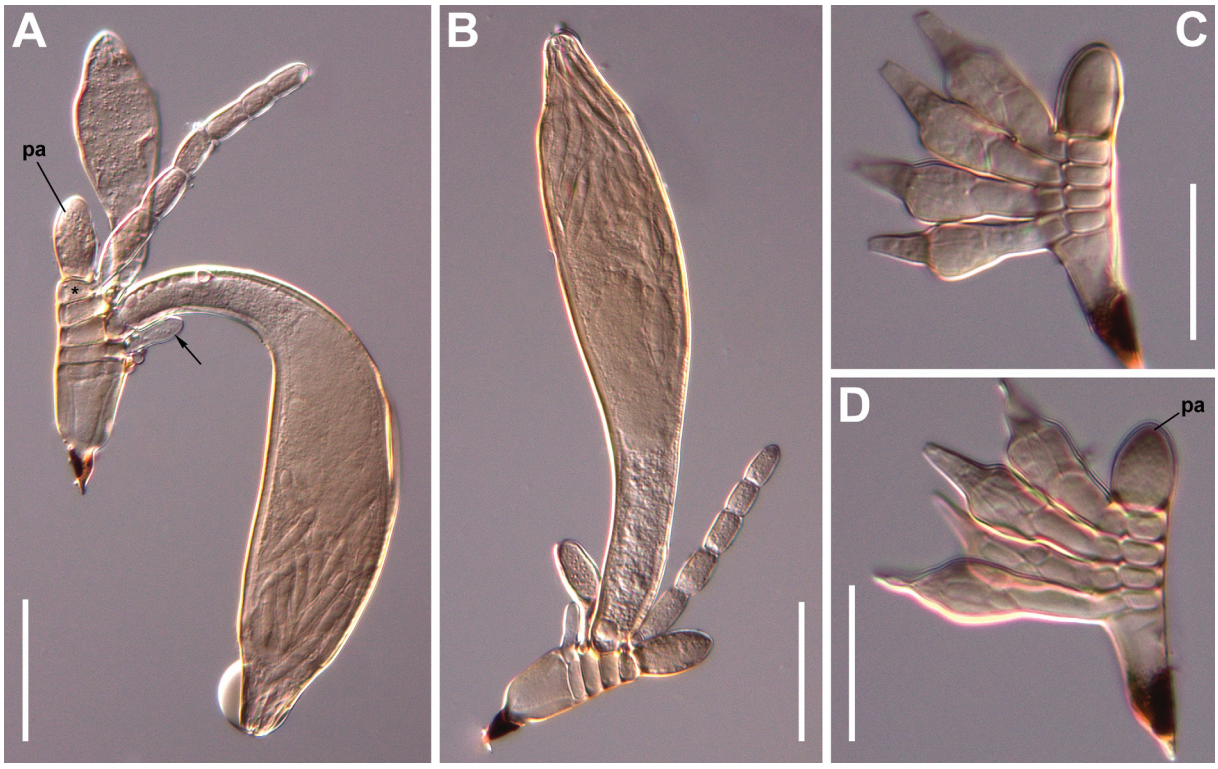

Fig. 71. *Dimeromyces corynetis* Thaxt. **A**–**B**. Female mature thalli with labelled primary appendage (pa), a unicellular secondary appendage (arrow), and the uppermost receptacular cell (*) in A. **C**–**D**. Male thalli showing primary appendage (pa). Scale bars: A–B = 50 µm; C–D = 25 µm. Photographs from slide ZMUC C-F-124099.

The uppermost cell supports a long, multicellular, unbranched secondary appendage and the rounded primary appendage (Fig. 71A, *). [Detailed descriptions: Thaxter 1924; Santamaria 2003; Majewski 2006]

Distribution and hosts

This species has been reported from Argentina (type), USA (Thaxter 1924), United Kingdom (Hincks 1960), France (Balazuc 1974f), Italy (Rossi 1975), Spain (Santamaria 1994), Poland (Majewski 2006), Sweden (Huggert 2010), and Czech Republic (Rossi *et al.* 2019b). Occurs on *Necrobia* (=*Corynetes*) (Col. Cleridae).

Collections examined from Denmark

On *Necrobia ruficollis* (Fabricius, 1775) (Col. Cleridae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Høvblege; 54°57.853′ N, 12°30.666′ E; UA49; 28 Jul. 2000; *JP Dry0029*; JP det.; ZMUC C-F-124099. – **Sydjylland (SJ)** • Åbenrå; 55°2.474′ N, 9°25.451′ E; NF29; 20 Sep. 2009; *JP Dry0030*; JP det.; ZMUC C-F-124100.

Remarks

First record from Denmark. This species shows a patchy distribution likely due to lack of investigation, probably because the capture of its hosts is complicated by its specialized habitat, viz., in rotting corpses and other unpleasant-smelling substances such as rotting grains where they feed on the meat-infesting larvae of blow flies (*Calliphora* Robineau-Desvoidy, 1830, Diptera Calliphoridae), Dermestidae (Coleoptera) and Piophilidae (Diptera). The cells above the basal cell may undergo divisions giving rise to additional secondary appendages or perithecia.

Dimeromyces oculatus Santam. sp. nov.
MB#840599
Fig. 72

Diagnosis

Similar to *Dimeromyces trilobatus* W.Rossi, Bernardi & J.A.Torres, but with female thalli differing by the two round prominences symmetrically flanking the straight snout-like perithecial tip, and smaller male thalli with fewer antheridia.

Etymology

The species epithet means “having eyes” and refers to the two protuberances on the perithecial tip which resemble two prominent eyes when seen in front view.

Type material

Holotype

DENMARK – **Sydsjælland (SZ)** • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; on *Longitarsus luridu*s (Scopoli, 1763) (Col. Chrysomelidae); 3 Jan. 2019; *JP 1271*; JP det.; ZMUC C-F-123799.

Isotype

DENMARK • same data as for holotype; ZMUC C-F-123800.

Paratype

DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; on *L. luridus*; 3 Jan. 2019; *JP 1304*; JP det.; ZMUC C-F-123838.

Description

Male thallus hyaline except for the blackened foot and a faint brown suffusion around the base and the apex of antheridia. Receptacle consisting of four cells obliquely superposed, the lowermost of which is obtriangular and 2–3 times as long as broad, the following two cells rhomboidal, giving rise to lateral antheridia, the uppermost cell trapezoidal, supporting the unicellular, subulate primary appendage (Fig. 72H, pa). Two flask-shaped antheridia with a variable, short stalk cell and the neck slightly curved outward.

Total length from foot to apex of appendage 58–73 µm. Length of antheridia (without stalk) 17–23 µm.

Female thallus nearly hyaline except for the blackened foot, the pale brown perithecial venter, and areas of the secondary appendage. Receptacle consisting of five cells: a large basal cell (cell I), two cells derived from cell II (II' and II"), and two distal small cells (probably resulting from division of cell III) which form the base for the unicellular, subulate primary appendage, which is almost identical to the appendage of male thalli (Fig. 72F). Cells I, II' and II" separated by oblique septa. Cell I extending upwards beside the lower II' till the basal cell of secondary appendage (Fig. 72, bc a). The latter whip-like, distally slender and flexuous, never reaching the perithecial apex in height; unicellular or once divided by a septum near the base (Fig. 72A, sa).

Perithecial stalk cell (VI), formed from cell II", vanishing upwards. Perithecium largely fusiform, about twice as long as receptacle, regularly enlarged above the stalk until the upper third of its length, then gradually narrower towards the apex. Tip of perithecium three-lobed above a constricted area, with a middle, snout-like lobe flanked symmetrically by the two other round lobes, which are prominences of the uppermost tier of wall cells (Fig. 72C–D, arrows).

Length from foot to apex of perithecium 142–188 µm. Perithecium (including stalk cell) 101–144 × 23–37 µm. Maximum length (chord) of secondary appendage 82–99 µm.

Thalli were found numerous on various body parts of the hosts. The hosts were sifted from fresh flood debris on coastal meadows.

Remarks

This species resembles *D. trilobatus*, described on *Apalotrius* Clark, 1860 and *Physimerus* Clark, 1860 (Col. Chrysomelidae Galerucinae Alticini Monoplatina) from Ecuador (Rossi *et al.* 2015) with regard to the peculiar three-lobed perithecial tip, although the lateral lobes are different: ear-shaped, more elongated in *D. trilobatus* and circular in *D. oculatus* sp. nov. The diagnosis given above highlights this and other characteristics that distinguish the two species. Similar lobes on the perithecial apex are also present in *D. pedalis* Thaxt. (Thaxter 1924) described on a fly from Borneo, which however differs from the new species by several characteristics such as the peculiar shape of the appendages in female thalli. Including *D. oculatus* sp. nov., 13 species of *Dimeromyces* have been described on Chrysomelidae so far (Haelewaters & Rossi 2015).

Dimeromyces oculatus sp. nov. is likely allied to *Dimeromyces longitarsi* Thaxt., the only species of *Dimeromyces* reported to date from Europe on flea beetles Chrysomelidae Alticini. The latter species was described on *Aphthona* Chevrolat, 1837 and *Longitarsus* from the USA and from Trinidad and Tobago (Thaxter 1914); it was subsequently recorded on *Longitarsus* from France, Poland, United Kingdom and Spain (Majewski 2008). The two species of fungi are very similar, especially as to the male thallus, but the female thallus of *D. longitarsi* lacks the "showy" perithecial outgrowths. *Dimeromyces bordei* Maire, described on *Thyamis* Stephens, 1831 from Algeria (Maire 1920), is considered a synonym of *D. longitarsi*.

Fig. 72. *Dimeromyces oculatus* Santam. sp. nov. **A**–**B**. Mature female thalli with labelling of secondary appendage (sa) and its basal cell (bc a) in A. **C**–**E**. Perithecial apex in detail, frontal view in C–D and side view in E; arrows point to septum separating the two distal wall cells. **F**. Lower area of a mature female thallus in detail focusing on certain cells, viz., primary appendage (pa), III, II', II", and I. **G**. Young male thallus. **H**–**J**. Male thalli at different focus levels, with primary appendage labelled in H. Scale bars: A–B = 50 µm; C–E = 10 µm; F–J = 20 µm. Photographs from slides ZMUC C-F-123800 (A–E) (isotype), ZMUC C-F-123799 (F–J) (holotype).

Genus ***Dimorphomyces*** Thaxt.
MB#1590

Proceedings of the American Academy of Arts and Sciences 28: 157 (Thaxter 1893). – Type species: *D. denticulatus* Thaxt.

Brief description

Dioecious. Male thalli consisting of a receptacle with a few cells, compound antheridia and an unbranched primary appendage. Female thalli consisting of a horizontal row of cells, underlain by the laterally elongated cell I. Cells of the receptacle give rise to perithecia, secondary appendages and an unbranched primary appendage. Perithecium with an undetermined number of cells in each vertical row of outer wall cells, only the 2–3 upper cells being visible at maturity. As perithecia matures, wall cells of stalk and basal cells degrade and vanish.

Remarks

The genus consists of 29 species, of which three in Europe, two in Denmark. The most recently described species is *D. carolinae* (Rossi 2010). *Dimorphomyces* and *Dimeromyces* are very closely related genera only distinguished because the female thalli of the former show a laterally elongate cell I which supports a row of cells (Tavares 1985).

Key to the Danish species

1. Perithecial apex showing a brown, almost darkened preapical suffusion in a bulging uppermost wall cell, near the subapical ostiole. Primary appendage three-celled, without dark septa, supporting a terminal, narrow and darker cell. On *Phloeopora* Erichson, 1837 (Col. Staphylinidae Aleocharinae)..... ***D. phloeoporae*** Thaxt.
– Perithecia uniformly coloured. Primary appendage three-celled, with darkened septa, supporting a terminal, narrow and paler cell. On other staphylinids..... ***D. myrmedoniae*** Thaxt.

Dimorphomyces myrmedoniae Thaxt.
MB#215212
Fig. 73A–F

Proceedings of the American Academy of Arts and Sciences 36: 409 (Thaxter 1900). – **Type**: "On *Myrmedonia flavicornis* Fauv., British Museum (Biologia Coll.), No. 766, Guatemala"; FH.

Diagnostic features

Male thalli consisting of a three-celled receptacle supporting a two-celled primary appendage, and a lateral flask-shaped compound antheridium. Female thalli consisting of an underlying cell I subtending a row of 6–14 cells; the first cell of the series (cell II) supports a three-celled primary appendage, where the two basal cells are inflated and separated by constricted and somewhat blackened septa, the distal cell narrower, longer, paler and often disintegrating. Perithecium with a ± perceptible tooth-like outgrowth near the apex (Fig. 73B, E, arrows). [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 2003]

Distribution and hosts

On members of the genera *Zyras* Stephens, 1835, *Myrmedonia* Erichson, 1837, *Tachyusa* Erichson, 1837 (in part as *Ischnopoda* Stephens, 1835), *Gnypeta* Thomson, 1858, *Atheta* Thomson, 1858, and *Dilacra* Thomson, 1858 (Col. Staphylinidae Aleocharinae). Type host is probably *Zyras* according to Majewski (1994b). It has been reported from Poland, Spain and Guatemala (Santamaria *et al.* 1991), USA (Seymour

1967, on *Myrmedonia*?), United Kingdom (Weir 1996), Italy, Greece (Castaldo *et al.* 2004), Bulgaria, Switzerland (Rossi *et al.* 2019a), and Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Dilacra vilis* (Erichson, 1837) (Col. Staphylinidae Aleocharinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1133*; JP det.; ZMUC C-F-123656, C-F-123657.

Other material examined

Type of *Dimorphomyces myrmedoniae*
GUATEMALA • "*Dimorphomyces myrmedoniae*, 2 slides from FH, #569, barcode 00313726, and #570, barcode 00313727, **type**, all over *Myrmedonia flavicornis* Fauv., from Guatemala, ex British Museum coll. no. 766"; FH[00313726] [slide #569 apparently does not include thalli; slide #570 includes seven mature female thalli and two mature male thalli, in very poor condition (Fig. 73F)]

Remarks

First record from Denmark. Thalli collected on *Dilacra vilis* from Denmark show a ± conspicuous protuberance near the perithecial apex, on the opposite side of where ostiole is found (Fig. 73E, arrow). This feature is neither mentioned nor illustrated in any other previous records of *D. myrmedoniae*. We have reviewed the Spanish material kept in BCB, and all the thalli show this same character, which was overlooked in our previous observations (Santamaria 2003). Figures and description by Thaxter (1908) do not show or mention this characteristic. To clarify if the American samples may perhaps correspond to a different species from those in Europe we have borrowed the type from FH (see above under other material examined). Unfortunately, the type slide is in very poor condition (Fig. 73F) and gives no additional information of interest. Given this situation, for the time being we should keep the European samples as they were classified.

Dimorphomyces phloeoporae Thaxt.
MB#215367
Fig. 73G–I

Proceedings of the American Academy of Arts and Sciences 36: 410 (Thaxter 1900, as *Dimorphomyces Thleoporae*). – **Type**: "On *Thleopora corticalis* Gz., Paris Museum, No. 297, Santa Anna, Madeira. On inferior surface of abdomen"; FH.

Diagnostic features

Male thalli consisting of a two- or three-celled receptacle supporting a three-celled primary appendage, and 1–2 lateral flask-shaped compound antheridia. Female thalli consisting of an underlying cell I subtending a row of 6–12 cells; the first cell of the series (cell II) supports a three-celled appendage, where the two basal cells are slightly inflated and the distal cell is narrower, darker, and usually disintegrates. Perithecium with a bulging, ± darkened preapical wall cell, beneath the ostiole. [Detailed descriptions: Thaxter 1908; Majewski 1999]

Distribution and hosts

Occurs on *Phloeopora* ("*Thleopora*" is a misspelling in the protologue) (Col. Staphylinidae Aleocharinae) from Madeira (type), Poland (Majewski 1999) and Sweden (Huggert 2010).

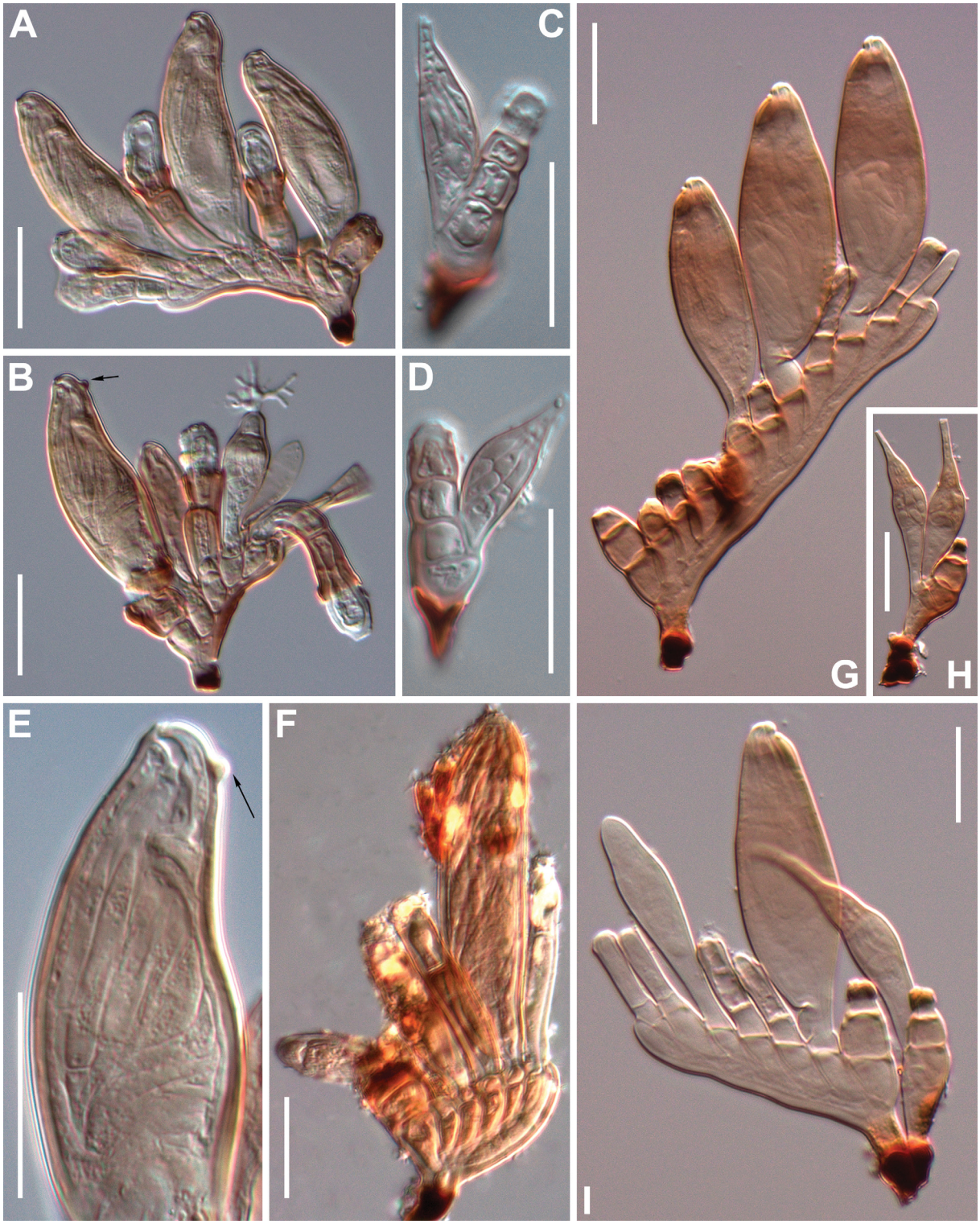

Fig. 73. *Dimorphomyces* spp. **A**–**F**. *D. myrmedoniae* Thaxt. **A**–**B**. Mature female thalli, showing perithecial outgrowth (arrow). **C**–**D**. Male thalli. **E**. Mature perithecium in detail showing perithecial outgrowth (arrow). **F**. Mature female thallus from type slide kept in FH. – **G**–**I**. *D. phloeoporae* Thaxt. **G**, **I**. Mature female thalli. **H**. Male thallus. Scale bars: A–B, F–I = 25 µm; C–E = 20 µm. Photographs from slides ZMUC C-F-123656 (A, C–D), ZMUC C-F-123657 (B, E), FH 00313727 (F) (type), ZMUC C-F-124218 (G–I).

Collections examined from Denmark

On *Phloeopora testacea* (Mannerheim, 1830) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Dyrehaven; 55°47.611′ N, 12°34.153′ E; UB48; 12 Mar. 1922; *Høeg Dry0152*; Høeg det.; ZMUC C-F-124218.

Remarks

First record from Denmark. The host is quite common and widespread in Denmark and not difficult to find under dead bark of various trees (mostly deciduous trees), but the fungus is apparently rarely collected. A photo of this species is given here for the first time.

Genus ***Trenomyces*** Chatton & F.Picard
MB#5531

Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 146: 201 (Chatton & Picard 1908). – Type species: *T. histophthorus* Chatton & F.Picard.

Brief description

Dioecious. Female and male thalli consist of a two-celled receptacle terminated by a two-celled apiculate appendage where the upper gives rise to several fertile branches which grow and corticate producing perithecia or antheridia. Cell I subspherical, forming a conspicuous haustorium. Blackened foot absent. Perithecia and antheridia as in *Dimeromyces* and *Dimorphomyces*.

Remarks

The genus consists of 11 species described on Mallophaga (biting lice of birds and mammals) (Phthiraptera) and Hippoboscidae (louse flies of birds and mammals) (Diptera). Six in Europe, one in Denmark. No new species have been described since *T. aquaticus*, *T. helveticus* and *T. thaxteri* by Eichler (1951). This genus seems understudied probably because of the difficulty to collect suitable hosts. Thaxter (1926) and more recently Tavares (1985) studied this genus in some depth, and the latter added a critical list with insect hosts, vertebrate hosts, and fungi. Eichler (1936, 1939, 1943a, 1943b, 1951, 1952) added abundant information but his descriptions were too brief and drawings too schematic. The genus requires a deep and detailed further study.

Trenomyces histophthorus Chatton & F.Picard
MB#149483
Fig. 74

Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 146: 201 (Chatton & Picard 1908, as *T. histophtorus*). – **Type**: [In ??] "La Laboulbéniacée que nous avons trouvée sur *Menopon pallidum* Nitzsch et sur *Goniocotes abdominalis* P., Mallophages recueillis sur les Poules domestiques à Banyuls-sur-Mer". [France]

Diagnostic features

Male thalli yellowish, including many antheridia per thallus; antheridial neck three times shorter than the venter. Female thalli yellowish, including many perithecia per thallus. Perithecia straight, clavate to cylindrical, wrinkled, with small indistinct lips. [Detailed descriptions: Thaxter 1912b, 1926; Bechet & Bechet 1960a, 1960b; Majewski 1994b]

Distribution and hosts

Occurs on Mallophaga (Phthiraptera) belonging to many genera of Menoponidae and Philopteridae like *Menopon* Nitzsch, 1818, *Goniocotes* Burmeister, 1838, *Menacanthus* Neumann, 1912, etc., recorded on several groups of birds (Tavares 1985). Reported from **Europe** (France, Poland, Germany, Romania, Czech Republic, Italy, Hungary), **America** (USA, Bahamas, Argentina, Guatemala, Jamaica), and Japan (Majewski 2008). A total revision of the records list would require a huge effort.

Collections examined from Denmark

On *Amyrsidea perdicis* (Denny, 1842) (Phthiraptera, Menoponidae), on the grey partridge, *Perdix perdix* (Linnaeus, 1758)

DENMARK – **Vestjylland (WJ)** • Esbjerg; 55°28.466′ N, 8°30.071′ E; MG64; 13 Apr. 1937; *H. Madsen 1584*; C. Overgaard det.; ZMUC C-F-124345.

On *Menopon gallinae* (Linnaeus, 1758) (Phthiraptera, Menoponidae), on the domestic chicken, *Gallus gallus* (Linnaeus, 1758)

DENMARK – **Østjylland (EJ)** • Viborg; 56°27.217′ N, 9°23.650′ E; NH25; 21 Jul. 1889; *C. A. Gad 1580*; C. Overgaard det.; ZMUC C-F-124341.

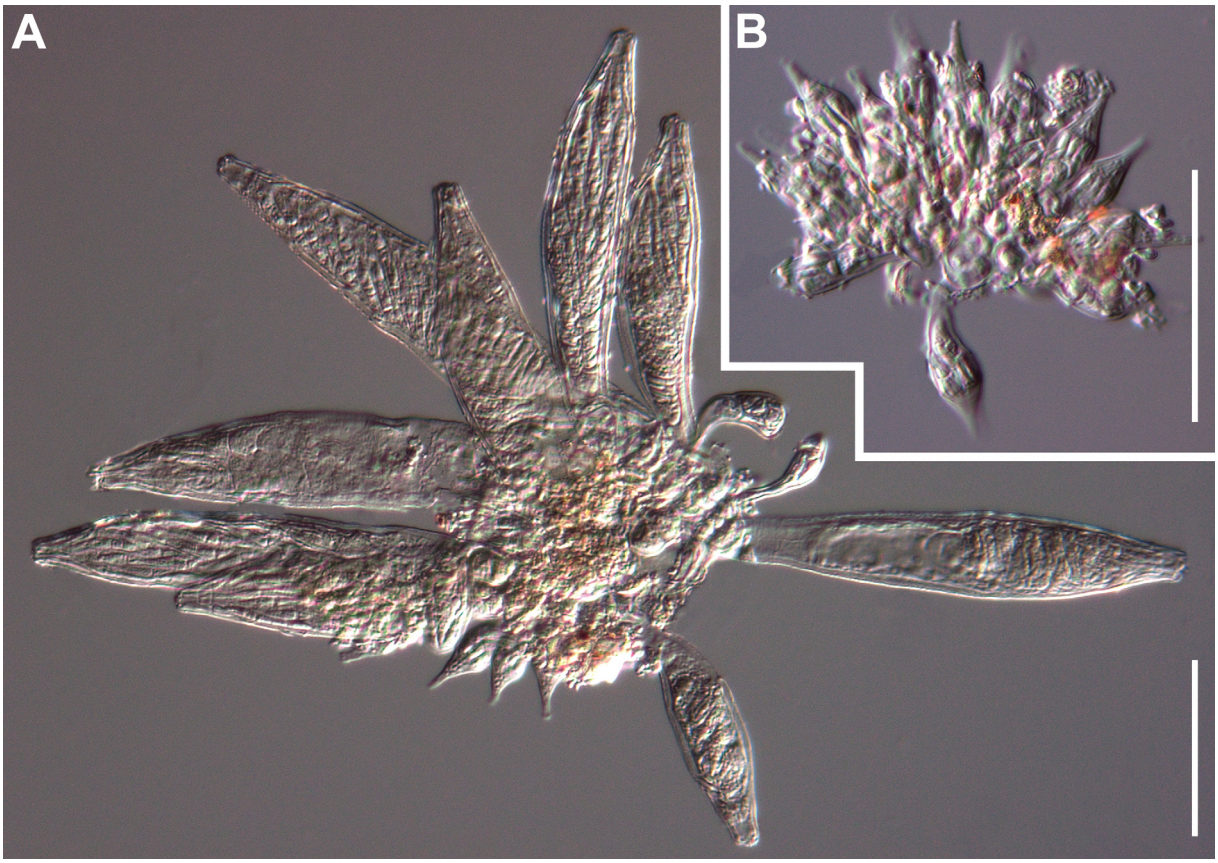

Fig. 74. *Trenomyces histophthorus* Chatton & F.Picard. **A**. Mature male and female thalli. **B**. One or more male thalli. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124344 (A), ZMUC C-F-124345 (B).

On *Menopon pallens* Clay, 1949 (Phthiraptera, Menoponidae), on the grey partridge, *Perdix perdix* (Linnaeus, 1758)

DENMARK – **Fyn (F)** • Bøjden; 55°6.142′ N, 10°6.564′ E; NG70; 26 Oct. 1937; *H. Madsen 1582*; C. Overgaard det.; ZMUC C-F-124343 • Broholm syd for Gudme; 55°8.195′ N, 10°43.782′ E; PG11; 6 Aug. 1937; *H. Madsen 1581*; C. Overgaard det.; ZMUC C-F-124342. – **Vestjylland (WJ)** • Esbjerg; 55°28.466′ N, 8°30.071′ E; MG64; 27 Apr. 1937; *H. Madsen 1583*; C. Overgaard det.; ZMUC C-F-124344.

Remarks

First record from Denmark. The presence of this fungus in Denmark is not surprising for such a widespread species. The collections are very old, and the fungi are in imperfect condition probably due to the unsuitable preservation fluid; nevertheless the species is perfectly identifiable.

Tribe Haplomyceteae Thaxt.

Genus ***Camptomyces*** Thaxt.
MB#780

Proceedings of the American Academy of Arts and Sciences 29: 100 (Thaxter 1894). – Type species: *C. melanopus* Thaxt.

Brief description

Monoecious. Receptacle three-celled (Fig. 75B). Primary appendage consisting of a flattened basal cell and a distal compound antheridium. Primary septum constricted and ± darkened. Antheridium ± conical, consisting of several regular rows of sterile cells and phialides; terminated with a pointed apex where the discharging pore is located (Fig. 75A, arrow). Perithecium with four cells in each vertical row of outer wall cells.

Remarks

The genus consists of nine species, with only *C. europaeus* known in Europe. The most recently described species is *C. africanus* (Rossi & Leonardi 2018). The terminal compound antheridium in the primary appendage relates this genus with others like *Haplomyces*, *Neohaplomyces*, *Euhaplomyces*, *Eucantharomyces*, and *Porophoromyces*. In *Camptomyces* and *Porophoromyces*, the original spore apex opens and transforms into the spermatia discharge pore, whereas in the other genera it remains as a closed spinous process.

Camptomyces europaeus W.Rossi & Cesari
MB#112155
Fig. 75A–B

Giornale Botanico Italiano 114(5): 187 (Rossi & Cesari Rossi 1981). – **Type**: "Sulla porzione posteriore dell'addome di alcuni esemplari di *Astenus thoracicus* Baudi (Paederinae) in località Colli del Forno, presso Montelibretti (Roma). *Holotypus in herbario Instituti Botanici apud Universitatem Studiorum Romae, n. 770*"; RO.

Diagnostic features

Cell I dark brown except for the paler distal portion. Cell II flattened, mostly blackish brown except for a paler ring above. Cell III showing a variably distinguished dark spot on its upper-inner side. Perithecial margin smooth. [Detailed description: Santamaria 2003]

Distribution and hosts

On *Astenus* (Col. Staphylinidae Paederinae) from Italy (type), Spain (Santamaria 1993a), and Sweden (Huggert 2010).

Collections examined from Denmark

On *Astenus gracilis* (Paykull, 1789) (Col. Staphylinidae Paederinae)

DENMARK – **Nordøstsjælland (NEZ)** • Asserbo Plantage; 56°1.794′ N, 12°1.589′ E; UC11; 15 Oct. 2017; *JP 577*; JP det.; ZMUC C-F-123063.

Remarks

First record from Denmark. There are few differences with *C. melanopus* Thaxt., but this applies to most species in the genus (Tavares 1985).

Genus ***Cantharomyces*** Thaxt.
MB#792

Proceedings of the American Academy of Arts and Sciences 25: 9 (Thaxter 1890). – Type species: *C. bledii* Thaxt.

Brief description

Monoecious. Receptacle three-celled, with the three cells (I, II and III) superposed and separated by ± horizontal septa. Primary appendage consisting of a basal cell which divides to form a compound antheridium and a few to many sterile cells. Above, the appendage may be simple to variably branched. Antheridium consisting of several irregularly arranged cells; the discharging pore is lateral. Perithecium with 4–5 cells in each vertical row of outer wall cells.

Remarks

The genus consists of 29 species, of which 13 are known in Europe, eight in Denmark. The most recently described species are *C. elongatus* (Haelewaters & De Kesel 2013) and *C. paschalis* W.Rossi & Santam. (Haelewaters *et al.* 2021). The genus is well-characterized by the compound antheridium which occupies part of the appendage basal cell (Fig. 75F, an).

Key to the Danish species (partially following Majewski 1994b and Santamaria 2003)

1. Cell II almost entirely blackened 2
– Cell II not so blackened, although some pigment, darkening or black spots may be present 3

2. Antheridium lateral on the appendage basal cell, which is narrower than cell III. Appendage unbranched. On *Dryops* (Col. Dryopidae)..... ***C. denigratus*** Thaxt.
– Antheridium occupying most of the appendage basal cell, which is almost spherical and broader than cell III. Appendage branched above the basal cell. On *Thinodromus* Kraatz, 1857 (Col. Staphylinidae Oxytelinae) ..... ***C. numidicus*** Maire

3. Primary appendage unbranched..... 4
– Primary appendage ± branched..... 5

4. Appendage basal cell, including antheridium, elongated, narrow. On *Dryops* (Col. Dryopidae) .... ***C. italicus*** Speg.
– Appendage basal cell, including antheridium, rounded or convex distally, broader than long. On *Syntomium* Curtis, 1828 (Col. Staphylinidae Oxytelinae)..... ***C. elongatus*** Haelew. & De Kesel

5. Antheridium occupying the middle side of appendage basal cell, without contacting upper and lower septa. On *Platystethus* Mannerheim, 1830 (Col. Staphylinidae Oxytelinae) ..... ***C. platystethi*** Thaxt.
– Antheridium occupying the corner or a lateral of the appendage basal cell, reaching either the upper and/or the lower septa 6

6. One to three cells above the appendage basal cell strongly flattened, inflated, separated by constricted and slightly darkened septa. On *Aploderus* Stephens, 1833 (Col. Staphylinidae Oxytelinae) ..... ***C. aploderi*** Huldén
– Otherwise 7

7. Cell III longer than broad. Appendage basal cell showing a papilla on the upper-inner corner, which probably represents an efferent neck. Cell VI elongate and strongly narrowing towards the basal portion. On *Bledius* (Col. Staphylinidae Oxytelinae) ..... ***C. papillatus*** Santam. sp. nov.
– Cell III broader than long. Appendage basal cell without papilla. Cell VI not as above. Usually on *Trogophloeus* Mannerheim, 1831 and allied genera (Col. Staphylinidae Oxytelinae) ..... ***C. orientalis*** Speg.

Cantharomyces aploderi Huldén
MB#124443
Fig. 75C–E

Karstenia 23: 45 (Huldén 1983). – **Type**: "*Host*. *Aploderus caesus* (Erichson) (Coleoptera, Staphylinidae). *Holotype.* Slide L. Huldén 24, in MZH. Collecting data of the host: U.S.S.R. Karelian A.S.S.R.: Zaoneskje, Sungu, leg. Poppius"; MZH. [Russia]

Diagnostic features

Cell II with a variable large dark spot on the dorsal margin (Fig. 75D, arrow). Cells I and II separated by a constricted septum; forming a geniculate stalk. One to three cells above the appendage basal cell, strongly flattened, inflated, separated by constricted and slightly darkened septa (Fig. 75D, *). Appendage branched above flat cells.

Distribution and hosts

Only known from the type, on *Aploderus* (Col. Staphylinidae Oxytelinae) from Russia.

Collections examined from Denmark

On *Aploderus caesus* (Erichson, 1839) (Col. Staphylinidae Oxytelinae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Engestofte; 54°45.767′ N, 11°33.506′ E; PF67; 12 Jul. 1951; *V. Hansen Dry0112*; V. Hansen det.; ZMUC C-F-124179 • ibid.; 13 Jul. 1951; *V. Hansen Dry0111*; V. Hansen det.; ZMUC C-F-124177, C-F-124178.

Remarks

First record from Denmark and the second after the original description. The host is considered rare in all parts of its distribution, thus the fungus is even more rare. A photo of this species is given here for the first time.

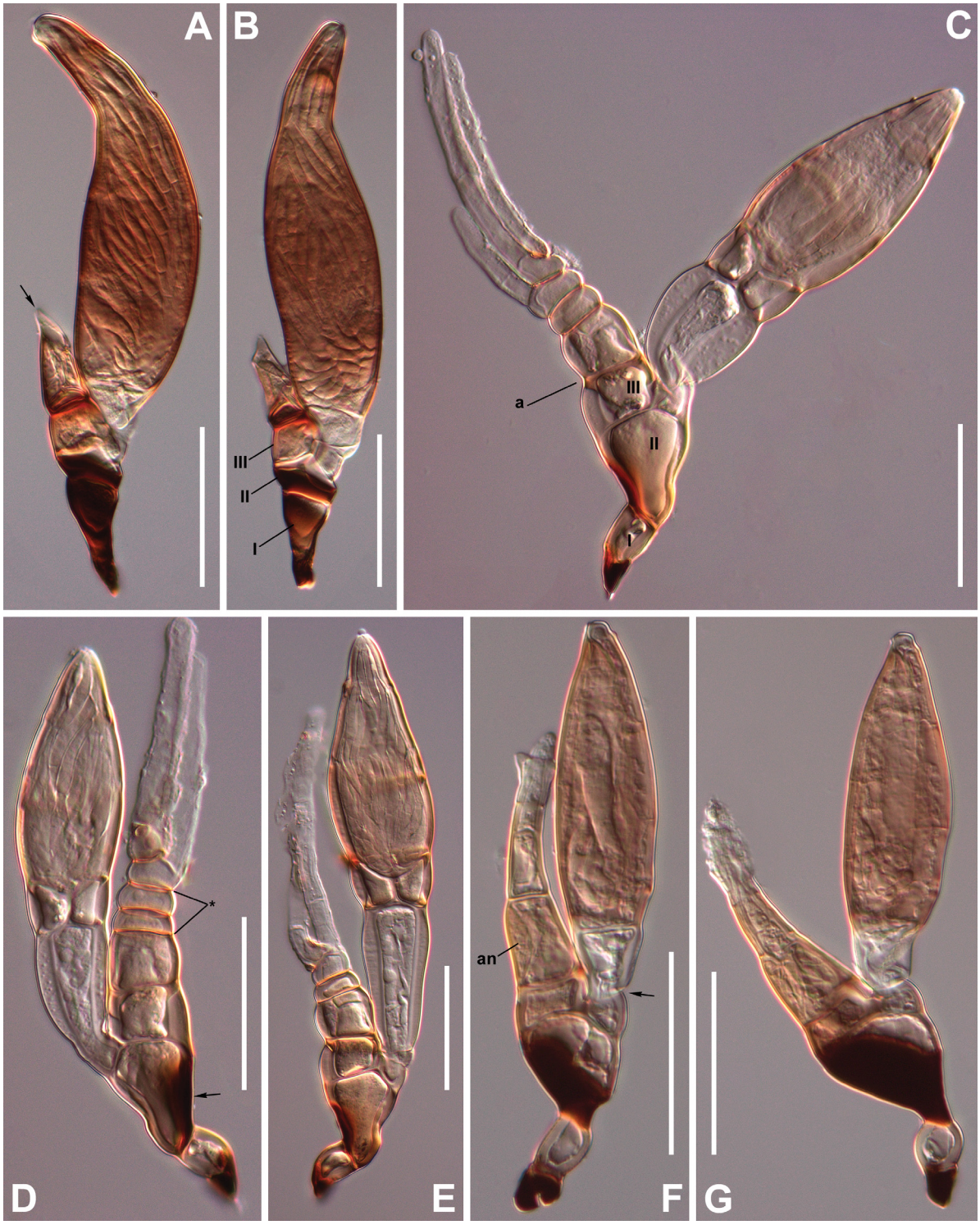

Fig. 75. A–**B**. *Camptomyces europaeus* W.Rossi & Cesari. Mature thalli showing discharge pore of antheridium (arrow) and cells I, II, III. – **C**–**E**. *Cantharomyces aploderi* Huldén. Mature thalli. **C**. Cells I, II, III and primary septum (a) are labelled. **D**. Arrow points to darkening of cell II, "*" delimits flattened cells of appendage, a diagnostic character. **E**. Mature thallus. – **F**–**G**. *Cantharomyces denigratus* Thaxt. Mature thalli showing antheridium (an) and constriction of cell VI (arrow). Scale bars: 50 µm. Photographs from slides ZMUC C-F-123063 (A–B), ZMUC C-F-124179 (C–D), ZMUC C-F-124178 (E), ZMUC C-F-123548 (F–G).

Cantharomyces denigratus Thaxt.
MB#262988
Fig. 75F–G

Memoirs of the American Academy of Arts and Sciences 16: 27 (Thaxter 1931). – **Type**: [Not designated] [Ind. loc.] "On *Parnus griseus* and *P. luridus*, New Forest, Hampshire, England; kindly communicated by Mr. F. Muir"; FH. [United Kingdom]

Diagnostic features

Thallus stocky. Cell II almost entirely blackened except for a small area below cells III and VI; this blackening spreads towards the dorsal margin of cell III. Cells I and II separated by a constricted septum; forming a geniculate stalk. Cell VI strongly constricted at the middle (Fig. 75F, arrow). Antheridium occupying the side of the appendage basal cell (Fig. 75F, an). Primary appendage unbranched. [Detailed descriptions: Majewski 1994b; Santamaria 2003; De Kesel & Haelewaters 2014b]

Distribution and hosts

On *Dryops* (Col. Dryopidae) from United Kingdom (type), Poland (Siemaszko & Siemaszko 1933), Spain (Santamaria 1992a), Sweden (Huggert 2010), and Belgium (De Kesel & Haelewaters 2014b).

Collections examined from Denmark

On *Dryops anglicanus* Edwards, 1909 (Col. Dryopidae)
DENMARK – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 26 Apr. 2020; *JP 1606*; JP det.; ZMUC C-F-124362.

On *Dryops auriculatus* (Geoffroy, 1785) (Col. Dryopidae)
DENMARK – **Sydjylland (SJ)** • Lakolk; 55°8.325′ N, 8°29.618′ E; MG62; 31 May 2013; *JP 107*; JP det.; ZMUC C-F-122584.

On *Dryops luridus* (Erichson, 1847) (Col. Dryopidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Røgbølle Sø ved Sørup; 54°42.497′ N, 11°34.760′ E; PF66; 3 Sep. 2019; *JP 1511*; JP det.; ZMUC C-F-124266.

On *Dryops similaris* Bollow, 1936 (Col. Dryopidae)
DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 15 Apr. 2018; *JP 1035*; JP det.; ZMUC C-F-123548 • Asserbo Plantage; 56°1.984′ N, 12°0.817′ E; UC11; 28 Apr. 2019; *JP 1454*; JP det.; ZMUC C-F-124004.

Remarks

First record from Denmark. *Cantharomyces denigratus* and *C. italicus* cannot be considered growth forms of the same species because there are no correlations with host sex and growing location.

Cantharomyces elongatus Haelew. & De Kesel
MB#800871
Fig. 76A–B

Mycotaxon 123: 468 (Haelewaters & De Kesel 2013). – **Type**: "The Netherlands, Prov. Gelderland, Rha, 52°02.9′N 6°08.5′E, on *Syntomium aeneum* (Müller, 1821) (*Coleoptera*, *Staphylinidae*, *Oxytelinae*, *Euphaniini*), 13 Oct. 2001, leg. O. Vorst, slides Haelewaters 69a (**holotype**, 2 mature and 4 immature thalli, found on left elytron and abdominal tergites, BR MYCO 173753-26)"; BR.

Diagnostic features

Cell I differs strikingly from cells II, III and basal cell of primary appendage by being paler and narrower. Primary appendage consisting of a large, distally rounded basal cell, mostly occupied by the antheridium, a small suprabasal cell and a simple branch formed by a series of elongate cells, exceeding the perithecial apex about three times the thallial length from foot to perithecial apex.

Distribution and hosts

Only known from the type, on *Syntomium* (Col. Staphylinidae Oxytelinae) from the Netherlands.

Collections examined from Denmark

On *Syntomium aeneum* (Müller, 1821) (Col. Staphylinidae Oxytelinae)

DENMARK – **Østjylland (EJ)** • Bygholm; 55°51.951′ N, 9°49.399′ E; NG59; 28 Nov. 1940; Høeg; Dry0108; Høeg det.; ZMUC C-F-124174 • Rugballegård ved Vejle; 55°43.981′ N, 9°27.852′ E; NG49; 22 Jul. 1895; *F. de Tengnagel Dry0106*; F. de Tengnagel det.; ZMUC C-F-124172 • Stensballe; 55°52.256′ N, 9°54.776′ E; NG59; 9 Nov. 1941; *Høeg Dry0107*; Høeg det.; ZMUC C-F-124173. – **Sydjylland (SJ)** • Favrdalen; 55°15.357′ N, 9°31.211′ E; NG32; 6 Nov. 1931; *Johs. Andersen Dry0109*; Johs. Andersen det.; ZMUC C-F-124175.

Remarks

First record from Denmark and the second after the original description. A photo of this species is given here for the first time.

Cantharomyces italicus Speg.
MB#159942
Fig. 76C–F

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 42 (Spegazzini 1915b). – **Type**: "Sobre el margen superior posterior del abdomen de *Dryops* (*Parnus*) *algiricus*, cazados en el torrente Monticano, Conegliano, Oct. 1913"; LPS. [Italy]

Diagnostic features

Thallus slender. Cell II pale, without blackening, sometimes slightly darker than cell I. Septum separating cells I and II not constricted. Cell VI strongly constricted at the middle (Fig. 76D). Antheridium occupying the side of the appendage basal cell (Fig. 76D, an). Primary appendage unbranched. [Detailed descriptions: Majewski 1994b; Santamaria 2003; De Kesel & Haelewaters 2014b]

Distribution and hosts

Occurs on *Dryops* (Col. Dryopidae). Widespread in **Europe**: Italy (type), United Kingdom (Thaxter 1931), Poland (Siemaszko & Siemaszko 1933), Finland, Russia (Huldén 1983), Hungary (Bánhegyi *et al.* 1985), Spain (Santamaria 1992a), Sweden (Huggert 2010), and Belgium (De Kesel & Haelewaters 2014b).

Collections examined from Denmark

On *Dryops anglicanus* Edwards, 1909 (Col. Dryopidae)

DENMARK – **Sydsjælland (SZ)** • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 26 Apr. 2020; *JP 1606*; JP det.; ZMUC C-F-124361.

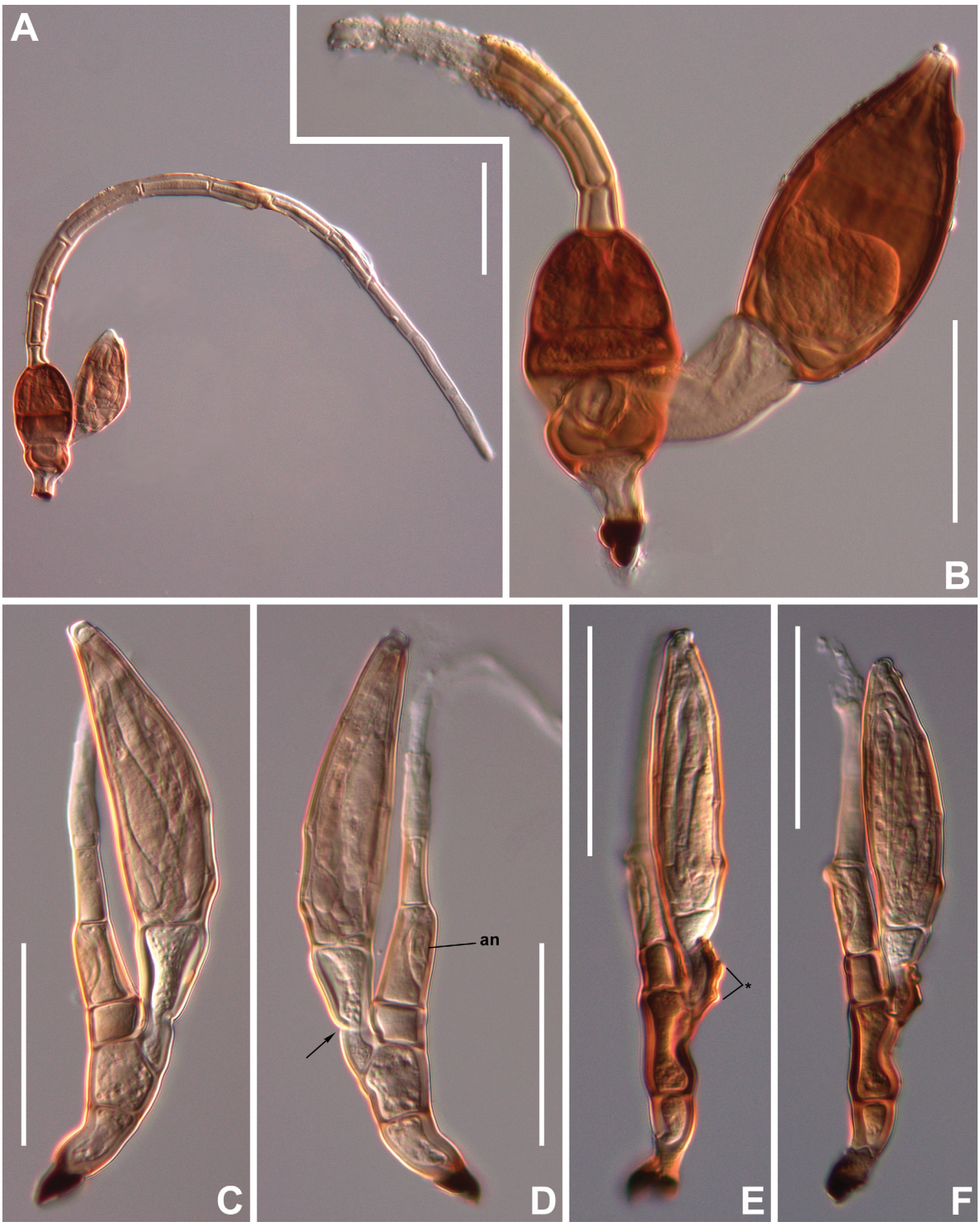

Fig. 76. *Cantharomyces* spp. **A**–**B**. *C. elongatus* Haelew. & De Kesel. **A**. Submature thallus with an undamaged appendage. **B**. Mature thallus. – **C**–**F**. *C. italicus* Speg. **C**–**D**. Typical thalli from the abdomen of the host, showing antheridium (an) and constriction of cell VI (arrow). **E**–**F**. Mature thalli from the pronotum of the host. In E, "*" points to cell VI corrugation. Scale bars: 50 µm. Photographs from slides ZMUC C-F-124174 (A), ZMUC C-F-124172 (B), ZMUC C-F-123549 (C–D), ZMUC C-F-124264 (E–F).

On *Dryops luridus* (Erichson, 1847) (Col. Dryopidae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Røgbølle Sø ved Sørup; 54°42.497′ N, 11°34.760′ E; PF66; 3 Sep. 2019; *JP 1511*; JP det.; ZMUC C-F-124263, C-F-124264, C-F-124265.

On *Dryops similaris* Bollow, 1936 (Col. Dryopidae)
DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°38.631′ N, 12°34.729′ E; UB47; 15 Apr. 2018; *JP 1035*; JP det.; ZMUC C-F-123549.

Remarks

First record from Denmark. This species often coexists with *C. denigratus* on the same host. *Cantharomyces italicus* was described on thalli from the upper surface of last abdominal tergites, and this seems to be its primary growing location, but heavily infected hosts may have thalli spreading to almost any part of the body. Thalli show rather interesting morphological differences depending on the host growth position, especially slenderer thalli growing on pronotum (on *Dryops luridus*, ZMUC C-F-124263, C-F-124264 and 124265) which have the cell VI with a corrugated and deeply brown pigmented lower dorsal surface (Fig. 76E, *) similar to thalli drawn from Belgium by De Kesel *et al.* (2020: fig. 4k), also collected from the pronotum. Further studies are needed to determine if these forms could be different species.

Cantharomyces numidicus Maire
MB#628283
Fig. 77A–C

Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 11(8): 132 (Maire 1920). – **Type**: [Type lost?!] "Sur un tibia de *Trogophloeus Mannerheimi* Kolen.: C. Bône, embouchure de la Seybouse, mars 1918 (De Borde)". [Algeria]

Cantharomyces japonicus K.Sugiy. (1973: 20) [MB#310380]

Diagnostic features

Cell II very large, elongate, almost entirely blackened, broadened distally. Cells I and II separated by a ± constricted septum; forming a geniculate stalk. Appendage basal cell very large, inflated, subspherical, forming the base of several short and crowded branchlets borne from many packed small cells. [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

On *Thinodromus*, a host genus name reported also as *Trogophloeus* or *Carpelimus* Leach, 1819 (Col. Staphylinidae Oxytelinae). *Trogophloeus* is now a synonym or a subordinate name of *Carpelimus* with a rank of a small subgenus. *Thinodromus* once was a part of *Carpelimus*. Type from Algeria, it has been reported from **Europe**: Italy (Rossi & Cesari Rossi 1978), Poland (Majewski 1986a), Spain (Santamaria 1989), Sweden (Santamaria *et al.* 1991), France (Duverger 1995), Greece (Castaldo *et al.* 2004), and Slovakia (Rossi *et al.* 2010). *Cantharomyces japonicus* has been reported on *Carpelimus* and *Thinodromus* from Japan (type) and on *Carpelimus* from China (Shen & Ye 2006).

Collections examined from Denmark

On *Thinodromus arcuatus* (Stephens, 1834) (Col. Staphylinidae Oxytelinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 18 Jan. 2015; *JP 450*; JP det.; ZMUC C-F-122935. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 19 Feb. 2017; *H. Liljehult 367*; JP det.; ZMUC C-F-122850. – **Sydsjælland (SZ)** •

Sorø Sø; 55°26.315′ N, 11°32.726′ E; PG64; 7 May 1996; *H. Liljehult Dry0110*; H. Liljehult det.; ZMUC C-F-124176.

Remarks

First record from Denmark. The finding of this species in Denmark is not surprising considering its presence in neighbouring countries.

Cantharomyces orientalis Speg.
MB#160059
Fig. 77D–F, 107A

Anales del Museo Nacional de Historia Natural de Buenos Aires 27: 43 (Spegazzini 1915b). – **Type**: "Sobre el dorso y el abdomen de un pequeño estafilino micófilo (*Quaedius* ?), en el bosquecillo Giustinian, cerca de Conegliano, Nov. 1914"; LPS. [Italy]

Cantharomyces thaxteri Maire (Maire 1916b: 100) [MB#175157]
Cantharomyces abbreviatus Maire (Maire 1920: 131) [MB#628282]

Diagnostic features

Cell III slightly flattened. The suprabasal cell of the appendage gives rise to a variable number of branches. Antheridium occupying a lateral position in the appendage basal cell, contacting with both septa above and below. [Detailed descriptions: Majewski 1994b; Santamaria 2003]

Distribution and hosts

On *Carpelimus* (Col. Staphylinidae Oxytelinae), or as *Trogophloeus*, but also on *Troginus* Mulsant & Rey, 1878. Records on other genera are questionable or due to host switch. From many countries in **Europe**: Belgium, Czech Republic, Finland, France, Germany, Greece, Hungary, Italy, the Netherlands, Poland, Russia, Slovakia, Spain, Sweden, Switzerland, United Kingdom (Majewski 2008), Bulgaria (Rossi *et al.* 2019a), and Slovenia (Rossi & Christian 2020); **Asia**: Philippines (Haelewaters & Yaakop 2014), Turkey (Rossi 2016), Thailand (Rossi & Bernardi 2018); and **Africa**: Algeria (Maire 1920). Remarkably, this species has recently been recorded on *Diglotta mersa* (Haliday, 1837) from Belgium by De Kesel *et al.* (2020); the host is a rove beetle inhabiting the fine gravel under small rocks in the intertidal zone.

Collections examined from Denmark

On *Carpelimus bilineatus* Stephens, 1834 (Col. Staphylinidae Oxytelinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Hobyskov; 54°44.069′ N, 11°15.296′ E; PF46; 25 Jan. 2018; *H. Liljehult 994*; JP det.; ZMUC C-F-123501. – **Nordøstsjælland (NEZ)** • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 29 Apr. 2016; *H. Liljehult 85*; JP det.; ZMUC C-F-122560 • ibid.; 28 Feb. 2017; *H. Liljehult 361*; JP det.; ZMUC C-F-122844 • Vest for Trørød; 55°50.223′ N, 12°31.185′ E; UB49; 13 Nov. 2016; *JP 143*; JP det.; ZMUC C-F-122621. – **Sydsjælland (SZ)** • Holtug Kalkbrud; 55°20.470′ N, 12°26.678′ E; UB33; 21 Sep. 2013; *JP 349*; JP det.; ZMUC C-F-122831 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 972*; JP det.; ZMUC C-F-123479.

On *Carpelimus corticinus* (Gravenhorst, 1806) (Col. Staphylinidae Oxytelinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 18 Jan. 2015; *JP 453*; JP det.; ZMUC C-F-122938 • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 535*; JP det.; ZMUC C-F-123019. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 692*; JP det.; ZMUC C-F-123180. – **Lolland, Falster, Møn (LFM)**

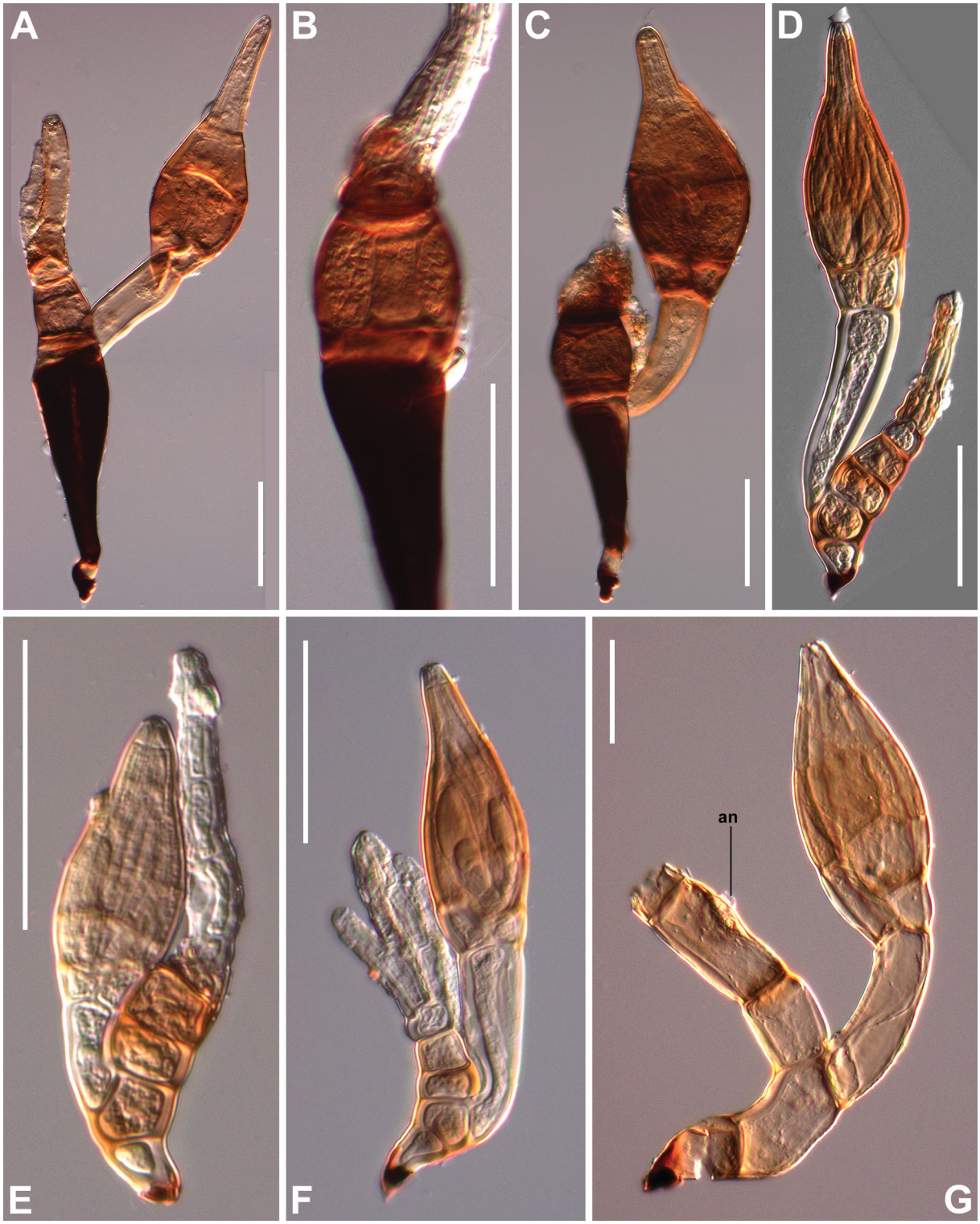

Fig. 77. *Cantharomyces* spp. **A**–**C**. *C. numidicus* Maire. **A**, **C**. Mature thalli. **B**. Appendage basal cell in detail. – **D**–**F**. *C. orientalis* Speg. Mature thalli. – **G**. *C. platystethi* Thaxt. Mature thallus with labelled antheridium (an). Scale bars: 50 µm. Photographs from slides ZMUC C-F-122850 (A), ZMUC C-F-122935 (B–C), ZMUC C-F-122482 (D), ZMUC C-F-122831 (E), ZMUC C-F-123217 (F), ZMUC C-F-124182 (G).

• Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1131*; JP det.; ZMUC C-F-123654 • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; *JP 1523*; JP det.; ZMUC C-F-124278 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1331*; JP det.; ZMUC C-F-123870. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 562*; JP det.; ZMUC C-F-123048. – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 724*; JP det.; ZMUC C-F-123217 • Halleby Å ved Bjerge Sydstrand; 55°33.194′ N, 11°10.079′ E; PG35; 24 Oct. 2018; *JP 1213*; JP det.; ZMUC C-F-123739 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 763*; JP det.; ZMUC C-F-123257. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 9 Apr. 2019; *JP 1424*; JP det.; ZMUC C-F-123970 • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1357*; JP det.; ZMUC C-F-123895 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1016*; JP det.; ZMUC C-F-123523 • ibid.; 25 Apr. 2019; *JP 1451*; JP det.; ZMUC C-F-124001 • Holtug Kalkbrud; 55°20.470′ N, 12°26.678′ E; UB33; 6 Sep. 2019; *JP 1512*; JP det.; ZMUC C-F-124267 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 971*; JP det.; ZMUC C-F-123478.

On *Carpelimus elongatulus* (Erichson, 1839) (Col. Staphylinidae Oxytelinae)

DENMARK – **Østjylland (EJ)** • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 984*; JP det.; ZMUC C-F-123491. – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; JP 691; JP det.; ZMUC C-F-123179. – **Lolland, Falster, Møn (LFM)** • Røgbølle Sø ved Sørup; 54°42.608′ N, 11°34.757′ E; PF66; 15 Oct. 2019; JP 1522; JP det.; ZMUC C-F-124277. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 725*; JP det.; ZMUC C-F-123218 • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 10*; JP det.; ZMUC C-F-122482. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 563*; JP det.; ZMUC C-F-123049. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 493*; JP det.; ZMUC C-F-122977 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1015*; JP det.; ZMUC C-F-123522 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; 31 Mar. 2019; *JP 1415*; JP det.; ZMUC C-F-123961 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 28 Feb. 2015; *JP 445*; JP det.; ZMUC C-F-122930 • ibid.; 17 Feb. 2019; *JP 1378*; JP det.; ZMUC C-F-123919 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1594*; JP det.; ZMUC C-F-124355.

On *Carpelimus erichsoni* (Sharp, 1871) (Col. Staphylinidae Oxytelinae)

DENMARK – **Nordøstsjælland (NEZ)** • Nordhavnstippen på Københavns Nordhavn; 55°43.091′ N, 12°37.088′ E; UB57; 29 Apr. 2018; *JP 1093*; JP det.; ZMUC C-F-123610.

On *Carpelimus foveolatus* (Sahlberg, 1832) (Col. Staphylinidae Oxytelinae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1330*; JP det.; ZMUC C-F-123869. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 726*; JP det.; ZMUC C-F-123219. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; 6 Feb. 2015; *JP 220*; JP det.; ZMUC C-F-122701 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 765*; JP det.; ZMUC C-F-123259. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1356*; JP det.; ZMUC C-F-123894 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1017*; JP det.; ZMUC C-F-123524 • Østerskov ved Langebæk; 54°59.572′ N, 12°6.715′ E; UA19; 3 Jan. 2019; *JP 1296*; JP det.; ZMUC C-F-123829.

Remarks

First record from Denmark. *Cantharomyces orientalis* is very variable, to the point that it can be considered a collective species. At the very least, *C. thaxteri* Maire and *C. abbreviatus* Maire may be accepted as synonyms. *Cantharomyces thaxteri* characterizes larger thalli, with a branched appendage. *Cantharomyces abbreviatus* represents a reduced form with short thalli and an unbranched appendage like those we have found on tarsi or antennae (Fig. 77E). Attempting to be very cautious we have not increased the list of synonyms but on this topic we should not forget other species, such as *C. venetus* Speg. (Spegazzini 1915b) which was described from Italy on a "little staphylinid" ("estafilino pequeño" in Spanish in the original description); for example, Majewski (1994b), questioned this possible synonymy because of the branched appendage drawn by Spegazzini (1914: fig. 8).

There are 14 different species described on *Carpelimus* (very often as *Trogophloeus*). Eleven of them form a confusion of forms (Santamaria 2003): (1) *C. abbreviatus*, (2) *C. andinus* (Thaxter 1918b) on *Troglophloeus* from Chile, (3) *C. chilensis* (Thaxter 1918b) on *Troglophloeus* from Chile, (4) *C. exiguus* (Thaxter 1931) on *Trogophloeus* and *Carpelimus* from Africa and Asia, (5) *C. haytiensis* (Thaxter 1931) on *Trogophloeus* from Haiti, (6) *C. orientalis*, (7) *C. pusillus* (Thaxter 1894) on *Trogophloeus* from USA, (8) *C. thaxteri*, (9) *C. trogophloei* (Spegazzini 1917) on *Trogophloeus* from Argentina, (10) *C. valdivianus* (Thaxter 1918b) on *Troglophloeus* from Chile, and (11) *C. venetus*. The other three species are: *C. numidicus*, its synonym *C. japonicus*, and *C. robustus* which are well-distinguished species. As a conclusion and in agreement with what has been mentioned in some literature (Santamaria 2003), the countless morphological variations with intermediates of this group of species makes the delimitation of taxa impossible without the use of molecular techniques.

Cantharomyces papillatus Santam. sp. nov.
MB#840595
Fig. 78

Diagnosis

The most remarkable characteristic refers to the presence of a papilla-like protuberance on the upper-inner corner of the appendage basal cell, which represents the antheridial efferent neck.

Etymology

The species epithet means "bearing a papilla", and refers to the prominence on the antheridium.

Type material

Holotype

DENMARK – **Nordøstjylland (NEJ)** • Fredrikshavn; 57°26.910′ N, 10°32.102′ E; NJ96; on *Bledius terebrans* (Schiødte, 1866) (Col. Staphylinidae Oxytelinae); Jul.1849; *Schiødte Dry0141*; Schiødte det.; ZMUC C-F-124208.

Isotype

DENMARK • same data as for holotype; ZMUC C-F-124209.

Description

Thallus pale yellowish-amber, slightly darker at the perithecial venter. Basal cell of receptacle (I) obconical, longer than broad. Suprabasal cell of receptacle (II) trapezoidal, as long as broad or slightly longer than broad, separated from cell VI by a strongly oblique septum. Cell III longer than cell II, 1.5 times as long as broad.

Fig. 78. *Cantharomyces papillatus* Santam. sp. nov. **A**–**C**. Basal area of appendage in detail with labelling of papilla-like prominence which represents the antheridial efferent neck (arrows). **D**–**F**. Mature thalli with labelled cell VII in E. Scale bars: A–C = 20 µm; D–F = 50 µm. Photographs from slides ZMUC C-F-124208 (holotype).

Primary appendage consisting of several superposed cells and is weakly branched above its suprabasal cell; not exceeding in length the perithecial apex. The basal cell of the primary appendage, which is slightly longer than broad, includes the compound antheridium and several sterile cells. The antheridial cells occupy the area around the upper inner corner of the appendage basal cell, surpassing to some extent the base of the suprabasal cell of the appendage (Fig. 78D–E) and giving rise to a papilla-like prominence which represents the antheridial efferent neck (Fig. 78A–C, arrows).

Perithecial stalk cell (VI) very elongated and strongly narrowing towards the base; abruptly constricted just below the perithecial base. Cells m and VII large, inflated, yet protruding outwards, especially cell VII. The separation of these cells from the perithecial ascogenous cavity is well-marked by constrictions. Perithecium pyriform, with a truncate, flat apex. Sometimes a second perithecium may develop from cell II (Fig. 78E–F).

Length from foot to apex of perithecium (121–)165–192 µm. Perithecium (including basal cells) (61–)71–89 × (24–)27–33 µm. Primary appendage (from primary septum to apex, when undamaged) 69–84 µm. Length of perithecial stalk cell (VI) (28–)40–59 µm.

Thalli were found on the legs and tarsi of the host. Nothing is known about the collecting circumstances of the host.

Remarks

Cantharomyces papillatus sp. nov. belongs to the group of species around *C. orientalis*, but may be readily recognized by several characteristics, e.g., the shape of the antheridium including a papilla (unknown in any other species), the long, very slender and narrowed cell VI, and the enlarged and inflated cells m and VII.

Cantharomyces orientalis has been reported on *Bledius* by Santamaria (2003). *Cantharomyces bledii* Thaxt. (Thaxter 1890) was described on *Bledius* from USA, being recorded later from Poland (Siemaszko & Siemaszko 1932); the record of this species from Spain (Santamaria 1989) belongs to *C. orientalis*. The other species described on *Bledius* is *C. occidentalis* Thaxt. (Thaxter 1896) from USA. Both taxa differ from *C. papillatus* sp. nov. by the above-mentioned characters.

Cantharomyces platystethi Thaxt.
MB#175399
Fig. 77G

Proceedings of the American Academy of Arts and Sciences 35: 415 (Thaxter 1900). – **Type**: "On abdomen of *Platystethus cornutus* Grav., British Museum, No. 449, Kilburn, England"; FH. [United Kingdom]

Diagnostic features

Cells III and the first two of the appendage form a divergent axis in relation to the perithecium and its stalk. Appendage basal cell longer than broad, including in the middle a small, lateral, lens-shaped, antheridium, which doesn't contact with upper and lower septa (Fig. 77G, an). Appendage branched above its second cell. [Detailed descriptions: Thaxter 1908; Santamaria 2003]

Distribution and hosts

Cantharomyces platystethi occurs on different species of *Platystethus* (Col. Staphylinidae Oxytelinae) from United Kingdom (type), Morocco (Maire & Werner 1937), Japan (Terada 1977), Spain (Santamaria &

Girbal 1987), India (Kaur & Mukerji 1996a), China (Zhang *et al.* 2001), Sweden (Huggert 2010), Turkey (Rossi 2016), and Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Platystethus cornutus* (Gravenhorst, 1802) (Col. Staphylinidae Oxytelinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Riserup; 54°53.732′ N, 11°49.746′ E; PF88; 2 Aug. 1872; *coll. unknown Dry0115*; det. unknown; ZMUC C-F-124182.

On *Platystethus nodifrons* Mannerheim, 1830 (Col. Staphylinidae Oxytelinae)
DENMARK – **Nordøstjylland (NEJ)** • Vendsyssel; no coordinates; Jun. 1872; *coll. unknown Dry0116*; det. unknown; ZMUC C-F-124183.

Remarks

First record from Denmark. The Danish thalli are in poor condition although perfectly identifiable; the samples come from two dried beetles from two very old Museum collections (year 1872).

Genus ***Haplomyces*** Thaxt.
MB#2232

Proceedings of the American Academy of Arts and Sciences 28: 159 (Thaxter 1893). – Type species: *H. californicus* Thaxt.

Brief description

Monoecious. Receptacle three-celled (Fig. 79B). Primary appendage entirely transformed into a compound antheridium. Primary septum constricted and ± darkened. Antheridium ellipsoidal to ovoidal, consisting of several irregularly arranged rows of sterile cells and phialides; bearing a spinous process on the upper, inner side (Fig. 79G, sx) and a discharging pore on the opposite side (Fig. 79G, po). Perithecium with four cells in each vertical row of outer wall cells.

Remarks

This genus consists of three species described by Thaxter (1893): *H. californicus*, *H. texanus* and *H. virginianus*, on *Bledius* spp. (Col. Staphylinidae Oxytelinae). Only *H. texanus* was reported later and occurs in Europe.

Haplomyces texanus Thaxt.
MB#232578
Fig. 79

Proceedings of the American Academy of Arts and Sciences 28: 160 (Thaxter 1893). – **Type**: "On abdomen and elytra of *Bledius rubiginosus* Er., Texas"; FH. [USA]

Diagnostic features

Cell II slightly flattened, pale to variably blackened towards the base and dorsal side. Cell III variable in shape and pigmentation. The spinous process on the antheridium may vary from a blunt inconspicuous prominence to a rather elongated, sharp, spinous process. Trichogyne stump conspicuous as a flat disk between w_2 and w_3 tiers (Fig. 79H, ts). [Detailed descriptions: Thaxter 1896; Majewski 1994b; Santamaria 2003]

Distribution and hosts

On several species of *Bledius* (Col. Staphylinidae Oxytelinae) from USA (type), United Kingdom, France, the Netherlands, Italy, Finland, Russia, Poland, Spain, Latvia, China (Majewski 2008), Sweden (Huggert 2010), Turkey (Rossi 2016), and Czech Republic (Rossi *et al.* 2019b).

Collections examined from Denmark

On *Bledius diota* Schiødte, 1866 (Col. Staphylinidae Oxytelinae)

DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°39.168′ N, 12°34.750′ E; UB47; 12 Jul. 1849; *Schiødte Dry0129*; Schiødte det.; ZMUC C-F-124196. – **Sydjylland (SJ)** • Sønderstrand på Rømø; 55°6.373′ N, 8°29.380′ E; MG60; 14 Mar. 2020; *JP 1620*; JP det.; ZMUC C-F-124365. – **Vestjylland (WJ)** • Esbjerg; 55°29.375′ N, 8°26.363′ E; MG64; 15 Jul. 1924; *V. Hansen Dry0130*; V. Hansen det.; ZMUC C-F-124197 • Skallingen; 55°31.076′ N, 8°14.838′ E; MG55; 21 Sep. 1951; *E. Bro Larsen Dry0128*; E. Bro Larsen det.; ZMUC C-F-124195 • ibid.; 11 Jun. 1960; *H. Gønget Dry0127*; H. Gønget det.; ZMUC C-F-124194.

On *Bledius dissimilis* Erichson, 1840 (Col. Staphylinidae Oxytelinae)

DENMARK – **Sydjylland (SJ)** • Kelstrup Strand; 55°11.503′ N, 9°35.000′ E; NG31; 22 Jul. 1930; *Høeg Dry0125*; Høeg; ZMUC C-F-124192.

On *Bledius femoralis* (Gyllenhal, 1827) (Col. Staphylinidae Oxytelinae)

DENMARK – **Nordvestjylland (NWJ)** • Hanstholm Vildtreservat; 57°4.208′ N, 8°34.593′ E; MJ72; 8°Jun. 1955; *U. Kornerup Dry0132*; U. Kornerup det.; ZMUC C-F-124199 • Nors; 57°1.232′ N, 8°40.706′ E; MJ81; 20 Aug. 1955; *V. Hansen Dry0131*; V. Hansen det.; ZMUC C-F-124198.

On *Bledius furcatus* (Olivier, 1811) (Col. Staphylinidae Oxytelinae)

DENMARK – **Nordøstjylland (NEJ)** • Kringelrøn; 57°13.308′ N, 11°0.233′ E; PJ24; 25 May 1993; *M. Hansen Dry0134*; M. Hansen det.; ZMUC C-F-124201.

On *Bledius gallicus* (Gravenhorst, 1806) (Col. Staphylinidae Oxytelinae)

DENMARK – **Nordøstjylland (NEJ)** • Skagen; 57°44.644′ N, 10°36.077′ E; NK90; Jul. 1849; *Schiødte Dry0135*; Schiødte det.; ZMUC C-F-124202.

On *Bledius longulus* Erichson, 1839 (Col. Staphylinidae Oxytelinae)

DENMARK – **Lolland, Falster, Møn (LFM)** • Slotsgavlene, Møns Klint; 54°59.586′ N, 12°32.065′ E; UA49; 9 Jul. 1894; *F. de Tengnagel Dry0137*; F. de Tengnagel det.; ZMUC C-F-124204. – **Vestjylland (WJ)** • Skallingen; 55°31.076′ N, 8°14.838′ E; MG55; 30 Apr. 1935; *E. Bro Larsen Dry0136*; E. Bro Larsen det.; ZMUC C-F-124203.

On *Bledius occidentalis* Bondroit, 1907 (Col. Staphylinidae Oxytelinae)

DENMARK – **Vestjylland (WJ)** • Esbjerg; 55°29.375′ N, 8°26.363′ E; MG64; 1901; *J.P. Johansen Dry0142*; J.P. Johansen det.; ZMUC C-F-124210.

On *Bledius opacus* (Block, 1799) (Col. Staphylinidae Oxytelinae)

DENMARK – **Nordøstjylland (NEJ)** • Fredrikshavn; 57°26.910′ N, 10°32.102′ E; NJ96; Jul.1849; *Schiødte Dry0143*; Schiødte det.; ZMUC C-F-124211. – **Nordøstsjælland (NEZ)** • Tisvilde Hegn; N 56°3.629′ N, 12°5.777′ E, UC11; 21 Jul. 1890; *F. de Tengnagel Dry0144*; F. de Tengnagel det.; ZMUC C-F-124212.

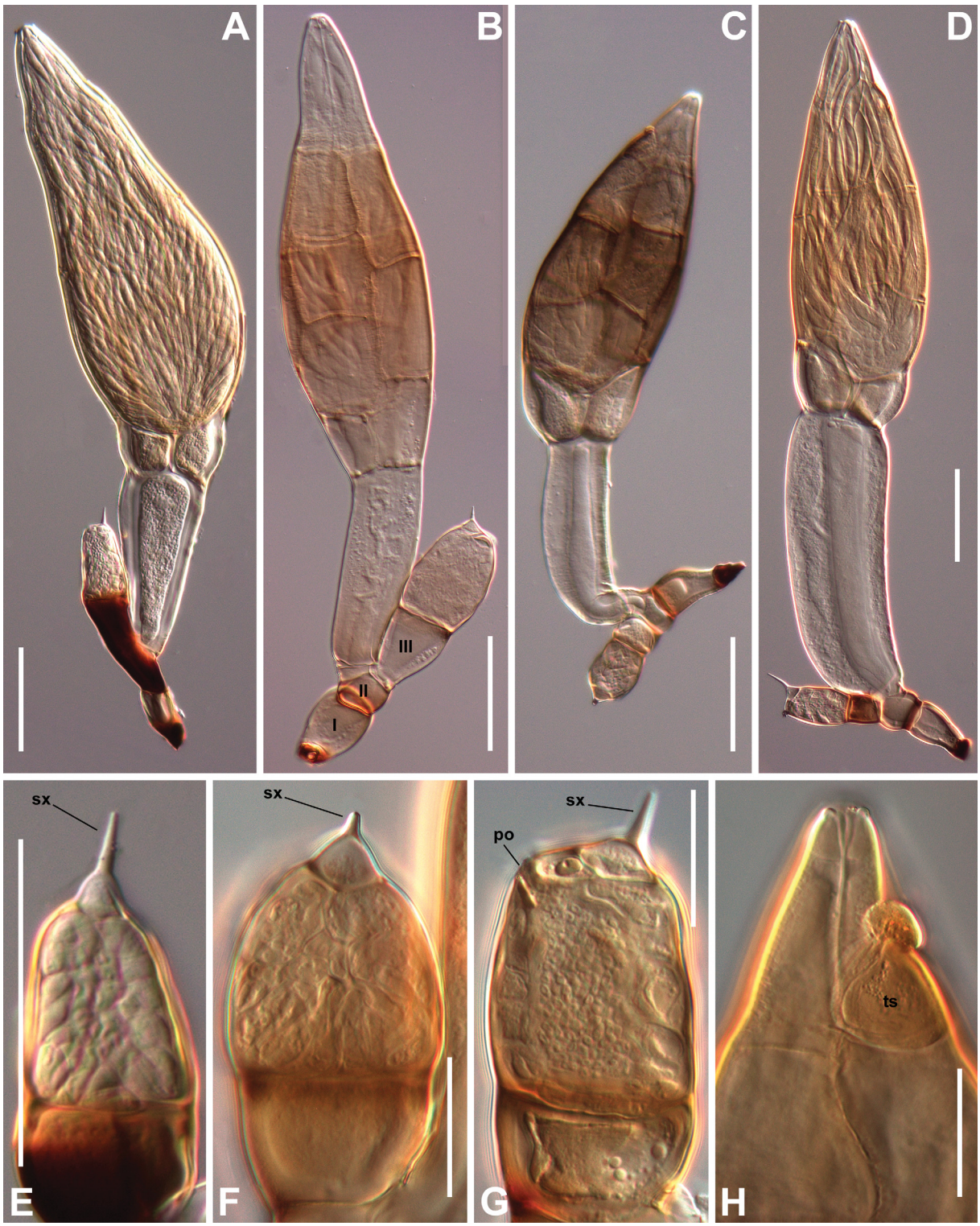

Fig. 79. *Haplomyces texanus* Thaxt. **A**–**D**. Mature thalli. In B, cells I, II, and III are labelled. **E**–**G**. Antheridia in detail showing the spinous process on the antheridium (sx) and the discharging pore (po) in G. **H**. Perithecial apex in detail showing conspicuous trichogyne scar (sc). Scale bars: 50 µm. Photographs from slides ZMUC C-F-124196 (A), ZMUC C-F-124192 (B), ZMUC C-F-124193 (C), ZMUC C-F-124201 (D), ZMUC C-F-124211 (E), ZMUC C-F-124212 (F–H).

On *Bledius pallipes* (Gravenhorst, 1806) (Col. Staphylinidae Oxytelinae)
DENMARK – **estjylland (WJ)** • Endrupholm; 55°31.202′ N, 8°43.026′ E; MG85; 28 Aug. 1932; *Johs. Andersen Dry0126*; Johs. Andersen det.; ZMUC C-F-124193.

On *Bledius tricornis* (Herbst, 1784) (Col. Staphylinidae Oxytelinae)
DENMARK – **Nordøstsjælland (NEZ)** • Amager Øststrand; 55°39.258′ N, 12°38.283′ E; UB57; 30 Jul. 1860; *Schiødte Dry0138*; Schiødte det.; ZMUC C-F-124205 • Vesterfælled; 55°40.198′ N, 12°32.371′ E; UB47; 24 Nov. 1895; *Rosenberg Dry0140*; Rosenberg det.; ZMUC C-F-124207. – **Vestjylland (WJ)** • Esbjerg; 55°29.375′ N, 8°26.363′ E; MG64; 25 Jun. 1897; *Dry0139*; ZMUC C-F-124206.

Remarks

First record from Denmark. The genus *Haplomyces* requires a thorough revision. The three described species were separated on the basis of subtle characters. Moreover, *H. texanus* alone is so variable that perhaps it should be considered as a collective species and includes some undescribed species. We had the opportunity to study many Danish samples from several species of *Bledius*. Not only are there differences between thalli from distinct hosts but also among those living on the same individual host. As written by Majewski (1994b): "possibly more than one taxon of *Haplomyces* occurs in Europe". The problem is to delimit the characteristics. This variability is illustrated in Fig. 79 and concerns almost any characteristic of the thallus. These variations were also described and illustrated by Santamaria (2003) for Iberian samples. Waiting the help of more accurate taxonomical techniques, we prefer to treat *Haplomyces texanus* as a single, very variable species.

Subfamily Monoicomycetoideae (Thaxt.) I.I.Tav.

Genus ***Monoicomyces*** Thaxt.
MB#3254

Proceedings of the American Academy of Arts and Sciences 35: 412 (Thaxter 1900). – Type species: *M. homalotae* Thaxt.

Brief description

Monoecious. Receptacle three-celled. Cell II supports one to several secondary axes (also known as secondary receptacles). Cell III in contact or not with cell I. Secondary axes consist of one to many superposed cells, derivatives from cell II, giving rise to antheridia and perithecia. The antheridia have been defined as of the compound type because their complex structure, which consists of 3–4 tiers of paired cells, where the 2nd or 2nd + 3rd tiers, respectively, bear the phialides. The antheridia also bear the secondary sterile appendages. Perithecium with four cells in each vertical row of outer wall cells.

Remarks

The genus consists of 53 species (including the four described here), of which 24 in Europe, 15 in Denmark. The most recently described species is *M. drusillae* (Santamaria *et al.* 2020a). The genus was described by Thaxter (1900) for species "showing a bicellular receptacle bearing fertile and sterile branches", where the fertile branches were regarded essential to delimit the genus at a time where only four species were known: *M. homalotae*, *M. britannicus*, *M. sanctae-helenae* and *M. invisibilis*. The description of this genus left open questions related to understanding the exact organization of three elements in the thallus: i.e., the primary receptacle, the primary appendage, and the antheridia. The first two are related because the primary appendage is separated from the primary receptacle by the primary septum. Therefore, determining the location of the primary septum is crucial. According to Majewski (1994b), the primary receptacle may be two- or three-celled. We question this judgement and consider

the receptacle invariably three-celled. The problem is that what some authors have described as "the basal cell of primary appendage" or simply "the appendage" is in fact the cell III.

The third issue refers to the antheridial structure. Inside the compound antheridia we find the spermatia-forming cells or phialides following the terminology of Tavares (1985). In *Monoicomyces*, this is a rather complex structure which usually consists of four tiers of cells: a 1st tier with a pair of sterile cells at the base, 2nd and 3rd tiers each consisting of a pair of sterile cells that support several flask-shaped phialides pointing to a central cavity, and a 4th tier with another pair of sterile cells. The first tier is supported by one ± long stalk consisting of one to a few cells which form the secondary receptacle, resulting from a division of cell II. The 4th tier typically bears secondary sterile branches in a variable number (1–4). Second and 3rd tiers are the most difficult to explain and understand. Some species reduce these two tiers to only one, but most species have two. The number of phialides may vary from (2–)4 to 8 for each antheridium. We suggest that this characteristic may be used to distinguish some species as, for example, *M. homalotae* from *M. britannicus*. But this area of the antheridium is even more complicated by the presence of several sterile cells which build an outer wall delimiting a central cavity where spermatia are released from phialides before being discharged through a pore located between secondary sterile appendages (Santamaria *et al.* 2020a).

Key to the Danish species

1. Thallus with a bilateral or symmetrical organization, with a fan-like disposition of antheridia and perithecia. Antheridia appear to be terminal because perithecia arise underneath and laterally from stalk cells of secondary axes. On Col. Staphylinidae Aleocharinae 2
– Thallus with a unilateral, asymmetrical organization. Antheridia situated laterally on the axis of the secondary receptacle which terminates with a single perithecium (some thalli may undergo branching showing almost bilateral patterns, but always one perithecium is on the top). On Col. Staphylinidae Oxytelinae 13

2. Outer surface of antheridia blackened 3
– Outer surface of antheridia not blackened 6

3. Thallus consisting of two secondary axes, each with 2–4 superposed cells giving rise to antheridia and perithecia in a unilateral series all pointing towards the inner margin. On *Bolitochara* Mannerheim, 1830 (Col. Staphylinidae Aleocharinae) ..... ***M. bolitocharae*** T.Majewski
– Thallus consisting of two to several secondary axes, each with only one cell giving rise to one antheridium and one perithecium 4

4. The appendages above cell III ± branched, darkened, very elongate and exceeding the perithecial apices. On *Ocalea* Erichson, 1837 (Col. Staphylinidae Aleocharinae) ..... ***M. fragilis*** Scheloske
– The appendage above cell III unbranched 5

5. Cell VI large, strongly broadened distally, then abruptly constricted below cell VII and perithecial basal cells. Basal cell of primary appendage bulging towards the inner margin and separated by strongly constricted septa from cells above and below. On *Oxypoda* Mannerheim, 1830 (Col. Staphylinidae Aleocharinae) ..... ***M. crassicaulis*** Santam. sp. nov.
– Characteristics not as above. On several genera of Col. Staphylinidae Aleocharinae..... ..... ***M. nigrescens*** Thaxt.

6. Perithecial stalk cell (cell VI) with narrower and darkened lower half 7
– Perithecial stalk cell (cell VI) neither narrower nor darkened 12

7. Perithecia bearing a horn-like protuberance near the apex. On *Gnypeta* (Col. Staphylinidae Aleocharinae)..... ***M. reboleirae*** Santam. sp. nov.
– Perithecia without protuberances..... 8

8. Secondary appendages absent or reduced to only one initial for each antheridium. Perithecium ham-shaped in side view. On various Aleocharinae (Col. Staphylinidae)..... ***M. athetae*** Thaxt.
– Secondary appendages well-developed. Perithecium not ham-shaped 9

9. Cell III supporting the unbranched primary appendage only. Cell VI very elongate, up to three times the perithecial length. On *Myllaena* Erichson, 1837 (Col. Staphylinidae Aleocharinae)..... ..... ***M. myllaenae*** Santam.
– Cell III supporting the primary appendage and another branch below and next to it..... 10

10. Fourth antheridial tier consisting of two prominent, auricle-like cells; bearing 2–4 short secondary appendages, which do not exceed in length the perithecial apices. Cell VI forming an almost right angle with the base of the perithecium. On *Drusilla* Leach in Samouelle, 1819 (Col. Staphylinidae Aleocharinae)..... ***M. drusillae*** Santam.
– All the above characters not found together 11

11. Appendages on cell III very elongate, exceeding in length the perithecial apices; the dorsal branch (i.e., the primary appendage) darkened, especially towards the dorsal margin. Base of primary appendage wrinkled. Antheridia slender, with the 4th tier not prominent, bearing two long secondary appendages arising close together, and then diverging strongly. On *Ocyusa* Kraatz, 1856 and *Atheta* (Col. Staphylinidae Aleocharinae)..... ***M. brachiatus*** Santam. sp. nov.
– Appendages on cell III short. Base of primary appendage smooth. Antheridia stocky, with a prominent 4th tier, bearing short secondary appendages. On *Atheta* and *Geostiba* Thomson, 1858 (Col. Staphylinidae Aleocharinae)..... ***M. validus*** Santam. sp. nov.

12. Cell III pale, in contact with cell I; supporting the primary appendage where the basal cell is darkened and strongly narrowed. Four phialides for each antheridium..... ***M. britannicus*** Thaxt.
– Cell III dorsally darkened; supporting the primary appendage where the basal cell is usually darkened, but separated from cell III by a not narrowed, paler septum. Eight phialides for each antheridium..... ***M. homalotae*** Thaxt.

13. Perithecium asymmetrical and bent. Secondary appendages absent or very reduced. On *Platystethus arenarius* (Geoffroy, 1785) (Col. Staphylinidae Oxytelinae)..... ***M. matthiatis*** T.Majewski
– Perithecium symmetrical and straight. Secondary appendages present, usually ± elongated. On *Oxytelus*, *Anotylus*, *Aploderus* and *Platystethus* (Co. Staphylinidae Oxytelinae)..... ..... ***M. invisibilis*** Thaxt.

Monoicomyces athetae Thaxt.
MB#257664
Fig. 80A–B

Memoirs of the American Academy of Arts and Sciences 16: 36 (Thaxter 1931). – **Type**: "On the inferior tip of the abdomen of *Atheta cinnamoptera* Thomp. No. 2193, New Forest, Brockenhurst, England (Muir)"; FH.

Diagnostic features

Primary appendage unbranched, not exceeding in length the perithecial apices. Cell III inflated, with lower portion blackened. Secondary appendages absent, or rudimentary and then at most one for each antheridium (Fig. 80A, arrow). Stalk cell of perithecium narrowing and darkening near the base (Fig. 80B, *). Perithecium strongly asymmetric in side view, "ham shaped"; the tip with two rounded protuberances at one side (Fig. 80B, *). [Detailed description: Majewski 1994b]

Distribution and hosts

This species is known from the United Kingdom, Germany, Poland, Czech Republic, Norway (Majewski 2008), and Sweden (Huggert 2010). Occurs on species of the genera *Atheta*, *Evanystes* Gistel, 1856 (as *Sipalia* Mulsant & Rey, 1853), and *Megaloscapa* Seidlitz, 1889 (Col. Staphylinidae Aleocharinae).

Collections examined from Denmark

On *Atheta picipes* (Thomson, 1856) (Col. Staphylinidae Aleocharinae)

DENMARK – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 678*; JP det.; ZMUC C-F-123167.

Remarks

First record from Denmark. Only two thalli were found on the tip of the host abdomen. This species is uncommon and difficult to detect because it grows partially concealed among the apical abdominal sternites of their hosts.

Monoicomyces bolitocharae T.Majewski
MB#363457
Fig. 80C

Polish Botanical Studies 7: 193 (Majewski 1994b). – **Type**: "Holotypus: Poloniae, Bialowieza, super *Bolitochara obliqua*, 11.V.1990, *leg. T. Majewski* (KRAM, No TM 4822)"; KRAM. [Poland]

Diagnostic features

Primary appendage unbranched, not exceeding in length the perithecial apices. Cell III inflated, dark brown. Thallus consisting of two divergent outwards dark brown secondary axes, which each include a series of 2–4 antheridia interspersed with perithecia or their initials. Antheridia dark brown except for the paler distal area, each bearing two dark brown apical secondary appendages. Stalk cell of perithecium narrowing and darkened near the base.

Distribution and hosts

Exclusive on *Bolitochara obliqua* (Col. Staphylinidae Aleocharinae) from Poland, United Kingdom (Weir 1996), and Belgium (De Kesel *et al.* 2020).

Collections examined from Denmark

On *Bolitochara obliqua* Erichson, 1837 (Col. Staphylinidae Aleocharinae)

DENMARK – **Bornholm (B)** • Svartingedalen ved Baggeå; 55°11.740′ N, 14 45.260′ E; VB81; 23 Jun. 2018; *JP 1153*; JP det.; ZMUC C-F-123677. – **Nordøstsjælland (NEZ)** • Fruebjerg i Strøgårdsvang; 55°58.539′ N, 12°16.659′ E; UC30; 18 Oct. 2018; *JP 1219*; JP det.; ZMUC C-F-123746.

Fig. 80. *Monoicomyces* spp. **A**–**B**. *M. athetae* Thaxt. Ascospores released from perithecia can be seen. **A**. Mature thallus showing a rudimentary secondary appendage (arrow). **B**. Mature thallus showing stalk cell of perithecium narrowing and darkening near the base (*) and rounded protuberance on one side of the perithecial tip (arrow). – **C**. *M. bolitocharae* T.Majewski. Mature thallus. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123167 (A–B), ZMUC C-F-123746 (C).

Remarks

First record from Denmark. This spectacular species, belonging to the "*nigrescens* group" (Santamaria 1996c), is unmistakable due to the particular organization of the antheridia and perithecia on the secondary axes. A photograph of this species is given here for the first time.

Monoicomyces brachiatus Santam. sp. nov.
MB#840606
Fig. 81

Diagnosis

Similar to *M. homalotae*, but differing by the dark and constricted cell VI (Fig. 81B, *), the appendage ramified inwards, the long outer branch (i.e., primary appendage) dorsally darkened, each antheridium bearing four phialides and two apical secondary appendages (Fig. 81F, *).

Etymology

The species epithet means "having branches", because the branched primary appendage and additional branches around.

Type material

Holotype

DENMARK – **Nordøstsjælland (NEZ)** • Klinten ved Selsø; 55°44.158′ N, 11°59.634′ E; PG88; on *Atheta sodalis* (Erichson, 1837) (Col. Staphylinidae Aleocharinae); 11 Mar. 2007; *JP 521*; JP det.; ZMUC C-F-123004.

Isotype

DENMARK • same data as for holotype; ZMUC C-F-123005.

Paratypes

DENMARK – **Østjylland (EJ)** • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; on *A. sodalis*; 10 Nov. 2018; *JP 1232*; JP det.; ZMUC C-F-123759. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; on *Ocyusa picina* (Aubé, 1850) (Col. Staphylinidae Aleocharinae); 12 Apr. 2016; *JP 6*; JP det.; ZMUC C-F-122477, C-F-122478.

Description

Thallus amber-coloured, with foot and outer margin of primary appendage blackened. Basal cell of receptacle (I) obconical and geniculate above the foot, about 1.5 times as long as broad. Suprabasal cell of the receptacle (II) small, triangular to trapezoidal, broader than long. Cell III variably cylindrical, ± inflated on the inner side, darkened on the outer, supporting the primary appendage and additional branches from the inner side. Usually, each thallus includes two secondary receptacles arising from cell II, bearing respective perithecia and antheridia.

Primary appendage unbranched or, rarely, once ramified, darkened along the entire outer margin, paler distally; sometimes with corrugated margins (Fig. 81C, pa). When seen in detail, the dark pigmentation shows a delicate roughness (Fig. 81D). Inner branch from cell III pale and ± ramified, sometimes simple and dorsally brownish (Fig. 81C, arrow).

Antheridia consisting of four superposed tiers of paired cells. Each of the four cells of the 2nd and 3rd tiers bear one phialide. The "sperm cavity" is sealed by four triangular cells on one side (Fig. 81E, far focus)

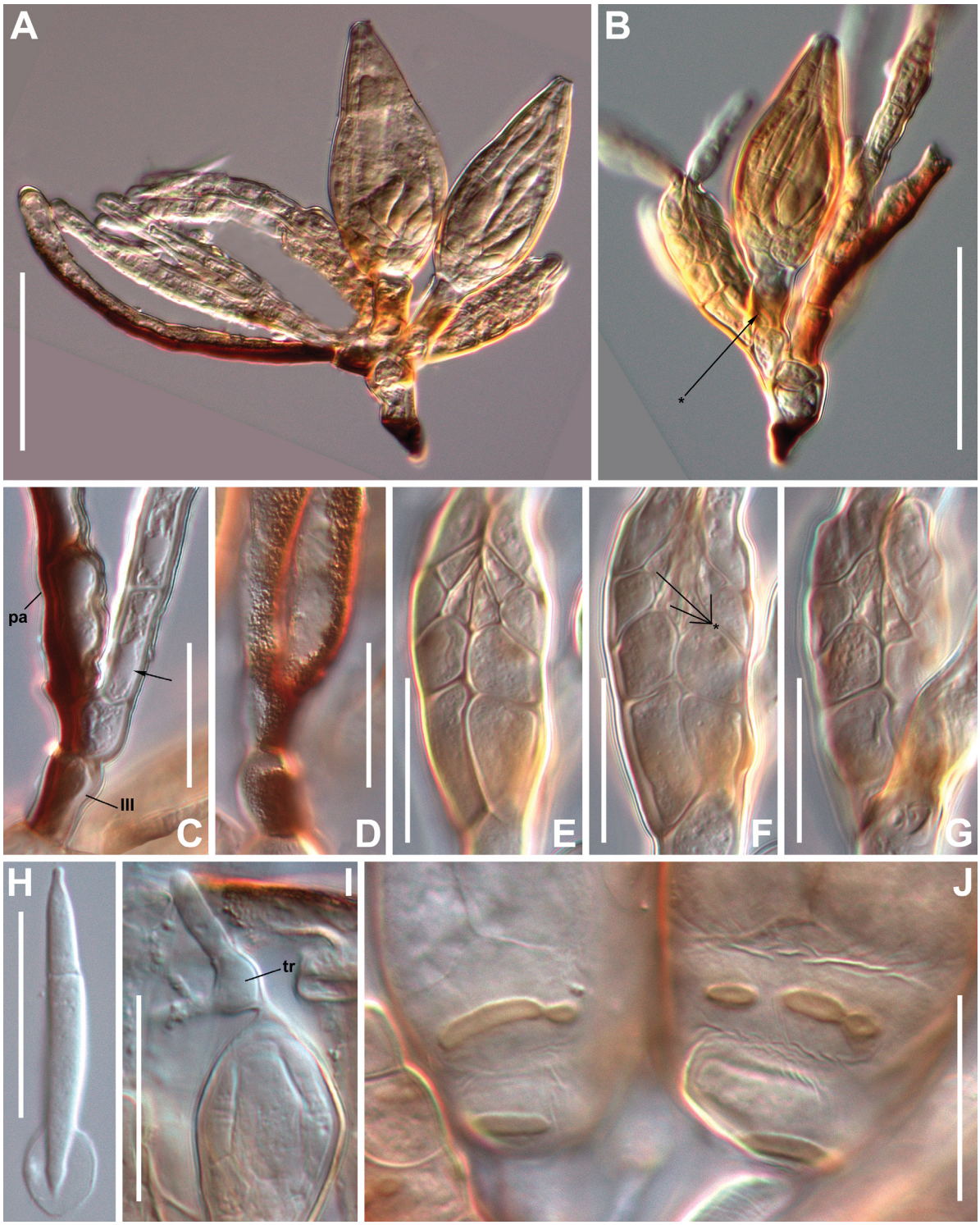

Fig. 81. *Monoicomyces brachiatus* Santam. sp. nov. **A**–**B**. Mature thalli. In B, "*" points to the narrowing and darkening lower half of cell VI. **C**. Primary appendage (pa) and additional branch (arrow) arising from cell III in detail. **D**. Delicate surface roughness of appendage in detail. **E**–**G**. Respectively, far, middle and near focus of antheridium in detail. In F, the asterisk * points to the four phialides. **H**. Ascospore. **I**. Young perithecium and trichogyne (tr) in detail. **J**. "Stigmata" in the lower area of two perithecia. Scale bars: A–B = 50 µm; C–J = 20 µm. Photographs from slides ZMUC C-F-123004 (A) (holotype), ZMUC C-F-122477 (B–C), ZMUC C-F-123759 (D–J).

and four on the opposite (Fig. 81G, near focus). Outer margins not protruding. The 4th tier bears two long and diverging secondary appendages.

Perithecial stalk cell (VI) about two times as long as broad, narrower and darkened in its lower half (Fig. 81B, *). Perithecia ovoid, symmetrical, with blunt and truncate apex. Perithecial basal cells (m, n, n') and VII provided with "stigmata" (Fig. 81J). Trichogyne consisting of a rounded base bearing few diverging, short branches (Fig. 81I, tr). Ascospores with the longer basal cell ending in a conical apex, and the apical shorter cell bearing a rounded and slightly prominent end (Fig. 81H). The spore wall expands in an elliptical outline into what will become the foot of the thallus (Fig. 81H).

Length from foot to tip of perithecia 106–135 µm. Perithecium (including basal cells) 61–80 × 27–36 µm. Antheridium (including pedicellar cell, without secondary appendages) 47–56 × 15–20 µm. Length of primary appendage (when undamaged) from primary septum above cell III 87–148 µm. Ascospores length (including expanded sheath at basal area) 34–38 µm.

Thalli were found on various body parts of the hosts. The hosts were sifted from moldy leaf litter along tree trunks and stubs in a shady deciduous forest, from moist rush and moldy leaf litter and mosses in a sun-exposed swamp along a rivulet, and from moist leaf litter and mosses at the edge of a light-open alder swamp.

Remarks

This species belongs to the *M. homalotae* group, which also includes *M. britannicus*, *M. drusillae* and *M. validus* sp. nov. It can be separated from the latter by a set of characteristics, such as the dark primary appendage, a constricted and darkened cell VI, four phialides per antheridium, and two secondary divergent appendages on antheridia.

Monoicomyces britannicus Thaxt.
MB#192361
Figs 82, 83A

Proceedings of the American Academy of Arts and Sciences 35: 413 (Thaxter 1900, as *M. brittanicus*). – **Type**: "On *Homalota insecta* Thorn., British Museum, No. 454, Hammer smith, England. On superior surface of abdomen"; FH.

Diagnostic features

Primary appendage usually branched once above the basal cell, rarely simple, with the dorsal branch deeply blackish-brown near the base. Cell III inflated, large, pale, in contact with cell I and separated from cell II by a ± vertical or oblique septum (Fig. 82C–D). Two to four secondary appendages for each antheridium. Each antheridium including four phialides (Fig. 82E–F, arrows). [Detailed descriptions: Thaxter 1908; Santamaria 1989]

Distribution and hosts

Reported on *Atheta* (in part as *Homalota* Mannerheim, 1831) from **Europe**: Finland, France, Germany, Italy, Poland, Spain, United Kingdom, Russia (Santamaria *et al.* 1991), Hungary (Bánhegyi *et al.* 1985), Belgium (De Kesel & Haghebaert 1991), Greece (Castaldo *et al.* 2004), Latvia (De Kesel & Krastina De Kesel 2006), Sweden (Huggert 2010), and the Netherlands (Haelewaters *et al.* 2014).

Collections examined from Denmark

On *Acrotona aterrima* (Gravenhorst, 1802) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstjylland (NEJ)** • Vandplasken ved Kærsgård Strand; 57°31.199′ N, 9°53.070′ E; NJ57; 21 Nov. 2017; *JP 806*; JP det.; ZMUC C-F-123301.

On *Acrotona fungi* (Gravenhorst, 1806) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordvestsjælland (NWZ)** • Flyndersø ved Dybesø; 55°58.151′ N, 11°45.621′ E; PH60; 4 Nov. 2017; *JP 723*; JP det.; ZMUC C-F-123216.

On *Acrotona pseudotenera* (Cameron, 1933) (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Kjellerup; 56°17.644′ N, 9°25.850′ E; NH23; 16 Feb. 2018; *JP 975*; JP det.; ZMUC C-F-123482. – **Lolland, Falster, Møn (LFM)** • Hobyskov; 54°44.069′ N, 11°15.296′ E; PF46; 7 Jan. 2018; *JP 956*; JP det.; ZMUC C-F-123462. – **Nordvestjylland (NWJ)** • Legind; 56°45.832′ N, 8°48.782′ E; MH89; 19 Oct. 2008; *JP 80*; JP det.; ZMUC C-F-122555. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 27 Apr. 2018; *JP 1087*; JP det.; ZMUC C-F-123605.

On *Acrotona* sp. (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Brønshøj; 55°42.234′ N, 12°30.135′ E; UB47; 2 Jul. 2012; *JP 38*; JP det.; ZMUC C-F-122513.

On *Aloconota sulcifrons* (Stephens, 1832) (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 14 Feb. 2019; *JP 1349*; JP det.; ZMUC C-F-123888.

On Atheta longicornis (Gravenhorst, 1802) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordvestsjælland (NWZ)** • Klintebjerg ved Klint; 55°57.351′ N, 11°34.463′ E; PH60; 1 May 2016; *JP 56*; JP det.; ZMUC C-F-122531. – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1012*; JP det.; ZMUC C-F-123519.

On *Atheta volans* (Scriba, 1859) (Col. Staphylinidae Aleocharinae)
DENMARK – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 973*; JP det.; ZMUC C-F-123480.

Remarks

First record from Denmark. Very often, cell II is difficult to distinguish because it is flat and wedge-shaped. In front view it appears almost concealed behind cell I and below cell III (Fig. 82D). In side view, the disposition of cells I, II and III is a characteristic that easily distinguishes *M. britannicus* from *M. homalotae* (Fig. 82C–D).

Thaxter (1908), when describing *M. britannicus*, wrote "too nearly related to *M. homalotae*, and may prove to be only a variety" and "general structure as in *M. homalotae*, the third cell of the primary appendage suffused with blackish brown, somewhat constricted below". Likely, Thaxter refers to the third cell of the receptacle or to the basal cell of the appendage.

Distinctiveness of *M. britannicus* from *M. homalotae* was questioned by Majewski (1994b) who considered the differences between the two species irrelevant and included *M. britannicus* among the synonyms of *M. homalotae* describing the latter with very broad characteristics.

The first author (SS) has studied the types of both species several years ago; in 1990 the type slide of *M. britannicus* (labelled FH2352) was borrowed from FH (Fig. 83A). The type slide contained only one thallus, as illustrated by Thaxter (1908). Although the photographs of the types are old and of low quality,

Fig. 82. *Monoicomyces britannicus* Thaxt. **A**–**B**. Mature thalli. **C**–**D**. Lower receptacle (I, II, and III) and base of primary appendage in detail. **E**–**F**. Antheridia showing four phialides in focus (arrows). Scale bars: A–B = 50 µm; C–F = 20 µm. Photographs from slides ZMUC C-F-123462 (A, C, E), ZMUC C-F-122513 (B), ZMUC C-F-123480 (D, F).

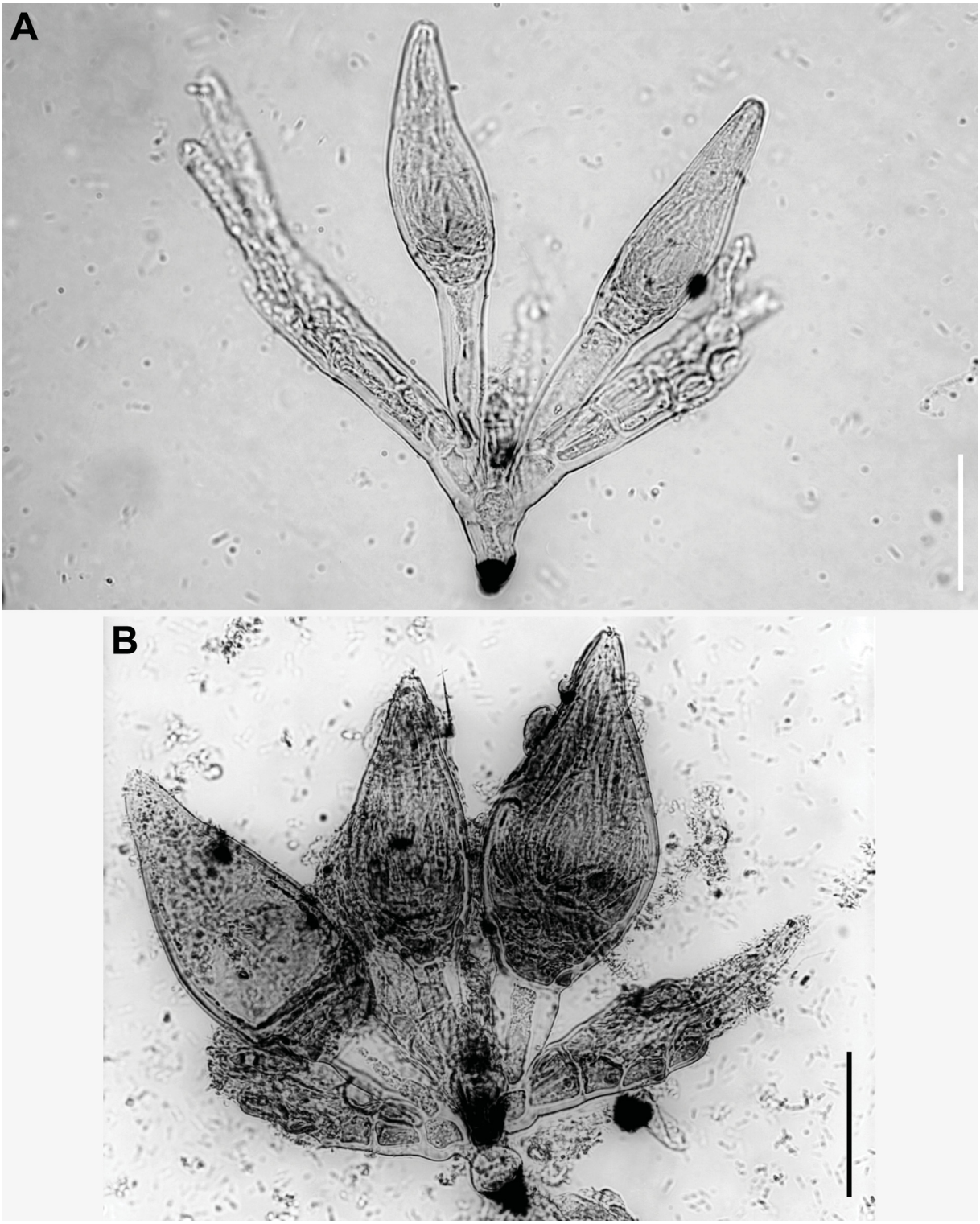

Fig. 83. *Monoicomyces* spp. Old photographs taken from FH type slides. **A**. *M. britannicus* Thaxt . (slide FH2353). **B**. *M. homalotae* Thaxt. (slide FH2402). Scale bars: 50 µm.

we reproduce them here for its documentary interest (Fig. 83A–B). An extended discussion appears below under the remarks of *M. homalotae*.

Monoicomyces crassicaulis Santam. sp. nov.
MB#840607
Figs 84, 107B

Diagnosis

Similar to *M. fragilis*, but differing by an enlarged, inflated cell VI, by a more elongated perithecia, with septa between wall cell tiers marked by elevations, and by a narrow, bent perithecial neck.

Etymology

The species epithet derives from *crassus*, "fat", and *caulis*, "stalk", referring to the inflated perithecial stalk cell.

Type material

Holotype

DENMARK – **Nordvestsjælland (NWZ)** • Garbølle; 55°34.107′ N, 11°34.293′ E; PG66; on *Oxypoda elongatula* Aubé, 1850 (Col. Staphylinidae Aleocharinae); 21 Apr. 2018; *JP 1059*; JP det.; ZMUC C-F-123576.

Paratypes

DENMARK – **Østjylland (EJ)** • Skallerund i Stenholt Skov; 56°11.410′ N, 9°20.787′ E; NH22; on *O. elongatula*; 24 Mar. 2019; *L. Kjær-Thomsen & L. Thomas 1401*; JP det.; ZMUC C-F-123947 • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; on *O. elongatula*; 24 Nov. 2019; *JP 1545*; JP det.; ZMUC C-F-124306. – **Nordøstsjælland (NEZ)** • Skodsborg Dam i Jægersborg Hegn; 55°49.068′ N, 12°33.937′ E; UB48; on *O. elongatula*; 18 Nov. 2018; *JP 1244*; JP det.; ZMUC C-F-123772 • Syd for Løjesø i Rude Skov; 55°49.866′ N, 12°28.551′ E; UB49; on *O. elongatula*; 12 Apr. 2018; *JP 1034*; JP det.; ZMUC C-F-123546. – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; on *O. elongatula*; 9 Apr. 2019; *JP 1425*; JP det.; ZMUC C-F-123971 • Holmegårds Mose; 55°17.685′ N, 11°47.928′ E; PG73; on *O. elongatula*; 31 Mar. 2019; *JP 1411*; JP det.; ZMUC C-F-123957 • Storskov syd for Sparresholm; 55°13.234′ N, 11°57.463′ E; PG82; on *O. elongatula*; 17 Feb. 2019; *JP 1389*; JP det.; ZMUC C-F-123932 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; on *O. elongatula*; 6 Jan. 2018; *JP 1592*; JP det.; ZMUC C-F-124353. – **Vestjylland (WJ)** • Sønderkær syd for Bindeballe; 55°39.107′ N, 9°16.682′ E; NG16; on *O. elongatula*; 10 Mar. 2002; *H. Liljehult 1469*; JP det.; ZMUC C-F-124049 • Velling; 56°3.078′ N, 8°18.596′ E; MH51; on *O. elongatula*; 16 Dec. 2018; *JP 1266*; JP det.; ZMUC C-F-123794.

Description

Thallus amber to brown, with darker antheridia, appendages, and foot. Basal cell of receptacle (I) obconical, about 1.5 times as long as broad. Suprabasal cell of receptacle (II) small, trapezoidal, broader than long. Cell III entirely darkened, with the inner side distinctly convex (Fig. 84G–H). Each thallus includes two to several secondary receptacles arising from cell II, with respective perithecia and antheridia.

Primary appendage unbranched, very elongated if unbroken, entirely brown, consisting of a short, inflated basal cell, and several very elongated cells, exceeding in length the perithecial apices. Basal cell of primary appendage between two constricted and darkened septa above and below; the latter is the primary septum (Fig. 84G–H, a).

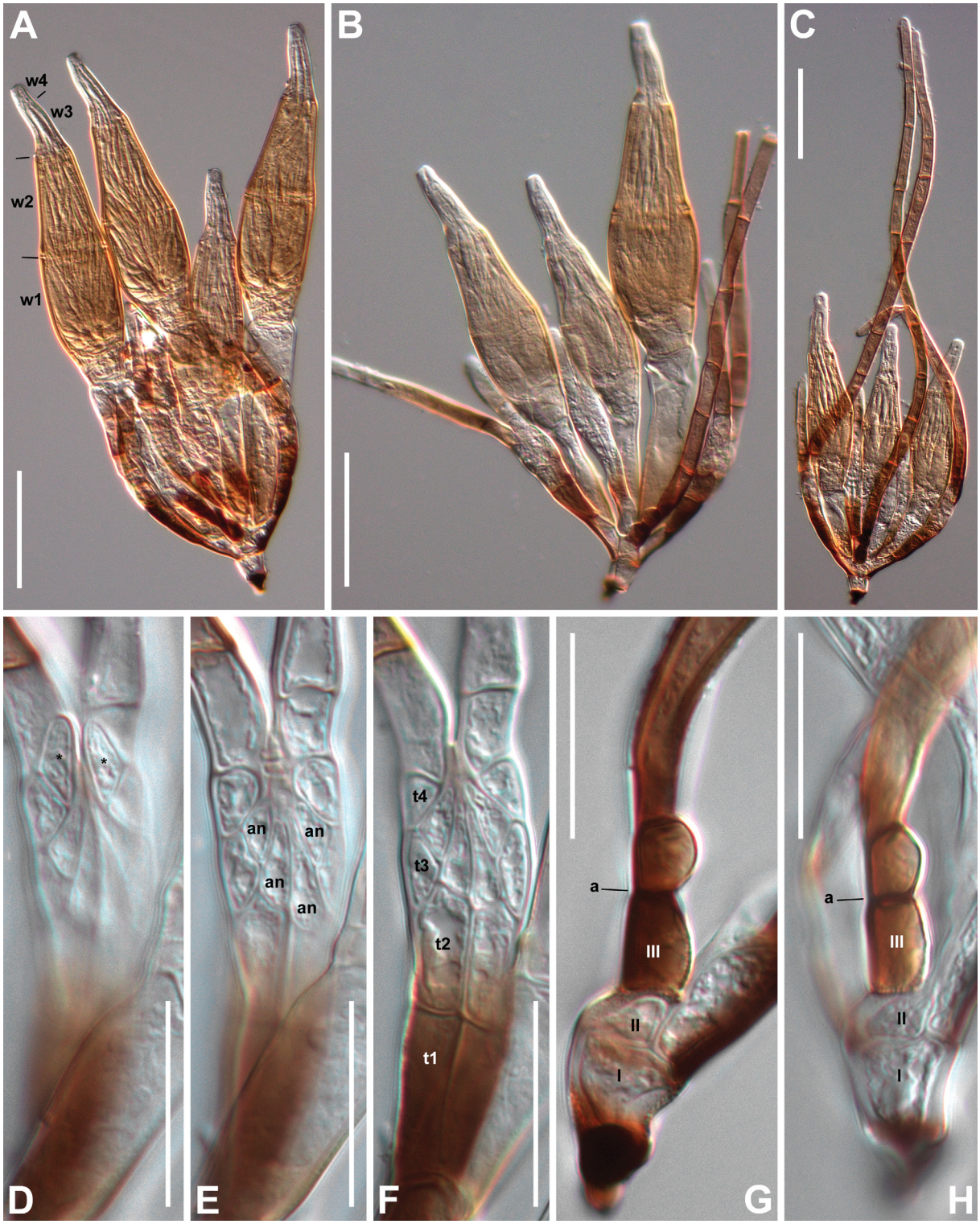

Fig. 84. *Monoicomyces crassicaulis* Santam. sp. nov. **A**–**C**. Mature thalli. In A, perithecial wall cell tiers ($w_{1–4}$) have been labelled. **D**–**F**. Respectively, near, middle and far focus of antheridium in detail. In E, the four phialides have been labelled (an). In F, the four tiers have been labelled (t1–4). **G**–**H**. Lower receptacle (I, II, and III) and primary appendage above the primary septum (a) in detail. Scale bars: A–C = 50 µm; D–H = 20 µm. Photographs from slides ZMUC C-F-123576 (A) (holotype), ZMUC C-F-123971 (B), ZMUC C-F-123794 (C–H).

Secondary receptacles including an externally darkened stalk supporting perithecia and antheridia with secondary appendages. Antheridia consisting of four superposed tiers of paired cells (Fig. 84D–F, tn). Each cell in the first tier is about three times as long as broad and fully dark brown. Brown suffusion occupies the basal area of 2nd tier, with cells about twice longer than broad. Cells of 3rd tier hyaline and subtriangular. The 2nd and 3rd tiers of cells bear four phialides altogether (Fig. 84E, an). The 4th tier consists of two subtriangular cells, smaller than cells of the 3rd tier; bearing two dark, very elongated secondary appendages which exceed in length the perithecial apices, and sometimes two cells representing initials for an additional pair of secondary appendages (Fig. 84D, *).

Perithecial stalk cell (VI) 3–4 times as long as broad, narrower and darkened at the base, distinctly inflated upwards, then abruptly constricted below the perithecial base. Perithecia elongate fusiform, with septa separating the two lower tiers of wall cells marked by slight elevations; broader at w_1-w_2 level which form a deeply pigmented venter (Fig. 84A). Tiers w_3 and w_4 almost hyaline, the w_3 forming a narrow neck which slightly bents laterally and ends in a blunt apex (Fig. 84A).

Maximum length from foot to tip of perithecium 175–242 µm. Perithecium (including basal cells) 115–133 × 27–34 µm. Antheridium (including pedicellar cell, without secondary appendages) 54–62 × 12–16 µm. Length of primary appendage (when undamaged) from primary septum above cell III 209–294 µm.

Thalli were found on various body parts of the hosts. The hosts were sifted from moist moss and leaf litter in a partly shady peat bog, beaten from rush in a sun-exposed swamp along a rivulet, sifted from moist beech leaf litter in a partly dried out forest pond, sifted from wet *Sphagnum* mosses and leaves around *Carex* tussocks in a sun-exposed *Sphagnum* bog, sifted from moist fine crumb and mice-nests in and under *Carex paniculata* tussocks at the edge of a sun-exposed forest pond, sifted from moist leaf litter and moss in a raised bog, sifted from moist moss and leaf litter in a partly sun-exposed alder swamp, sifted from wet, fresh flood debris along the banks of a river and sifted from moist leaf litter and moss in an open willow/birch/alder swamp.

Remarks

Majewski (1994b) already mentioned that thalli on *Oxypoda* differ from those on *Ocalea* although he did not formally describe any new taxa. After studying the abundant material from Danish *Oxypoda elongatula*, we conclude that a new species should be erected because the differences are stable and remarkable. As mentioned above, in comparison with the closely allied *M. fragilis*, thalli of *M. crassicaulis* sp. nov. are larger, with narrower perithecia having a well-distinguished, bent neck, with a simple primary appendage, with both cells III as well as the basal cell of appendage producing a very characteristic figure, in addition to a broadened and distally inflated cell VI.

Monoicomyces drusillae Santam.
MB#834606
Fig. 85A–B

Nova Hedwigia 110 (3-4): 359 (Santamaria *et al.* 2020a). – **Type**: "Spain, Barcelona, Mura, Riera de Nespres, 41°41′55″ N, 1°58′33″ E, 449 m a.s.l., 14.IX.1991, S. Santamaria, on *Drusilla canaliculata* (Fabricius) (Coleoptera Staphylinidae), det. S. Santamaria, slide BCB-SS1099b (HOLOTYPE)"; BCB.

Diagnostic features

Primary appendage simple or once branched above the basal cell. Cell III barrel-shaped, longer than broad, with a darkened outer margin. Two to four secondary appendages for each antheridium. Fourth tier

of antheridium consisting of two prominent cells. Each antheridium including four phialides. Perithecial stalk cell narrower and darkened in its lower half.

Distribution and hosts

Recently described on *Drusilla canaliculata* (Col. Staphylinidae Aleocharinae) from Spain (type), probably also from United Kingdom (Weir & Beakes 1993) and from Poland (Majewski 2008) where the records on the same host as the type were referred to *M. homalotae*.

Collections examined from Denmark

On *Drusilla canaliculata* (Fabricius, 1787) (Col. Staphylinidae Aleocharinae)

DENMARK – **Nordøstjylland (NEJ) •** Bønderskoven i Tofte Skov; 56°49.955′ N, 10°14.981′ E; NH79; 8–22 Aug. 2013; *I. Aggerholm 934*; JP det.; ZMUC C-F-123434.

Remarks

First record from Denmark. As mentioned in the protologue, this species should be carefully compared with *M. homalotae* from which it may be distinguished by the constricted and darkened cell VI, the four phialides in the antheridium, and by the secondary receptacles showing constrictions at the septa separating the antheridial tiers. Also, its special ecology supports the distinctiveness of this species from others occurring on Aleocharinae rove beetles, such as *M. britannicus* and *M. homalotae*. *Drusilla canaliculata* is a rove beetle that catches ants (myrmecophagous).

Monoicomyces fragilis Scheloske

MB#334445

Fig. 85C–E

*Parasitologische Schriftenreihe*19: 138 (Scheloske 1969). – **Type**: "An allen Teilen der Körperoberfläche von *Ocalea picata* (Col., Staphylinidae, Aleocharinae). Das Material stammt aus Gesiebe aus Bruchwäldern bei Schwand/Nürnberg und Erlangen. Deutschland. Holotypus Abb. 39". [Germany]

Diagnostic features

Cell III darkened, supporting two appendages: an outer blackened and irregularly branched primary appendage (Fig. 85D, pa), and an inner pale to variably darkened, simple or branched subsidiary appendage (Fig. 85D, arrow). Thalli with two to several secondary receptacles. Antheridia bearing two often very elongated secondary appendages, darker at the base, paler towards the apex, separated from the 4th antheridial tier by a contrasting dark and constricted septum. Antheridia dark brown towards the base and margins, paler distally and around the middle area. Each antheridium includes four phialides. Stalk cell of perithecium narrowing and darkened near the base. [Detailed descriptions: Majewski 1994b; Weir 1994; Santamaria 1996c]

Distribution and hosts

Described from Germany on *Ocalea picata* (Stephens, 1832) (Col. Staphylinidae Aleocharinae), it has been later reported from Spain, United Kingdom, France, Belgium, Poland (Majewski 2008), and Denmark (Høier 2009). Also reported on *Oxypoda* (Col. Staphylinidae Aleocharinae) but these records probably belong to *M. crassicaulis* sp. nov.

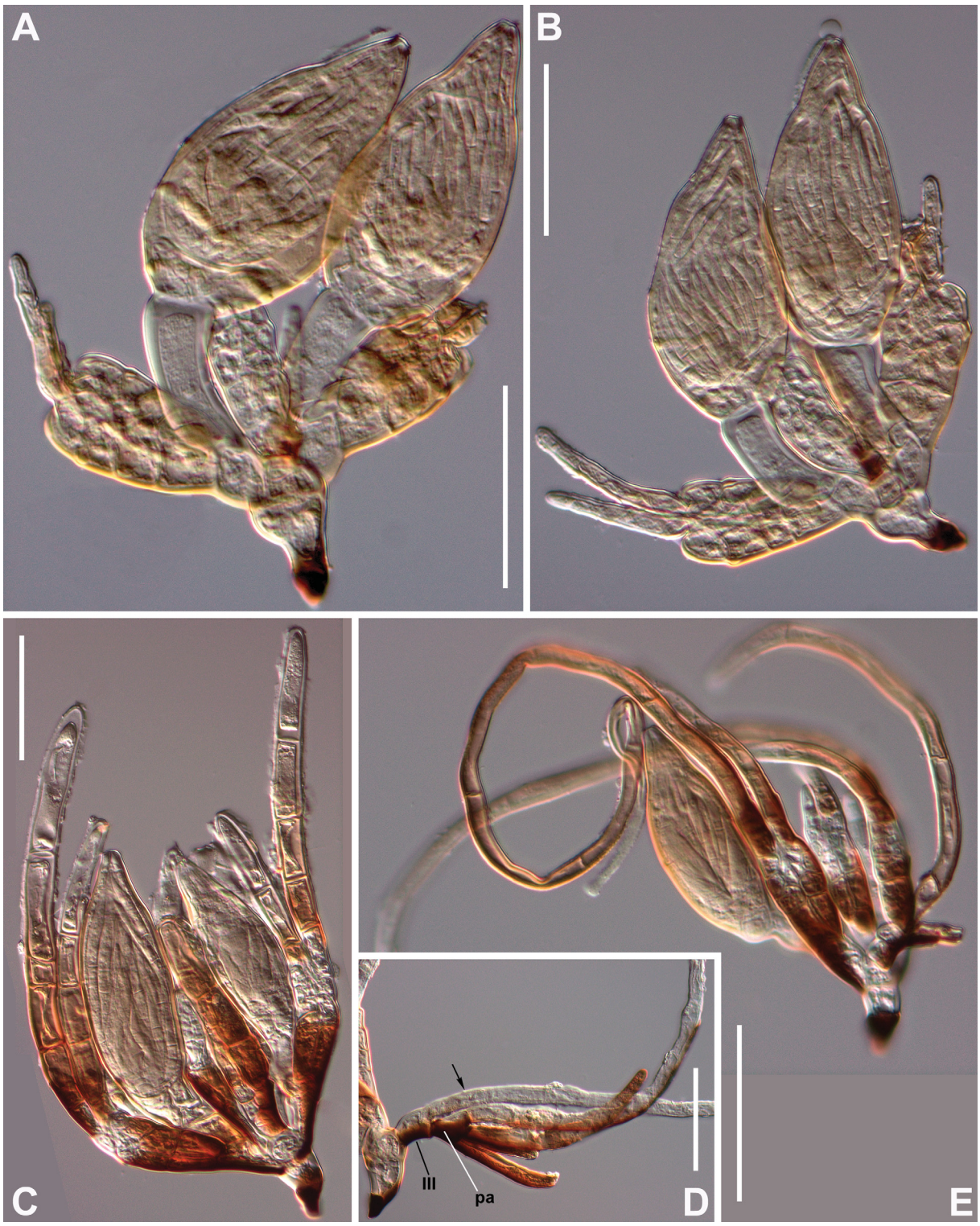

Fig. 85. *Monoicomyces* spp. **A**–**B**. *M. drusillae* Santam. Mature thalli. – **C**–**E**. *M. fragilis* Scheloske. **C**, **E**. Mature thalli. **D**. Primary appendage (a) and additional branch (arrow) arising from cell III. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123434 (A–B), ZMUC C-F-122963 (C), ZMUC C-F-123928 (D), ZMUC C-F-123758 (E).

Collections examined from Denmark

On *Dinaraea aequata* (Erichson, 1837) (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; 10 Nov. 2018; *JP 1231*; JP det.; ZMUC C-F-123758.

On *Dinaraea angustula* (Gyllenhal, 1810) (Col. Staphylinidae Aleocharinae)
DENMARK – **Sydsjælland (SZ)** • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1013*; JP det.; ZMUC C-F-123520.

On *Ocalea concolor* Kiesenwetter, 1847 (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 14 Feb. 2019; *JP 1346*; JP det.; ZMUC C-F-123885.

On *Ocalea picata* (Stephens, 1832) (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 14 Feb. 2019; *JP 1347*; JP det.; ZMUC C-F-123886 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 986*; JP det.; ZMUC C-F-123493. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1134*; JP det.; ZMUC C-F-123658 • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1338*; JP det.; ZMUC C-F-123877. – **Nordøstsjælland (NEZ)** • Eriksholm Skov; 55°41.771′ N, 11°47.912′ E; PG77; 4 Nov. 2017; *JP 729*; JP det.; ZMUC C-F-123222 • Mølleå ved Farum Lillevang; 55°49.093′ N, 12°18.496′ E; UB38; 24 Feb. 2018; *JP 991*; JP det.; ZMUC C-F-123498. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 891*; JP det.; ZMUC C-F-123389. – **Sydsjælland (SZ)** • Broby Vesterskov; 55°23.332′ N, 11°35.794′ E; PG64; 2 Mar. 2019; *L. Kjær-Thomsen & L. Thomas 1396*; JP det.; ZMUC C-F-123939 • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 495*; JP det.; ZMUC C-F-122979 • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1361*; JP det.; ZMUC C-F-123899 • Gammel Kalvehave; 54°59.745′ N, 12°8.232′ E; UA19; 24 Mar. 2018; *JP 1011*; JP det.; ZMUC C-F-123518 • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 17 Feb. 2019; *JP 1384*; JP det.; ZMUC C-F-123926 • Villa Gallina i Hesede Skov; 55°16.335′ N, 11°56.850′ E; PG82; 8 Mar. 2015; *JP 479*; JP det.; ZMUC C-F-122963.

On *Ocalea rivularis* Miller, 1851 (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 18 Jan. 2015; *JP 451*; JP det.; ZMUC C-F-122936. – **Sydsjælland (SZ)** • Krobæk i Sjolte Skov; 55°10.772′ N, 12°0.863′ E; UB11; 28 Feb. 2015; *JP 443*; JP det.; ZMUC C-F-122928 • ibid.; 17 Feb. 2019; *JP 1385*; JP det.; ZMUC C-F-123927, C-F-123928.

Remarks

Distinctiveness of this species with respect to *M. infuscatus* (which is reported on Xantholininae rove beetles, Santamaria 1996c) should be revaluated with further studies. *Dinaraea* spp. is mentioned here for the first time as host for this species

Monoicomyces homalotae Thaxt.
MB#181116
Figs 83B, 86

Proceedings of the American Academy of Arts and Sciences 35: 412 (Thaxter 1900). – **Type**: "On *Homalota putrescens* Woll., British Museum, No. 412, Azores"; FH.

Monoicomyces ternatus Speg. (Spegazzini 1915b: 67) [MB#191957]

Monoicomyces unilateralis Speg. (Spegazzini 1915b: 68) [MB#192287]

Diagnostic features

Cell I ± globose, often heart-shaped (Fig. 86A–B). Primary appendage variably branched. Cell III barrel-shaped, longer than broad, usually broadened distally, with a darkened outer margin. Usually four secondary appendages for each antheridium. Each antheridium with eight phialides. [Detailed descriptions: Thaxter 1908; Majewski 1988, 1994b; Santamaria 1989]

Distribution and hosts

Reported on many genera and species of Aleocharinae (Col. Staphylinidae), mostly *Atheta*, but also on others like *Evanystes*, *Geostiba*, *Ischnopoda*, etc. (Majewski 2008). Its geographical distribution is difficult to delimit because of confusion with similar species, in particular *M. britannicus*. It has been recorded from **Europe**: Finland, France, Germany, the Netherlands, Italy, Spain; **Africa**: Algeria; **America**: Argentina, USA; **Asia**: Japan; and Azores (Santamaria *et al.* 1991). Reported subsequently from Zaire (Rossi & Santamaria 1992), Poland (Majewski 1994a), United Kingdom (Weir 1996; record on *Drusilla* may be *M. drusillae*), Greece (Castaldo *et al.* 2004), Norway (Majewski 2008), Slovakia, Czech Republic (Rossi *et al.* 2010), Sweden (Huggert 2010), Belgium (De Kesel 2010), Turkey (Rossi 2016), China, Armenia, and Bulgaria (Rossi *et al.* 2019a).

Collections examined from Denmark

On *Aloconota gregaria* (Erichson, 1839) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Asserbo Plantage; 56°1.984′ N, 12°0.817′ E; UC11; 28 Apr. 2019; *JP 1455*; JP det.; ZMUC C-F-124006. – **Sydsjælland (SZ)** • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 6 Jan. 2018; *JP 1593*; JP det.; ZMUC C-F-124354.

On *Atheta castanoptera* (Mannerheim, 1830) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Nærum; 55°49.077′ N, 12°32.686′ E; UB48; 1 Dec. 2019; *JP 1565*; JP det.; ZMUC C-F-124325.

On *Atheta graminicola* (Gravenhorst, 1806) (Col. Staphylinidae Aleocharinae)
DENMARK – **Østjylland (EJ)** • Klostermølle; 56°2.432′ N, 9°41.629′ E; NH41; 14 Feb. 2019; *JP 1348*; JP det.; ZMUC C-F-123887 • Tange å vest for Kjellerup; 56°17.959′ N, 9°23.462′ E; NH23; 17 Feb. 2018; *JP 985*; JP det.; ZMUC C-F-123492 • Vest for Ørnsø ved Silkeborg; 56°9.126′ N, 9°30.588′ E; NH32; 10 Nov. 2018; *JP 1230*; JP det.; ZMUC C-F-123757 • Viemose ved Ringkloster; 56°0.632′ N, 9°57.400′ E; NH50; 12 Mar. 2017; *JP 536*; JP det.; ZMUC C-F-123020. – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1339*; JP det.; ZMUC C-F-123878. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 19 Mar. 2017; *JP 677*; JP det.; ZMUC C-F-123166 • Kongelunden; 55°34.369′ N, 12°34.189′ E; UB46; 26 Sep. 2013; *H. Liljehult 208*; JP det.; ZMUC C-F-122687. – **Nordvestjylland (NWJ)** • Nord for Landting ved Vinderup; 56°30.049′ N, 8°45.384′ E; MH86; 19 Jan. 2015; *JP 560*; JP det.; ZMUC C-F-123046 • Vest for Vinderup; 56°28.727′ N, 8°44.810′ E; MH85; 19 Jan. 2015; *JP 767*; JP det.; ZMUC C-F-123261. – **Nordvestsjælland (NWZ)** • Bognæs Skov på Tuse Næs; 55°44.966′ N, 11°45.817′ E; PG78; 10 Dec. 2013; *JP 892*; JP det.; ZMUC C-F-123390 • Nordøstbredden af Tissø; 55°35.612′ N, 11°18.461′ E; PG46; 1 May 2013; *JP 761*; JP det.; ZMUC C-F-123255 • Vesterlyng; 55°44.195′ N, 11°17.276′ E; PG47; 9 Feb. 2014; *JP 635*; JP det.; ZMUC C-F-123124. – **Sydsjælland (SZ)** • Even Bro; 55°8.694′ N, 12°0.601′ E; UB11; 17 Feb. 2019; *JP 1362*; JP det.; ZMUC C-F-123900 • Holtug Kalkbrud; 55°20.470′ N, 12°26.678′ E; UB33; 21 Sep. 2013; *JP 351*; JP det.; ZMUC C-F-122833 • Tryggevælde Å ved Varpelev; 55°21.055′ N, 12°15.877′ E; UB23; 5 Jan. 2013; *H. Liljehult 209*; JP det.; ZMUC C-F-

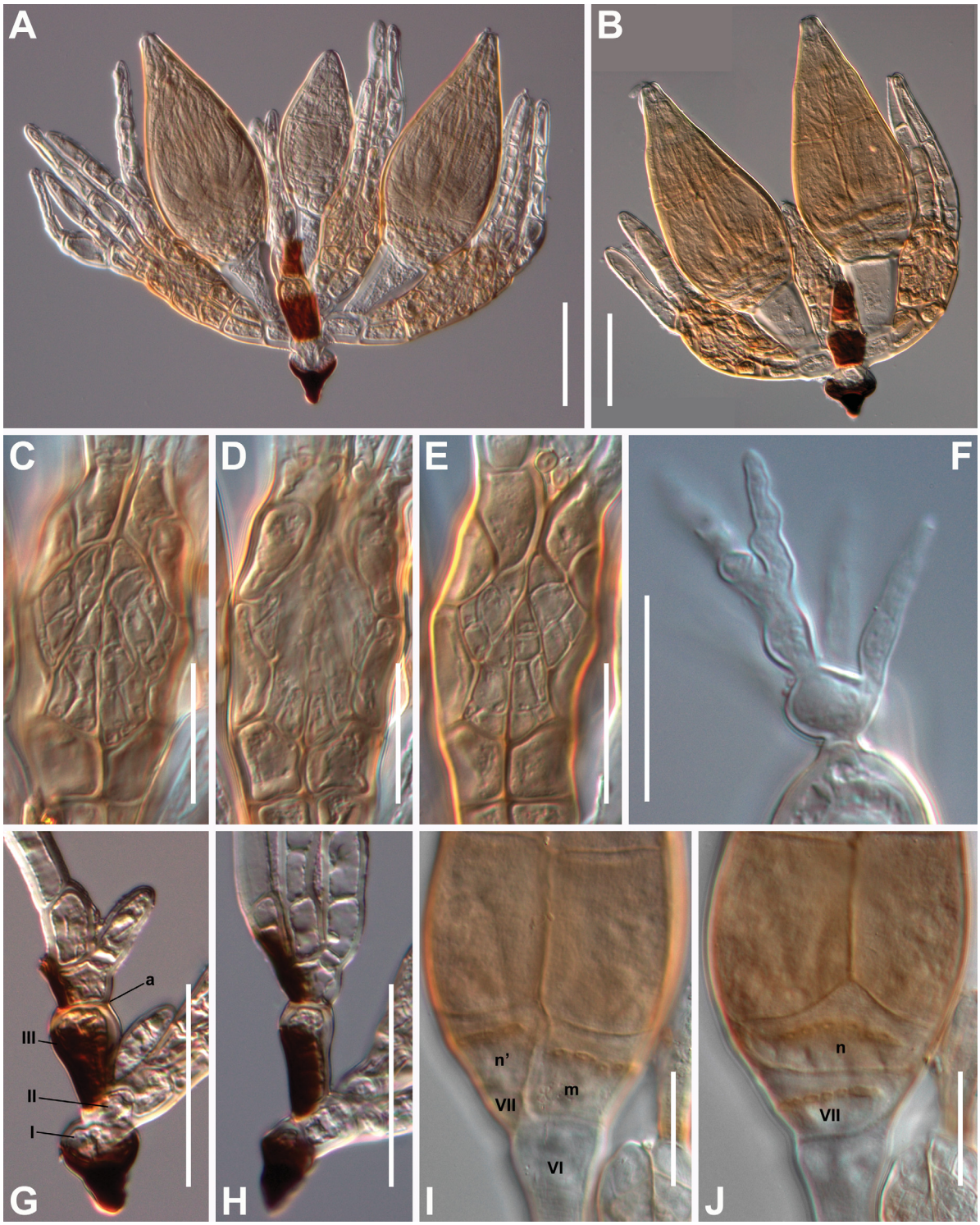

Fig. 86. *Monoicomyces homalotae* Thaxt. **A**–**B**. Mature thalli. **C**–**E**. Respectively, near, middle and far focus of antheridium in detail. In D, the middle focus, phialides and spermatia can be seen. **F**. Trichogyne in detail. **G**–**H**. Lower receptacle (I, II, and III) and base of primary appendage in detail; the primary septum (a) is labelled in G. **I**–**J**. Perithecial base in two focusing levels to see basal cells (m, n, n'), secondary stalk cell (VII), and stalk cell (VI). Scale bars: A–B, G–H = 50 µm; C–F, I–J = 20 µm. Photographs from slides ZMUC C-F-123255 (A), ZMUC C-F-122687 (B), ZMUC C-F-123046 (C–E), ZMUC C-F-123757 (F), ZMUC C-F-123020 (G), ZMUC C-F-123492 (H), ZMUC C-F-123793 (I–J).

122688. – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1264*; JP det.; ZMUC C-F-123792.

On *Atheta melanocera* (Thomson, 1856) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Amager Fælled; 55°39.168′ N, 12°34.750′ E; UB47; 14 Apr. 2001; *H. Liljehult 388*; JP det.; ZMUC C-F-122871.

On *Atheta triangulum* (Kraatz, 1856) (Col. Staphylinidae Aleocharinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Vest for Bandholm; 54°50.303′ N, 11°28.050′ E; PF57; 3 Jan. 2019; *JP 1340*; JP det.; ZMUC C-F-123879.

On *Atheta pallidicornis* (Thomson, 1856) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Åsen ved Lellinge; 55°27.948′ N, 12°8.785′ E; UB15; 26 Jun. 2019; *JP 1485*; JP det.; ZMUC C-F-124070.

On *Geostiba circellaris* (Gravenhorst, 1806) (Col. Staphylinidae Aleocharinae)
DENMARK – **Vestjylland (WJ)** • Velling; 56°3.078′ N, 8°18.596′ E; MH51; 16 Dec. 2018; *JP 1265*; JP det.; ZMUC C-F-123793.

On *Schistoglossa aubei* (Brisout de Barneville, 1860) (Col. Staphylinidae Aleocharinae)
DENMARK – **Sydsjælland (SZ)** • Denderup Sø i Denderup Vænge; 55°15.075′ N, 11°57.366′ E; PG82; 5 May 2016; *JP 497*; JP det.; ZMUC C-F-122981.

Remarks

First record from Denmark. Efforts to distinguish *M. homalotae* and *M. britannicus* begun soon after their original descriptions. Thaxter (1908) thought that the receptacle of both species was two-celled. He described *M. homalotae* with "the basal cell of the primary appendage" ± deeply suffused including blackish brown. After examination of many thalli we believe what Thaxter called the basal cell of primary appendage corresponds to cell III.

The compound antheridium of *M. homalotae* seems to have been misunderstood by Thaxter (1908) and therefore his drawings are imprecise. Thaxter failed also regarding the number of phialides formed by the two middle tiers (2nd and 3rd) of the antheridium. Although not described, his drawings show four phialides. Nowadays, the correct observation of this part of the thallus requires a high-quality microscope with high magnification, preferable with DIC optics, because the planes of focus are very close and difficult to discern. Upper (Fig. 86C) and lower focus (Fig. 86E) of the antheridium consists of several cells which seem to serve as wall cells for sealing the central cavity where phialides eject their spermatia. The middle focus shows the area with phialides and the cavity with spermatia (Fig. 86D). We think the number of phialides is very important for distinguishing *M. homalotae* from other very similar species, with eight (two for each cell in 2nd and 3rd tiers) in *M. homalotae* (Fig. 86D), whereas the phialides are four (one for each cell) in other species, as the related but distinct *M. britannicus*.

Thaxter (1908) increased the confusion by including under *M. homalotae* thalli with constricted and darkened perithecial stalk cells; this seems inappropriate, and probably some of these forms belong to species described here, such as *M. brachiatus* sp. nov. and *M. validus* sp. nov. In 1989, 17 slides of *M. homalotae* were borrowed from FH (labelled with references FH2402 to 2418) by SS (see *M. britannicus*). In Fig. 83B the only thallus included in the type slide (FH2402) is reproduced with an old photograph taken at that time. The material was in very poor condition but it is easy to deduce that this is the thallus which appears in Thaxter (1908: fig. 8).

The perithecial basal cells (m, n, n') and the secondary stalk cell (VII) are provided with darker and prominent spots ("stigmata") of unknown function and origin (Fig. 86I–J), which are also present on other species, such as *M. drusillae* (Santamaria *et al.* 2020a).

Monoicomyces invisibilis Thaxt.
MB#189243
Figs 87, 88A–C

Proceedings of the American Academy of Arts and Sciences 35: 414 (Thaxter 1900). – *Eumonoicomyces invisibilis* (Thaxt.) Thaxt. (Thaxter 1901b: 21) [MB#245519]. – **Type**: "On *Homalota putrescens* Woll., British Museum, No. 412, Azores"; FH. [This is a mistake because Thaxter exactly repeated the type of *M. homalotae.* Thaxter (1931: 43) reported that the type material is scanty, in bad condition and erroneous in relation to the host reference which is not *Homalota* but *Oxytelus*. The material reported in this latter work as a "locotypic indication" included: on *Oxytelus hostilis* Bernh. Nos. 3339 and 3452 from Fort de Koch, Sumatra, figures 3 and 6; on *O. sulcifer* Fauv., No. 3393, from Los Chorros, Venezuela.]

Eumonoicomyces californicus Thaxt. (Thaxter 1901b: 22) [MB#245492]. – *Monoicomyces californicus* (Thaxt.) Thaxt. (Thaxter 1931: 38) [MB#259377]
Eumonoicomyces argentinensis Speg. (Spegazzini 1912: 188) [MB#139851]
Monoicomyces affinis Speg. (Spegazzini 1915b: 65) [MB#186507]
Monoicomyces furcatus Thaxt. (Thaxter 1931: 41) [MB#265593]
Monoicomyces oxyteli Huldén [MB#108233], **syn. nov.** (Huldén 1983: 61, as *M. oxytelis* [MB#271607])

Diagnostic features

Receptacle consisting of a basal cell (I) supporting 2–12 flattened cells oriented diagonally which are cell II derivatives; the uppermost cell bears a solitary perithecium. Antheridia and sterile appendages borne laterally on cells of the main axis. Compound antheridium consisting of three tiers of paired cells (Fig. 88A–C), the 2nd tier giving rise to four phialides (Fig. 88B, an), the 3rd bearing (2–)4 secondary sterile appendages which are variable in length and pigmentation (Fig. 88A, C, bc sap1 and bc sap2). [Detailed descriptions: Thaxter 1908; Santamaria 1989; Majewski 1994b]

Distribution and hosts

Widely distributed in **Europe** (Czech Republic, Finland, France, the Netherlands, Italy, Norway, Poland, Spain, Sweden, Russia), **America** (Argentina, Guatemala, Haiti, Jamaica, Uruguay, USA, Venezuela), **Asia** (Sumatra) and Azores Islands (Santamaria *et al.* 1991), on *Oxytelus*, *Anotylus*, *Aploderus* and *Platystethus* (Col. Staphylinidae Oxytelinae) beetles usually found in herbivore dung. Further records not included in Santamaria *et al.* (1991): Belgium (De Kesel & Haghebaert 1991), United Kingdom (Weir 1996), China (Shen & Ye 2006), Ecuador (Proaño Castro & Rossi 2008), and Slovakia (Rossi *et al.* 2019b).

Collections examined from Denmark

On *Anotylus inustus* (Gravenhorst, 1806) (Col. Staphylinidae Oxytelinae)
DENMARK – **Fyn (F)** • Gyldenstens inddæmmede Strand; 55°34.447′ N, 10°7.211′ E; NG75; 2 Apr. 2014; *JP 689*; JP det.; ZMUC C-F-123177 • Kratholm ved Bellinge; 55°19.710′ N, 10°19.335′ E; NG83; 18 May 2016; *JP 89*; JP det.; ZMUC C-F-122564. – **Sydsjælland (SZ)** • Bimose i Broby Overdrev; 55°23.921′ N, 11°35.499′ E; PG64; 1 Jul. 2013; *JP 197*; JP det.; ZMUC C-F-122676.

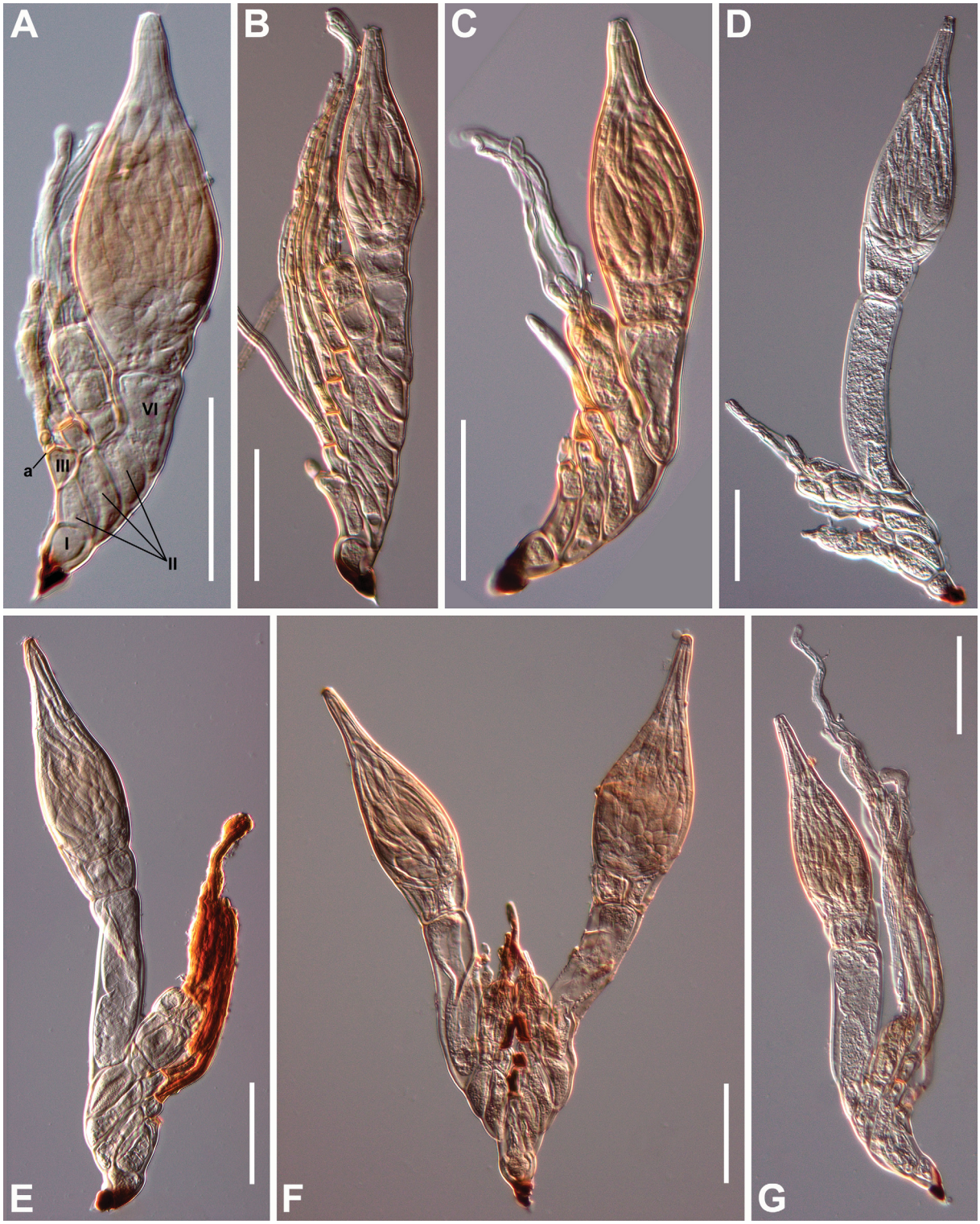

Fig. 87. *Monoicomyces invisibilis* Thaxt. **A**. Mature thallus from *Platystethus arenarius* showing cells I, II (subdivided into three cells), III, VI, and primary septum (a). **B**–**C**. Mature thalli from *Oxytelus fulvipes*. **D**, **F**. Mature thalli from *Anotylus sculpturatus*. **E**, **G**. Mature thalli from *Anotylus inustus*. Scale bars: 50 µm. Photographs from slides ZMUC C-F-123613 (A), ZMUC C-F-122951 (B), ZMUC C-F-123161 (C), ZMUC C-F-123406 (D), ZMUC C-F-122676 (E), ZMUC C-F-123003 (F), ZMUC C-F-123177 (G).

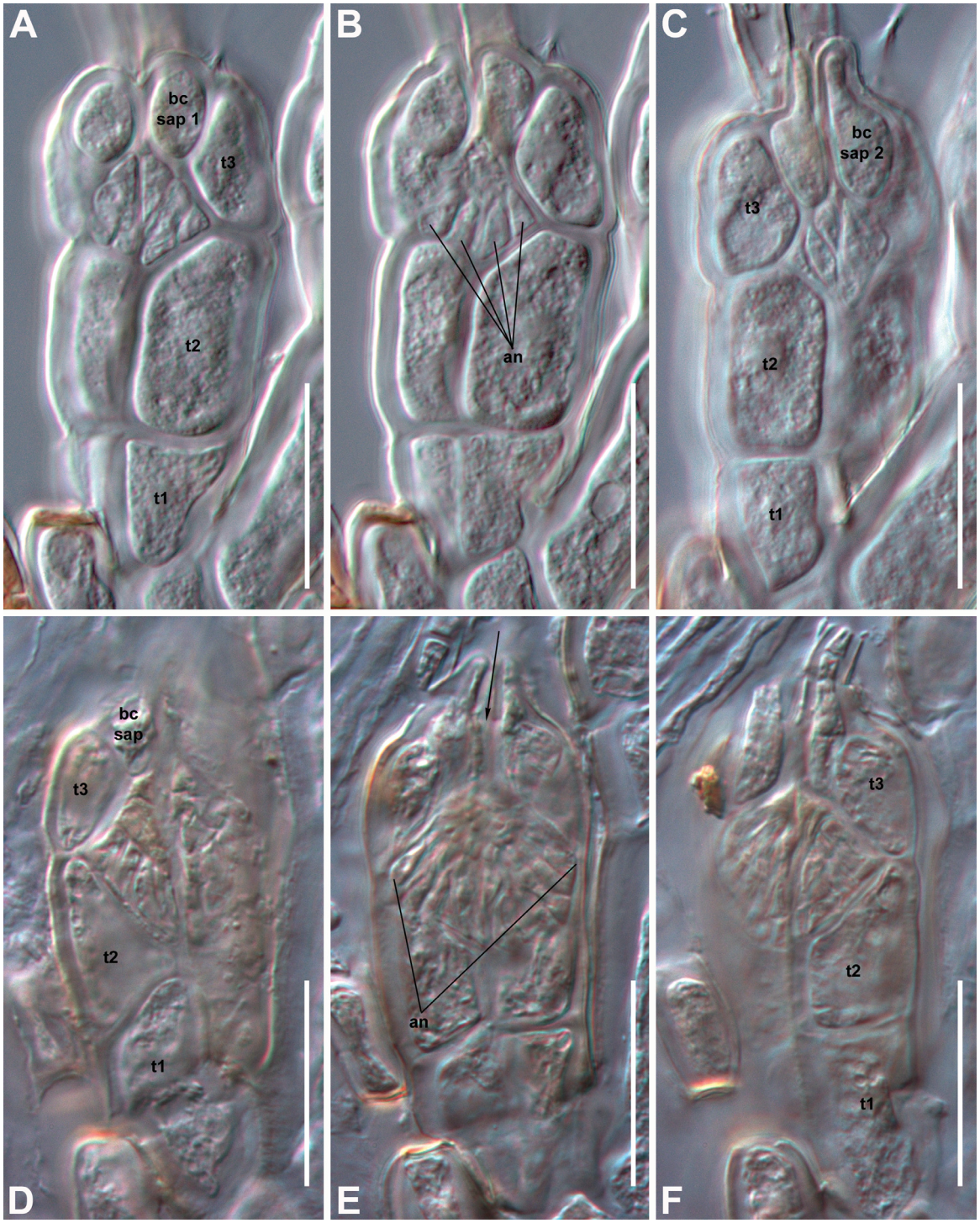

Fig. 88. Comparison of antheridia from *Monoicomyces invisibilis* Thaxt. and *Eumonoicomyces papuanus* Thaxt. **A**–**C**. *M. invisibilis*. Respectively, near, middle and far focus of antheridium in detail. The three tiers of paired cells are labelled (t1–3), the basal cells of secondary appendages (bc sap 1–2), and in the middle focus (B), "an" points to the four phialides. – **D**–**F**. *E. papuanus*. Respectively, near, middle and far focus of antheridium in detail. The three tiers of paired cells are labelled (t1–3), the basal cells of a secondary appendages (bc sap), and in the middle focus (E), "an" points to the phialides and the arrow to the opening through which the spermatia flow out. Scale bars: 20 µm. Photographs from slides ZMUC C-F-123406 (A–C), FH2092 barcode 00313728 (D–F) (type).

On *Anotylus sculpturatus* (Gravenhorst, 1806) (Col. Staphylinidae Oxytelinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Krenkerup Haveskov; 54°46.408′ N, 11°39.955′ E; PF77; 8 Jul. 1993; *S. Langemark & O.E. Meyer 908*; JP det.; ZMUC C-F-123406. – **Nordøstsjælland (NEZ)** • Klinten ved Selsø; 55°44.158′ N, 11°59.634′ E; PG88; 11 Mar. 2007; *JP 520*; JP det.; ZMUC C-F-123003 • Ledøje; 55°42.601′ N, 12°17.977′ E; UB37; 18 Apr. 2018; *JP 1047*; JP det.; ZMUC C-F-123563 • Tokkekøb Hegn; 55°52.334′ N, 12°22.229′ E; UB39; 6 May 2013; *JP 332*; JP det.; ZMUC C-F-122810.

On *Oxytelus fulvipes* Erichson, 1839 (Col. Staphylinidae Oxytelinae)
DENMARK – **Østjylland (EJ)** • Ørnsø ved Silkeborg; 56°9.446′ N, 9°31.488′ E; NH32; 20 May 2013; *JP 380*; JP det.; ZMUC C-F-122863. – **Lolland, Falster, Møn (LFM)** • Lysemose ved Maribo; 54°46.971′ N, 11°28.959′ E; PF57; 4 Jun. 2018; *JP 1130*; JP det.; ZMUC C-F-123653. – **Nordøstsjælland (NEZ)** • Indelukket ved Frederiksborg Slot; 55°56.191′ N, 12°17.861′ E; UC30; 12 Apr. 2016; *JP 3*; JP det.; ZMUC C-F-122473 • ibid.; 19 Mar. 2017; *JP 672*; JP det.; ZMUC C-F-123161 • Stampeskov ved Rådvad; 55°48.332′ N, 12°33.138′ E; UB48; 23 Mar. 2017; *JP 467*; JP det.; ZMUC C-F-122951. – **Nordvestsjælland (NWZ)** • Nordbredden af Skarresø; 55°39.425′ N, 11°22.998′ E; PG47; 1 May 2013; *JP 849*; JP det.; ZMUC C-F-123344.

On *Platystethus alutaceus* Thomson, 1861 (Col. Staphylinidae Oxytelinae)
DENMARK – **Sydjylland (SJ)** • Juvre; 55°11.050′ N, 8°33.568′ E; MG71; 8 Mar. 2020; *JP 1641*; JP det.; ZMUC C-F-124369.

On *Platystethus arenarius* (Geoffroy, 1785) (Col. Staphylinidae Oxytelinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°59.171′ N, 12°31.954′ E; UA49; 2 May 2018; *JP 1096*; JP det.; ZMUC C-F-123613, C-F-123614. – **Vestjylland (WJ)** • Skallingen; 55°31.076′ N, 8°14.838′ E; MG55; 28 May 1955; *U. Kornerup Dry0114*; U. Kornerup det.; ZMUC C-F-124181 • Tipperne; 55°52.452′ N, 8°14.261′ E; MG59; Oct. 1973; *E. Rald Dry0113*; E. Rald det.; ZMUC C-F-124180.

Other material examined

Type of *Eumonoicomyces papuanus*
PAPUA NEW GUINEA • "*Eumonoicomyces papuanus*, two slides from FH, #2092, barcode 00313728, and #2195, barcode 00313729, **type**, all over *Oxytelus*, from Ralum, prope New Guinea, New Pomerania (Papua New Guinea), ex Berlin Museum coll. no. 1012"; FH[00313728] [slide #2092 consists of five mature thalli in poor condition; slide #2195 consists of seven mature thalli in very poor condition, buried by crystals]

Remarks

First record from Denmark. *Monoicomyces invisibilis* is mostly accepted as a variable species. It may be a collective species, with discrepancy of opinions among the different authors as to which species should be placed among the synonyms.

In the protologue, Thaxter (1900) described small thalli (110–140 µm) with three receptacular cells or axial receptacle cells (i.e., those intermediate cells located between cell I and cell VI, derivatives from cell II; see Fig. 87A). The species was shortly after transferred to *Eumonoicomyces* by Thaxter (1901b). Years later, Thaxter (1931) again reallocated it to the genus *Monoicomyces* because of the characteristics of the phialides which are arranged in a single tier instead of two as for *Eumonoicomyces*. As described below, this two-tiers arrangement of phialides in *Eumonoicomyces* is not seen in the type slide (Fig. 88E, an). Moreover, Thaxter had doubts about the structure of the antheridia because of the difficulty of observing them in an adequate alignment. Also, he corrected some aspects of the type material (see above under the Type paragraph), and reduced *M. affinis* (Spegazzini 1915b) to synonymy with *M. invisibilis*.

At this point it seems quite appropriate to take a look at the genus *Eumonoicomyces*. This genus was described by Thaxter (1900) including two species: *E. papuanus* and *E. californicus*. The latter was quickly transferred to *Monoicomyces* by Thaxter himself (1901b). *Monoicomyces invisibilis* and *Eumonoicomyces argentinensis* (the latter now a synonym of the former) went through this genus. Only *E. platystethi* was added later as a second species (Thaxter 1931); no more species have been described in the genus until today. Seemingly, the only difference between *Eumonoicomyces* and *Monoicomyces* lies in the structure of the antheridium. According to its author, in *Eumonoicomyces*, the phialides are obliquely arranged in two rows, in an area which entirely replaces the 2nd and 3rd tiers of cells in the antheridia of most species of *Monoicomyces*. Our observations of the type slides do not agree with this conclusion.

It is necessary to review Thaxter's writings to understand the uncertainty that pervaded his description. Thaxter (1908) wrote (sic): "the only material from which it is possible to form an approximately accurate idea of the structure of the antheridium in this genus is that of *E. papuanus*". Subsequently, in the same publication, Thaxter provided a very detailed explanation about the structure of the compound antheridium but admitted many doubts related to the inappropriate orientation of the antheridia, which he himself defined as a cause of confusion. We have borrowed the type of *E. papuanus* from FH (see above under "other material examined"). The two slides include 12 thalli in rather poor condition, variably squashed, showing some degree of cell shifting, apparently due to inadequate handling during slide restoration. Despite all the drawbacks, a patient study of these slides does not agree with Thaxter's description. Based on our observations, we conclude that the compound antheridium consists of three tiers: the 1st tier includes a pair of cells, the 2nd tier includes a pair of cells supporting about eight phialides (maybe more) arranged in a single row divided into two sets (Fig. 88E, an), the 3rd and uppermost tier bears the secondary sterile appendages (Fig. 88D, bc sap) and delimits the opening through which the spermatia flow out (Fig. 88E, arrow). Some additional cells around the 2nd tier level serve to separate the spermatia cavity from the outside (Fig. 88D, F), as in other species of *Monoicomyces*. The oblique orientation of antheridia easily leads to misunderstanding the real position of the cells.

According to these observations, there is probably no strong support for the distinction between *Eumonoicomyces* and *Monoicomyces*, either morphologically or phylogenetically (Goldmann & Weir 2018), but we prefer to be conservative because the material at our disposition, including the type, was in imperfect condition. Moreover, the absence of photographs in records of *Eumonoicomyces* after Thaxter's description does not help at all to verify the identifications or to understand a structure thought confusing by Thaxter (1908) himself. Likewise, we cannot confirm the presence of *E. papuanus* in Denmark, which was reported by Rostrup (1916), also because none of the numerous specimens we have studied fits its description.

Another matter concerns the possible synonyms of *M. invisibilis*. *Monoicomyces californicus* (initially described in *Eumonoicomyces* by Thaxter 1901b) differs from *M. invisibilis* according to the original description by its dark sterile appendages, "as well as by other points of difference" as written by Thaxter (1901b). The Fig. 87E and G from *Anotylus inustus* represents two of such thalli. *Monoicomyces furcatus* was distinguished from *M. invisibilis* by the bifurcate condition, "although this species is subject to much variation in size and may rarely be simple, instead of furcate" as written by Thaxter (1931). Figure 87F from *Anotylus sculpturatus* represents one such, rather common, bifurcate thallus. Rossi (1975) already suggested the synonymy of *M. furcatus* and *M. californicus* under *M. invisibilis* because (1) the furcate condition of *M. furcatus* is very variable and not clearly delimitated, and (2) the appendages may vary from hyaline to dark brown (as the thalli of *M. californicus* would be) with all the intermediate degrees of shading. Recently, De Kesel *et al.* (2020) kept *M. californicus* separate from *M. invisibilis.* To conclude the discussion of probable synonymies, a third species, *Monoicomyces oxyteli* (Huldén 1983) was separated from *M. invisibilis* by showing more numerous and narrower receptacular cells. Majewski (1999) accepted the distinctiveness of this taxon by the difference in number of receptacular cells, 2–3(–4) in *M. invisibilis*

against 4–12 in *M. oxyteli*, as well as because this latter is exclusively for *Oxytelus fulvipes* Erichson (Fig. 87B–C). This does not agree with our observations, either for the number of receptacular cells which is extremely variable, or for the supposed exclusivity of *O. fulvipes* (Fig. 87D represents a thallus with four axial cells found on *Anotylus sculpturatus*). We therefore suggest to include also *M. oxyteli* among the synonyms of *M. invisibilis*.

Monoicomyces matthiatis T.Majewski
MB#128602
Fig. 89A–C

Acta Mycologica 25 (1): 49 (Majewski 1990a, as *M. mathiatis*). – **Type**: "On *Platystethus arenarius* (Fourcr.) (Col., Staphylinidae): Biala Woda near Szczawnica (Nowy Sacz voiv.), cow feces on pasture near Biala Woda stream, alt. about 640 m, 5.9.1987, leg. T.Majewski (TM.3825 – holotype)"; KRAM. [Poland]

Diagnostic features

Primary appendage two-celled, consisting of a basal inflated cell separated from the elongated apical cell by a darkened, oblique septum (Fig. 88C, arrow). Thallus with only one developed antheridium, which consists of three tiers of cells, the 2nd including two phialides (Fig. 89B). No secondary appendages from the 3rd tier are formed. [Detailed descriptions: Majewski 1994b; De Kesel 2010]

Distribution and hosts

Only known from Poland (type) and Belgium (De Kesel 2010), on *Platystethus arenarius* (Col. Staphylinidae Oxytelinae). The host species is found in cow dung in pastures.

Collections examined from Denmark

On *Platystethus arenarius* (Geoffroy, 1785) (Col. Staphylinidae Oxytelinae)
DENMARK – **Lolland, Falster, Møn (LFM)** • Jydelejet, Møns Klint; 54°59.171′ N, 12°31.954′ E; UA49; 2 May 2018; *JP 1096*; JP det.; ZMUC C-F-123613.

Remarks

First record from Denmark. This is a very interesting species that occurs in company with *Monoicomyces invisibilis* on the same host. The first tier of paired cells of the antheridium seems to include two inner triangular cells that seem to be phialide initials, but none of the studied thalli show their functionality. This characteristic is not observed in any other species of the genus since these cells only exists in the 2nd tier and above, not in the 1st tier. Cell II directly supports the 1st tier of paired cells in the antheridium (Fig. 89B, t1) without the presence of any intermediate cell serving as a pedicel. A photograph of this species is given here for the first time.

Monoicomyces myllaenae Santam.
MB#521398
Fig. 89D–E

Nova Hedwigia 82 (3–4): 358 (Santamaria 2006). – **Type**: "SPAIN. Asturias: Parque Nacional de Somiedo, Pigüeces, on the abdominal apex of *Myllaena elongata* Matthews (Coleoptera, Staphylinidae, Aleocharinae), 22 June 2000, *S. Santamaria*, …. HOLOTYPE: slide BCB–SS2329c"; BCB.

Diagnostic features

Primary appendage unbranched, with darkened lower and dorsal margins. Cell III with a darkened outer margin. Antheridium with 1st and 2nd tiers of cells elongate and forming more than half of its total length. Each antheridium including four phialides. Perithecial stalk cell very elongated, up to three times the perithecial length.

Distribution and hosts

Only known from Spain (type) and the Netherlands (Haelewaters *et al.* 2014), exclusively on *Myllaena elongata* (Col. Staphylinidae).

Collections examined from Denmark

On *Myllaena elongata* (Matthews, 1838) (Col. Staphylinidae Aleocharinae)
DENMARK – **Sydjylland (SJ)** • Nordborg Præstegårdshave; 55°3.646′ N, 9°44.362′ E; NG40; 12 Aug. 1936; *Johs. Andersen Dry0148*; Johs. Andersen det.; ZMUC C-F-124215.

Remarks

First record from Denmark. The Danish material is in very poor condition although identifiable (Fig. 89E). A photograph of the type is added for comparison (Fig. 89D).

Monoicomyces nigrescens Thaxt.
MB#189290
Fig. 89F–G

Proceedings of the American Academy of Arts and Sciences 38: 10 (Thaxter 1902). – **Type**: "U.S.A.: On *Calodera* sp., Intervale, N.H., Jul. 1909, R. Thaxter 1359 (FH–2452, type) (according to Santamaria 1996c)"; FH.

Diagnostic features

Cell III entirely darkened (Fig. 89F). Primary appendage unbranched, short, consisting of up to four cells. Antheridia dark towards the base and margin, bearing two secondary appendages. Each antheridium including four phialides. Stalk cell of perithecium narrowed and darkened near the base. [Detailed descriptions: Thaxter 1908; Majewski 1994b; Santamaria 1996c]

Distribution and hosts

Reported on many genera and species of Aleocharinae (Col. Staphylinidae) like *Atheta* and *Tachyusa*, but also on others. Recorded from **Europe**: the Netherlands, Germany, Italy, Poland, Spain, United Kingdom, Portugal (Majewski 2008), Sweden (Huggert 2010), Czech Republic (Rossi *et al.* 2010), and Belgium (De Kesel *et al.* 2020); **America**: USA (type), Argentina (Spegazzini 1912), and Uruguay (Spegazzini 1917); and **Asia**: Japan (Majewski 1988). The record from Sri Lanka (Thaxter 1931) was described as a separate species by Santamaria (1996c) (*M. ceylonensis*).

Collections examined from Denmark

On *Dilacra luteipes* (Erichson, 1837) (Col. Staphylinidae Aleocharinae)
DENMARK – **Nordøstsjælland (NEZ)** • Ledreborg; 55°36.740′ N, 11°58.456′ E; PG86; 21 Apr. 1885; *leg. unknown Dry0150*; det. unknown; ZMUC C-F-124217.

Fig. 89. *Monoicomyces* spp. **A**–**C**. *M. matthiatis* T.Majewski. **A**. Mature thallus. **B**. Lower receptacle (I, II, and III) and antheridium (tiers of cells labelled with t1–3) in detail. **C**. Central area of a thallus in detail showing cell III, the primary septum (a), and the darkened, oblique septum separating the basal inflated cell from the elongated apical cell of the primary appendage (arrow). – **D**–**E**. *M. myllaenae* Santam. **D**. Mature thallus from Spanish type slide kept in BCB. **E**. Broken and damaged thallus from Denmark. – **F**–**G**. *M. nigrescens* Thaxt. **F**. Primary appendage in detail showing cell III at the base. **G**. Immature thallus. Scale bars: A, D–E, G = 50 µm; B–C = 20 µm; F = 25 µm. Photographs from slides ZMUC C-F-123613 (A–C), BCB-SS2329c (D) (holotype), ZMUC C-F-124215 (E), ZMUC C-F-124217 (F–G).

Remarks

First record from Denmark. Danish thalli were immature but identifiable and in agreement with the key by Santamaria (1996c).

Monoicomyces reboleirae Santam. sp. nov.
MB#840608
Fig. 90

Diagnosis

Cell VI darkened and constricted below. Primary appendage and cell III pale yellow. Perithecium asymmetric, bearing a conspicuous horn-like outgrowth near the base of the tip which is distinctly bent.

Etymology

Named after Sofia Reboleira, Portuguese student of millipedes and their fungi, who has actively collaborated in this project.

Type material

Holotype

DENMARK – **Lolland, Falster, Møn (LFM)** • Gedser; 54°33.588′ N, 11°58.187′ E; PF95; on *Gnypeta carbonaria* (Mannerheim, 1830) (Col. Staphylinidae Aleocharinae); 29 Sep. 1895; *F. de Tengnagel Dry0149*; F. de Tengnagel det.; ZMUC C-F-124216.

Description

Thallus amber-coloured, with a blackened foot. Basal cell of receptacle (I) obconical, about 1.5 times as long as broad. Suprabasal cell of receptacle (II) small, triangular to trapezoidal, slightly broader than long. Cell III pale yellowish, cylindrical, 1.5 times as long as broad, sometimes slightly constricted at middle height. Primary septum distinctly constricted (Fig. 90D, a). Each thallus includes two secondary receptacles arising from cell II, including respective antheridia and perithecia or their initials.

Primary appendage unbranched, entirely pale, consisting of up to six cells gradually longer and slenderer from below upwards, not exceeding in length the perithecial apex.

Antheridia pale yellowish, consisting of four superposed tiers of paired cells (Fig. 90E). Each of the four cells of the 2nd and 3rd tiers bear one phialide. The 4th tier bears two short secondary appendages, arising side by side but immediately diverging.

Perithecial stalk cell (VI) about 1.5 times as long as broad, strongly narrower and darker on its lower half, abruptly inflated upwards, then constricted below the perithecial base. Perithecium more deeply pigmented than surroundings, asymmetric in side view, with an inflated venter. A horn-like outgrowth (remains of the trichogyne base) is found on the base of w_3 wall cell tier, on the same side where the perithecium is much convex, pointing upwards and darker than the perithecial venter (Fig. 89C, arrow). Perithecial neck short, poorly distinguished, below a rounded, stout, laterally bent apex.

Length from foot to tip of perithecium 121–151 µm. Perithecium (including basal cells) 67–79 × 31–43 µm. Antheridium (including pedicellar cell, without secondary appendages) 36–44 × 11–14 µm. Maximum length of primary appendage (when undamaged) from primary septum above cell III 86 µm. Length of preapical outgrowth 10–12 µm.

Fig. 90. *Monoicomyces reboleirae* Santam. sp. nov. **A**. A pair of mature thalli. **B**. Mature thallus. **C**. Perithecium in detail with arrow pointing to outgrowth. **D**. Basal area of a thallus in detail showing the primary appendage at left with labelled primary septum (a), the lower receptacle with cells I, II, and III, and the antheridium including labelled stalk (II') and four tiers of cells (t1–4). **E**. Base of a thallus in detail, with labelled cells I, II, III and VI. Scale bars: A–B = 50 µm; C–E = 20 µm. Photographs from slide ZMUC C-F-124216 (holotype).

Thalli were found very concealed in the last retracted segments of the abdomen of the host. Nothing is known about the collecting circumstances of the host.

Remarks

This is a well-distinguished species that grows on the last abdominal segment of its host. Thalli are very small and difficult to be detected. It may be compared with *M. denticulatus* Thaxt. which also has a horned perithecium, but differs by the darkened secondary receptacles lacking secondary appendages. *Monoicomyces denticulatus* was described from Java and Sumatra on *Stenomastax* Cameron, 1933 and *Atheta* (as *Homalota*) (Col. Staphylinidae Aleocharinae) by Thaxter (1915).

Monoicomyces validus Santam. sp. nov.
MB#840609
Fig. 91

Diagnosis

Similar to *M. homalotae* Thaxt., but differing by the dark and constricted cell VI, and by the very stout, rounded, conspicuously convex antheridia, which are 1.5 times as long as broad (not considering the very short secondary appendages), each with four phialides.

Etymology

The species epithet means "stout", because of the stocky antheridia.

Type material

Holotype

DENMARK – **Fyn (F)** • Sprogø; 55°20.012′ N, 10°58.263′ E; PG23; on *Atheta vestita* (Gravenhorst, 1806) (Col. Staphylinidae Aleocharinae); 7 Sep. 2013; *JP 214*; JP det.; ZMUC C-F-122693.

Paratypes

DENMARK – **Lolland, Falster, Møn (LFM)** • Gedser Odde; 54°33.687′ N, 11°57.806′ E; PF95; on *Aleochara grisea* Kraatz, 1856 (Col. Staphylinidae Aleocharinae); 21 Apr. 2019; *JP 1429*; JP det.; ZMUC C-F-123976 • ibid.; on *A. vestita*; ZMUC C-F-123974, C-F-123975. – **Nordvestjylland (NWJ)** • Syd for Stårup; 56°34.792′ N, 9°5.958′ E; NH07; on *A. vestita*; 6 Feb. 2015; *JP 222*; JP det.; ZMUC C-F-122703. – **Nordvestsjælland (NWZ)** • Dybesø ved Rørvig; 55°58.117′ N, 11°45.004′ E; PH70; on *A. vestita*; 17 May 2019; *JP 1465*; JP det.; ZMUC C-F-124045 • Kongstrup Klint på Røsnæs; 55°43.730′ N, 10°58.299′ E; PG27; on *Geostiba circellaris* (Gravenhorst, 1806) (Col. Staphylinidae Aleocharinae); 20–26 Sep. 2014; *JP 236*; JP det.; ZMUC C-F-122716 • Stold Skydeterræn; 55°45.124′ N, 11°17.634′ E; PG48; on *A. vestita*; 25 May 2014; *JP 378*; JP det.; ZMUC C-F-122861.

Description

Thallus amber coloured, with a blackened foot and outer margin of primary appendage. Basal cell of receptacle (I) obconical, often geniculate, about 1.5 times as long as broad, almost entirely dark. Suprabasal cell of receptacle (II) small, triangular to trapezoidal, broader than long. Cell III cylindrical, darkened outwards, supporting the primary appendage and, sometimes, an additional branch borne from the inner side. Usually, each thallus includes two secondary receptacles arising from cell II, including respective perithecia and antheridia.

Primary appendage unbranched or, rarely, once ramified, darkened along its entire outer margin; short to very short, not exceeding in length the perithecial apex.

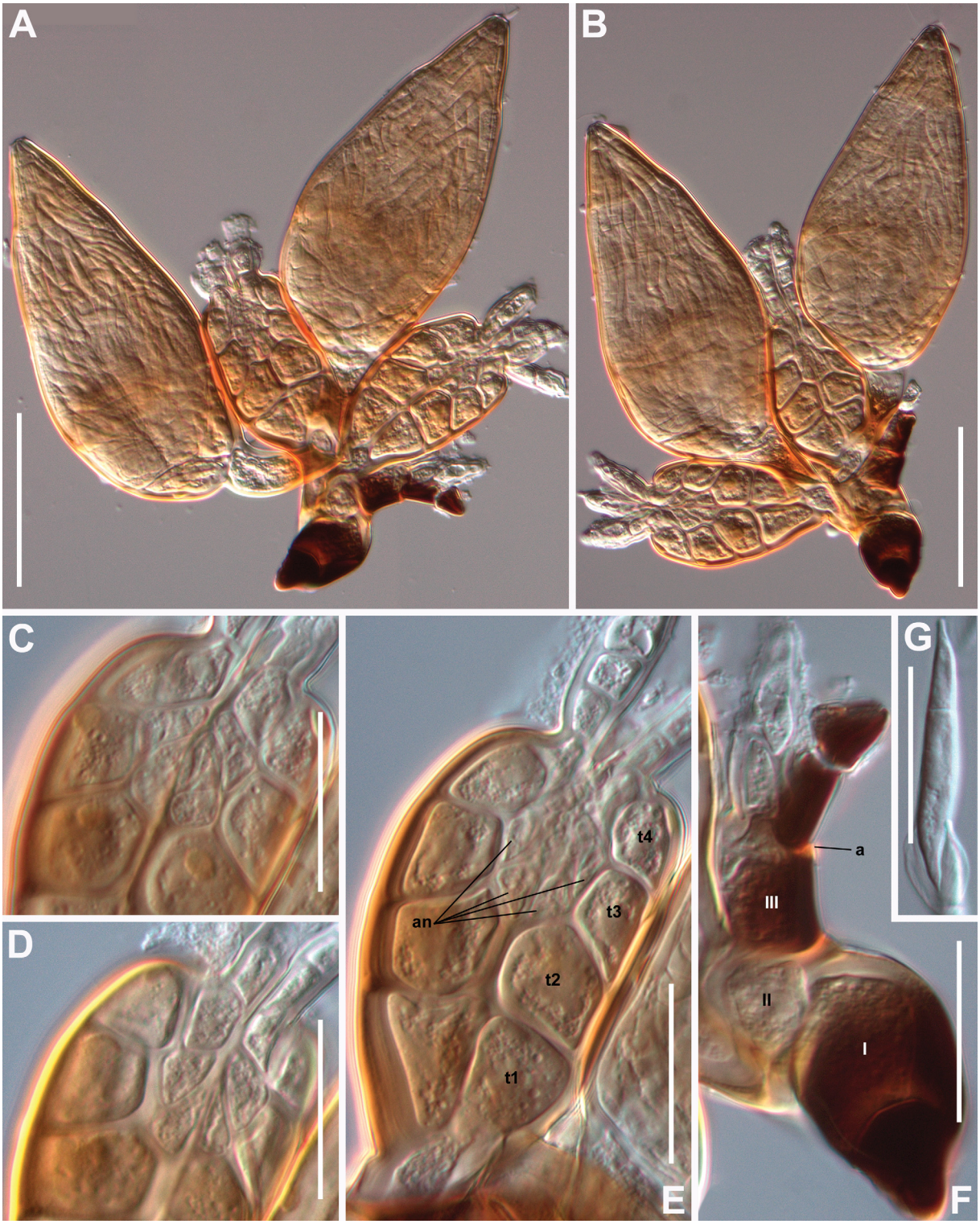

Fig. 91. *Monoicomyces validus* Santam. sp. nov. **A**–**B**. Mature thalli. **C**–**E**. Antheridium at three focusing levels. **C**–**D**. Respectively in near and far focus. **E**. Middle focus in detail with the four tiers of cells (t1–4), and four phialides (an). **F**. Lower receptacle (I, II, and III) and primary appendage in detail above the primary septum (a). **G**. Ascospore. Scale bars: A–B = 50 µm; C–G = 20 µm. Photographs from slide ZMUC C-F-122693 (holotype).

Antheridia consisting of four superposed tiers of paired cells, stout, stocky, rounded in outline, about 1.5 times as long as broad (not considering the secondary appendages). Cells of the four tiers shortening from below upwards. Each of the four cells of 2nd and 3rd tiers bear a phialide. The "sperm cavity" is sealed by four to several cells on both sides. Outer margins strongly convex (Fig. 91C–E). The 4th tier bears 2–4 short, pale secondary appendages.

Perithecial stalk cell (VI) 2–3 times as long as broad, narrower and darkened in its lower half. Perithecia ovoid, symmetrical, with a subacute, pointed apex. Perithecial basal cells (m, n, n') and VII provided with "stigmata". Ascospores with the basal cell (the longer) ending in a conical apex, and the apical cell (the shorter) bearing a rather pointed, but rounded tip (Fig. 91G). The spore wall expands into what will become the forthcoming foot of the thallus in an almost ellipsoidal outline.

Length from foot to tip of perithecium 160–181 µm. Perithecium (including basal cells) 103–116 × 49–52 µm. Antheridium (including pedicellar cell, without secondary appendages) 57–63 × 31–35 µm. Length of primary appendage (when undamaged) from primary septum above cell III 27–73 µm. Ascospores length (including expanded sheath at basal area) 34–35 µm.

Thalli were found on various body parts of the hosts. The hosts were sifted from rotten seaweed on a stony sea shore, from rotten seaweed at the base of a coastal soft clay cliff, from semi-fresh flood debris on a coastal meadow, from moist rotten seaweed on a stony beach, from dry lichens and herbs on sun-exposed sandy ground, and in pitfall traps on a sun-exposed, dry meadow.

Remarks

This species, which belongs to same group of *M. homalotae* (see additional explanations under *M. brachiatus* sp. nov.), may be easily separated at first sight by the stockier antheridia.

Discussion

How many species of "Laboulbeniales" are expected to exist in Denmark? Comparison with other European countries

Danish districts are shown on Fig. 92; Figs 93–94 provide geographical data on Laboulbeniales in Denmark.

On the map of Europe with state boundaries (Fig. 95, bottom) we have included approximate numbers of "Laboulbeniales" species known from each country. These numbers have been acquired from an updated and unpublished Access™ database created by the first author (SS) over more than 30 years ago, where all information from the literature covering these fungi has been constantly updated. This is part of an ongoing project to update the already outdated check-list of European Laboulbeniales (Santamaria *et al.* 1991). For a better understanding and comparison we have also included a map of Europe with the numerical data of Laboulbeniales by country built from the data of Santamaria *et al.* (1991) (Fig. 95, top). This will help us to compare the ranking of knowledge of these fungi in Denmark in comparison with the rest of the countries. The figures for Denmark are quite impressive when compared with other European countries with a large tradition of "floristic" studies, either by monographs, or by a ± long and continuous series of papers. But these "impressive" figures are the result of the degree of investigation, with an entomologist (JP) and a laboulbeniologist (SS) dedicated intensively to this particular project. Countries where laboulbeniologists and entomologists can operate almost full-time are likely to get also "impressive" results. Others, with their so called "floristic" studies, did their best, and will hopefully get there as well.

The European list of Laboulbeniales published by Santamaria *et al.* (1991) recognized 378 taxa (with 356 species and 22 subspecific taxa) and 75 genera. One of the problems of that list was to define the synonymies. According to the time the list was made, a fairly lumping strategy was adopted to avoid the perpetuation of the use of unnecessary names. That compilation included 73 heterotypic synonyms. After three decades, the current number is 507 species (the subspecific taxa are assimilated under the nominal form) and 108 other names including homo- and heterotypic synonyms, as well as infraspecific taxa.

It is important to bear in mind that some countries have changed boundaries or even their integrity along the history, therefore their figures should be taken with care and only as a help to get an approximate idea of what there may be. This especially affects the data from the former Yugoslavia (now divided into seven countries) and the former USSR (now divided into Russia and 13 other countries), but also to other territories as, for example, Austria and Hungary and many adjacent areas belonging to the former Austro-Hungarian Empire before World War I. It has not always been possible for us to establish the actual geographical countries to which old records refer, since in such old literature the localities were often not recorded with excessive precision.

If we make a top ten ranking of countries having the most records of Laboulbeniales species, we will see that Denmark now enters in the fourth position. The countries and numbers are: (1) Spain, 284 spp.; (2)

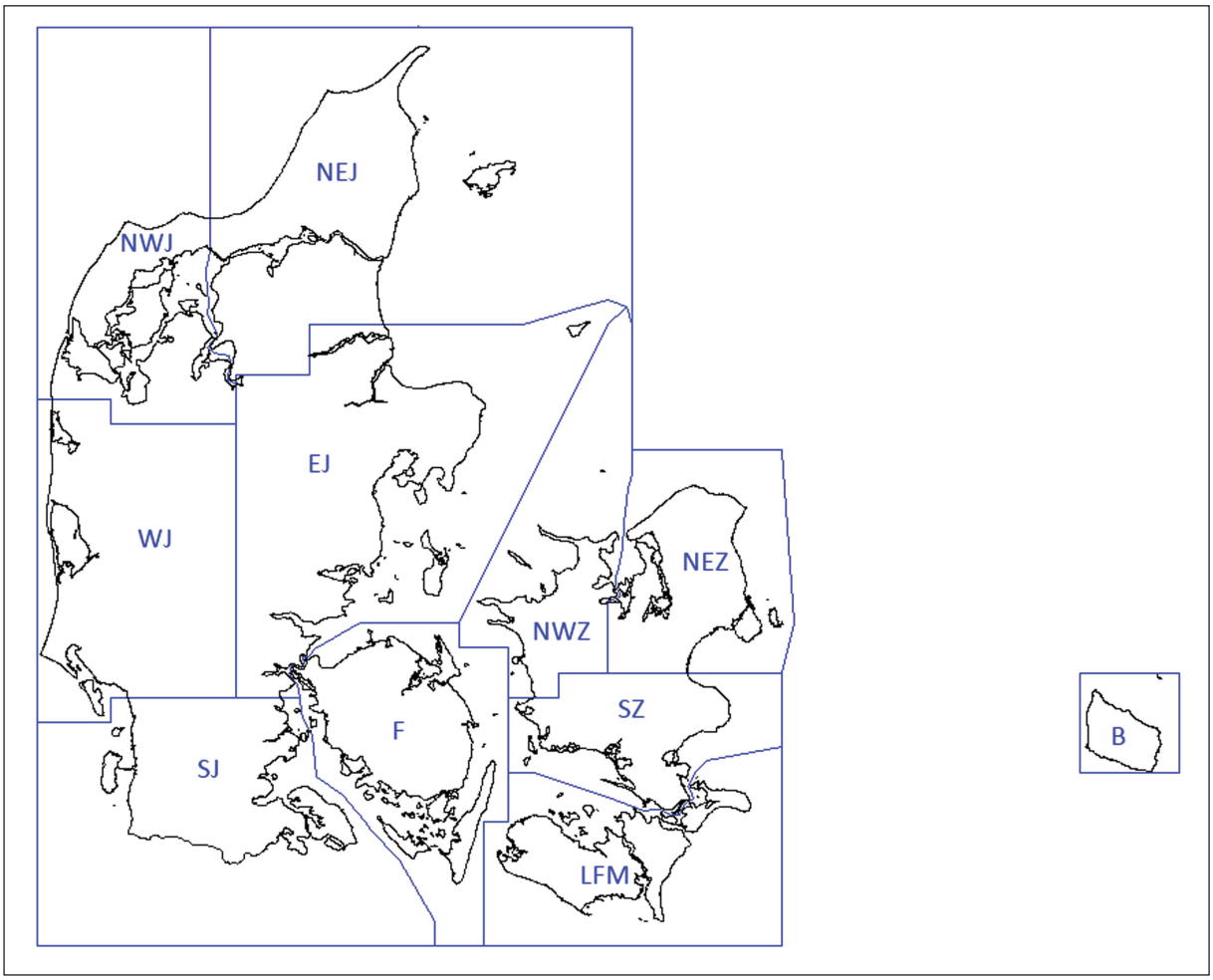

Fig. 92. Danish districts. See the text for abbreviations and names (under Material and methods – Localities).

Poland, 215 spp.; (3) Italy, 213 spp.; (4) Denmark, 195 spp.; (5) France, 160 spp.; (6) United Kingdom, 119 spp.; (7) Belgium, 118 spp.; (8) Germany, 108 spp.; (9) Sweden, 102 spp.; and (10) Hungary, 93 spp. Appendix 1 lists the names of the species reported for these countries which should help us to get an idea of the species that could still be found in Denmark and which species can we expect in the neighboring countries of Denmark.

If we compare the data of these countries with those of Denmark, we can calculate degrees of similarity based on the shared species. Thus, we observe that Belgium and the United Kingdom coincide with Denmark in 83% and 81% of the species, respectively. Neighbouring Germany (74%) and Sweden (79%) also show high degrees of similarity. Poland (65%) and Hungary (68%) maintain reasonable similarity data. As we get closer to southern Europe, the numbers decrease, as with France, where only 60% of the species coincide with those in Denmark. For Spain (46%) and Italy (51%) the similarity data are much lower which is logical given the geographical location, far from Denmark.

It is amazing that we have found 16 undescribed species in Denmark, relatively small in surface area and among the most heavily urbanized countries in the world. However, considering that Laboulbeniomycetes is a severely understudied group of fungi, with only a handful of researchers working on them at any given time, this is perhaps not surprising.

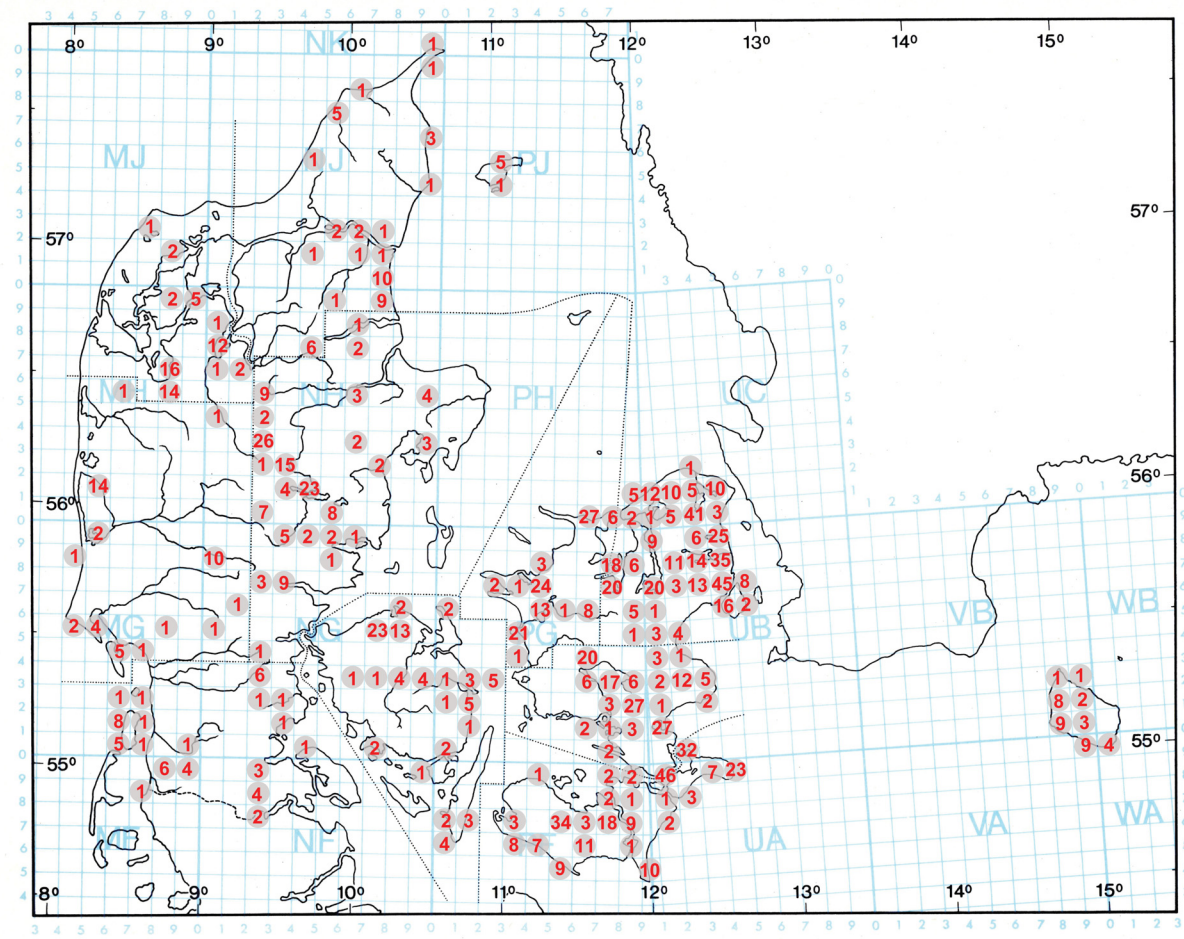

Fig. 93. Number of species of Laboulbeniomycetes in UTM 10×10 km squares.

Which additional species of Laboulbeniales can be expected in Denmark? Where should we direct our research?

It stands to reason that since the European Laboulbeniales list contains 507 species and the Danish list 195, there is still scope for new findings. But the possibilities are highly dependent on the country's "entomological" richness as there are specific arthropod host species that simply do not live in Denmark. To find out if a certain host species is found in Denmark, we have checked Skipper (2017). In other cases we have looked at species lists from neighbouring countries to get an idea of what potential host species occur there which still have not been found in Denmark, but most likely will at some point.

Of the four big insect orders, Lepidoptera does not host Laboulbeniales, and among the Hymenoptera, only ants (Formicidae) are hosts of a few species, but none of these have been found in Denmark. The vast majority of Danish hosts for Laboulbeniales belong to Diptera, with 24 species out of ca 5100 known Danish species (Petersen & Meier 2001), corresponding to 0,5% of the known Danish fauna, and especially Coleoptera (342 species out of ca 3900 known Danish species (Hansen & Jørum 2017), corresponding to 8,8% of the known Danish fauna). This agrees with the fact that worldwide, most Laboulbeniales have been reported from Coleoptera and Diptera, with 90% (80% and 10%, respectively) of the global diversity of these fungi (Weir & Hammond 1997).

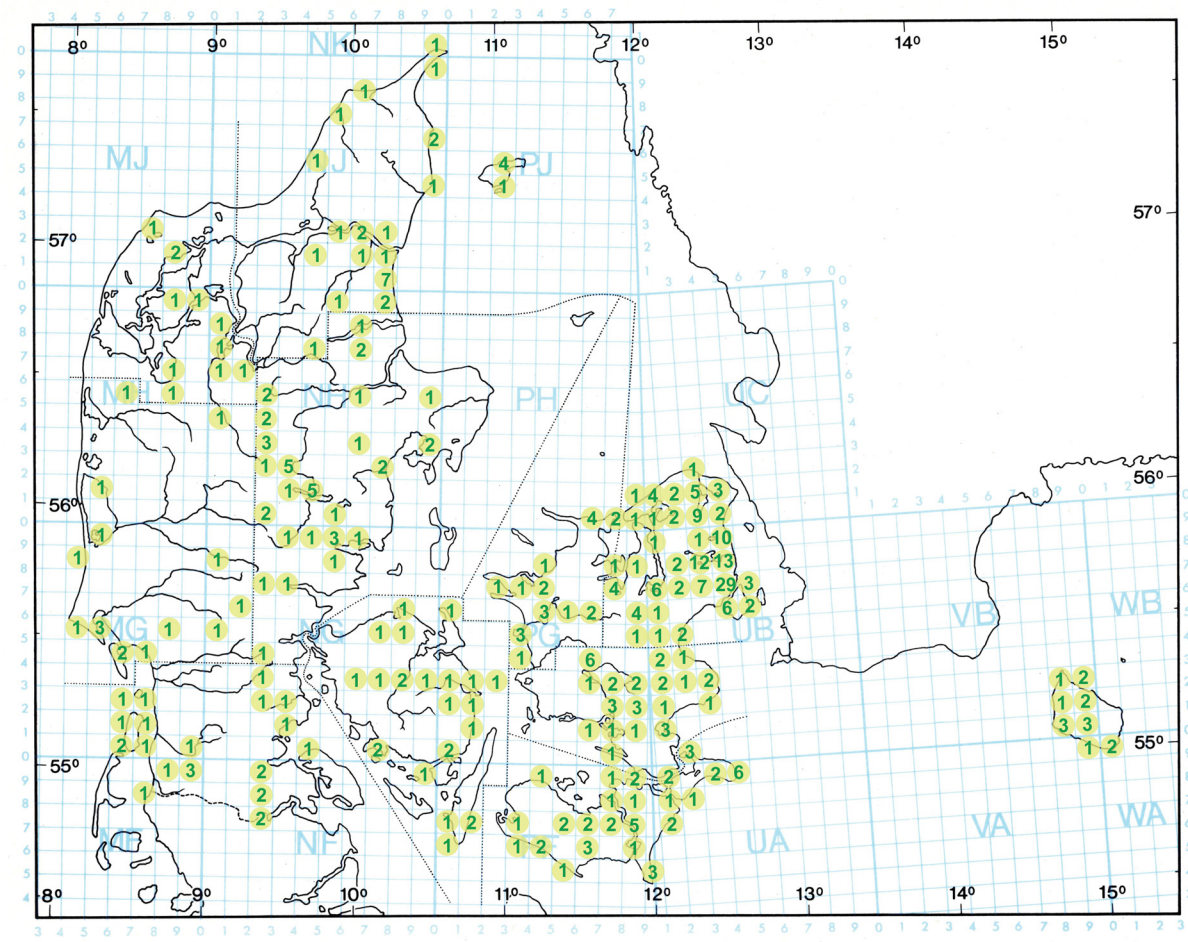

Fig. 94. Number of localities with sampled Laboulbeniomycetes for UTM 10×10 km squares.

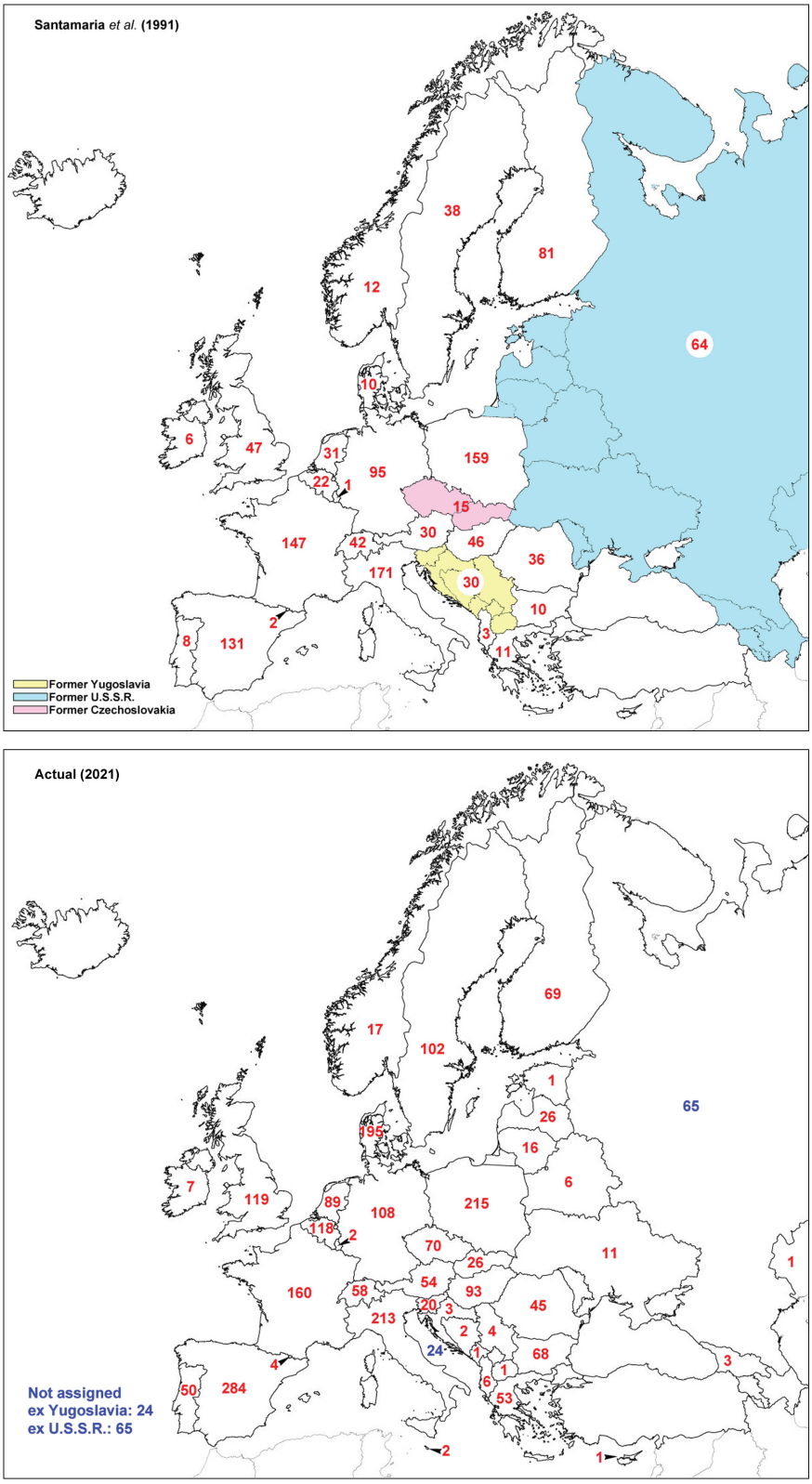

Fig. 95. Political maps of Europe showing the number of species of Laboulbeniomycetes at the moment of the European check-list published in 1991 by Santamaria *et al.* (top), and according to current data (bottom).

Other groups including potential hosts, such as the aquatic Heteroptera Veliidae and Hydrometridae (Gerromorpha) have been examined with no success. Recently collected Hebridae (Heteroptera Gerromorpha) have yielded *Tavaresiella hebri* but no other European species like *Tavaresiella santamariae*, *Triceromyces hebri* and *Rhizopodomyces mexicanus* R.K.Benj. Corixidae (Heteroptera, Nepomorpha) are commonly infected with five species of *Coreomyces* in Europe, three of them have been found in Denmark. The studied cockroaches (Blattodea), hosted the three mostly typical and widespread species of the genus *Herpomyces* (now in Herpomycetales), of the five species existing in Europe. Recently, the study of about a thousand specimens of Phthiraptera (bird lice) have provided some interesting records of *Trenomyces*, and a single member of Dermaptera (Forficulidae) has been found infected with *Distolomyces forficulae* after reviewing hundreds of specimens. Laboulbeniales from Danish millipedes (Diplopoda) have been the subject of special studies (Santamaria *et al.* 2014; Enghoff & Santamaria 2015); three species have been found, but *Rickia dendroiuli* and *Troglomyces manfrediae*, recently recorded from Belgium (De Kesel *et al.* 2020) may also occur. There are many other groups of insects like ants (Hymenoptera, Formicidae), and even other arthropods like mites (Acarina) that should be checked for these fungi in Denmark.

If we compare the data included in Appendix 1, we can see some gaps that can probably be filled with continued search for and study of the appropriate insects in Denmark. We only mention those that perhaps can be considered more likely examples. The genus *Acompsomyces* is represented in Europe with six species, only *A. stenichni* has been found in Denmark; the five species that occur on Cryptophagidae and Lathridiidae beetles are missing, such as *A. atomariae* Thaxt. and *A. pauperculus* Thaxt. on *Atomaria* and *A. ootypi* Santam. on *Ootypus* Ganglbauer, 1899, as well as *A. brunneolus* Thaxt. and *A. corticariae* Thaxt. on *Corticaria* Marsham, 1802. The two species of fungi from *Corticaria* seem to have a fairly southern European distribution, but our experience from this project has shown that there is no obstacle to such southern species occurring in Denmark. Also *Phaulomyces ephistemi* (Thaxter) on *Ephistemus* (Col. Cryptophagidae), a very common and widespread genus, is likely to occur in Denmark. *Amorphomyces italicus* Speg. is a rather common species infesting rove beetles of the genus *Carpelimus* that probably may be found in Denmark.

We should focus on Hydrophilidae beetles belonging to the common genus *Laccobius* to find *Autoicomyces crassus* Speg. and on the likewise common genus *Berosus* to find *A. falcifer* (Thaxt.). Several species of *Colon* Herbst, 1797 (Col. Leiodidae) were reported in Skipper (2017), therefore it would be very interesting to search for *Colonomyces appendiculatus* R.K.Benj., a probably underrecorded species which has been found in the neighbouring countries Sweden (Huggert 1973), Germany (Markovskaja 2004) and Czech Republic (Rossi & Máca 2006). Probably, we also have missed some species of *Corethromyces*, as for example those that occur on Col. Staphylinidae like *Medon* Stephens, 1833 (e.g., *C. laminifer* Thaxt.) and *Scopaeus* Erichson, 1839 (*C. striatus* Santam.); although the genus *Corethromyces* is always a source of surprises and it would not be surprising to find other species that live on other staphylinid genera (as *Pseudomedon* Mulsant & Rey, 1878). *Dimorphomyces tuzsonii* (Bánhegyi) I.I.Tav. is a common species on a less common beetle of the genus *Corticeus* Piller & Mitterpacher, 1783 (Col. Tenebrionidae). Also on members of the same beetle family (Col. Tenebrionidae), *Dimeromyces balazucii* W.Rossi & Cesari and *D. strongylii* Thaxt. on *Scaphidema metallica* (Fabricius, 1792) and *Platydema violacea* (Fabricius, 1790), respectively, two relatively common and widespread species in the southern parts of Denmark, could be found. More Anthicidae beetles should be investigated for additional species of *Dioicomyces. Erichsonius cinerascens* (Gravenhorst, 1802) is a not uncommon staphylinid that has to be searched for *Diplomyces clavifer* W.Rossi & Cesari. The genus *Eucantharomyces* is represented by eight species in Europe, none in Denmark; perhaps *E. stammeri* Scheloske may be found on *Calathus* and *Agonum* (Col. Carabidae), and *E. fennoscandicus* Huldén on *Sericoda* Kirby, 1837 (Col. Carabidae); although we should recognize that all species in this genus of Laboulbeniales are very uncommon. It would also be interesting to look closely at the riparian species of the genus *Stenus* Latreille, 1796 (Col. Staphylinidae Steninae)

in search of *Ilyomyces mairei* F.Picard, especially the *Stenus* species with yellow dots on the elytra, such as *Stenus guttula* Müller, 1821 and *Stenus bimaculatus* Gyllenhal, 1810, since the first author (SS) has only been able to find these fungi on this specific group of *Stenus* species.

The genus *Laboulbenia*, with 107 species in Europe and 47 in Denmark is a particular case. If we review the list of European species and those that are missing in Denmark, we should focus our attention on very specific examples. The genus *Laboulbenia* is reasonably well-represented in Denmark. However, there are species that call our attention due to their absence. It is very unexpected that we have not found *L. fennica* Huldén although a significant number of its possible hosts of the genus *Gyrinus* (Col. Gyrinidae) have been studied, and only *L. gyrinicola* has been collected. Maybe, as a curiosity, *Tachyta nana* (Gyllenhal, 1810), a corticicolous carabid (i.e., living under the bark of tree trunks), should be studied for *L. nana* K.Sugiy. The ripicolous (i.e., living on the banks of rivers and streams) *Zorochros dermestoides* (Herbst, 1806) (Col. Elateridae) should be studied to find the very common and widespread *L. patrata* Speg. Also, it is surprising not to have found *L. proliferans* Thaxt. among the amounts of *Pterostichus* subgenus *Melanius* beetles studied. To end with this massive genus, we should not forget to continue reviewing more species of the genus *Bembidion* (Col. Carabidae) that harbour a plethora of species (e.g., *L. carelica* Huldén, *L. etrusca* Speg. and *L. tenera* T.Majewski) in addition to those we have already found (*L. vulgaris*, *L. pedicellata*, etc.).

There are some species of *Monoicomyces* that still could be searched for in Denmark, as it is a pretty broad genus, of which species inhabit the diverse group of rove beetles of the Athetini tribe. Among these we can mention *M. similis* Thaxt. and *M. zealandicus* Thaxt. The "Almindelig bækløber" is the common Danish name for *Velia caprai* Tamanini, 1947 (Hemiptera Veliidae), a true bug that should be studied for the presence of *Prolixandromyces triandrus* Santam. Although the number of species of *Rhachomyces* in Denmark may seem very low (32 in Europe, only six in Denmark), it should be taken into account that many of the absent species belong to the interesting subterranean habitat, which Denmark lacks. Although the genus *Rickia* is widespread, its species seem to prefer tropical regions, which have the largest known diversity (Weir & Hammond 1997; Santamaria & Espadaler 2015); including 156 species, only 16 occurs in Europe, and five have been found in Denmark; especially *R. wasmannii* Cavara deserves to be mentioned since it is an extremely common and widespread species occurring on ants of the genus *Myrmica* Latreille, 1804, absent until now from Denmark, which is a little strange since it has been searched for in vain at several suitable locations in most of the country. Furthermore the lack of *R. nephanis* Scheloske and *R. ptiliidarum* T.Majewski on two of the smallest beetle species in Denmark, *Nephanes titan* (Newman, 1834) and *Ptiliola kunzei* (Heer, 1841) (Col. Ptiliidae), respectively, is most likely due to their very small size which makes them easily overlooked since the host species are not rare animals. *Rickia* species on mites seem to be very rare and difficult to find but nevertheless it cannot be ruled out that these could also be found in Denmark, especially when it is taken into account that there are four species of this genus found on various Acari species in neighbouring Poland.

The large genus *Stigmatomyces*, specialized on Diptera, includes 156 described species, 49 in Europe, 14 in Denmark. The number of the Danish Funga for this genus is certainly low, and an effort must be made to study more samples of Diptera. We can, for example, search for *S. asteiae* W.Rossi & Cesari on *Asteia* Meigen, 1830 (Asteiidae), *S. baeri* (Knoch) Peyrit. on *Musca* Linnaeus, 1758 (Muscidae), *S. ceratophorus* Whisler on *Fannia* Robineau-Desvoidy, 1830 (Fannidae) and *S. oecotheae* Thaxt. as well as *S. preisleri* W.Rossi on members of the family Heleomyzidae, but above all we should examine a lot more specimens in the diverse and species rich families of Ephydridae and Sphaeroceridae which is where additional species of *Stigmatomyces* are still to be discovered.

It is obvious that the above-mentioned species represent only a relatively small part of the species of Laboulbeniales that can be expected in Denmark, since there are many potential hosts for these fungi.

Taking a look at which species have been found in the nearest neighbouring countries (Belgium, Czech Republic, Germany, Estonia, Finland, Great Britain, Latvia, Lithuania, Norway, Poland, Slovakia, Sweden and the Netherlands), a list of roughly 100 species of fungi results, occurring on many hundreds of host species that already exist in Denmark, many of these are even quite common and widespread. Likewise, there are a number of host species not yet found in Denmark, but which will most likely be found in the foreseeable future. Not least in the light of a very mobile force of skilled collectors and an increasingly warmer climate.

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Appendix 1 (continued on next 16 pages). Species of Laboulbeniales reported in the ten most diverse European countries.

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Acallomyces	***homalotae***									•		**1**
Acompsomyces	***atomariae***							•	•			**2**
Acompsomyces	***brunneolus***								•			**1**
Acompsomyces	***corticariae***								•			**1**
Acompsomyces	***ootypi***								•			**1**
Acompsomyces	***stenichni***		•					•				**2**
Acompsomyces	***pauperculus***			•	•				•	•	•	**5**
Amorphomyces	***falagriae***								•			**1**
Amorphomyces	***hernandoi***								•			**1**
Amorphomyces	***italicus***					•	•	•	•			**4**
Amorphomyces	***ventricosus***		•									**1**
Aphanandromyces	***audisioi***	•	•	•			•	•	•	•	•	**8**
Aporomyces	***szaboi***					•			•			**2**
Arthrorhynchus	***acrandros***						•					**1**
Arthrorhynchus	***diesingii***			•		•	•	•			•	**5**
Arthrorhynchus	***nycteribiae***		•	•		•	•	•	•	•		**7**
Asaphomyces	***cholevae***	•	•	•	•	•	•	•	•	•	•	**10**
Autoicomyces	***aquatilis***		•	•	•	•	•	•	•	•		**8**
Autoicomyces	***crassus***					•	•	•	•			**4**
Autoicomyces	***falcifer***							•	•			**2**
Autoicomyces	***fragilis***						•					**1**
Autoicomyces	***humilis***		•				•					**2**
Autoicomyces	***marginicola***								•			**1**
Bordea	***coronata***						•		•			**2**
Bordea	***denotata***		•									**1**
Botryandromyces	***heteroceri***	•	•	•	•	•	•	•	•	•	•	**10**
Camptomyces	***europaeus***		•				•		•	•		**4**
Cantharomyces	***ancyrophori***			•			•		•			**3**
Cantharomyces	***aploderi***		•									**1**
Cantharomyces	***bledii***							•	•			**2**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Cantharomyces	***bordei***						•		•			**2**
Cantharomyces	***denigratus***	•	•					•	•	•	•	**6**
Cantharomyces	***elongatus***		•									**1**
Cantharomyces	***italicus***	•	•			•	•	•	•	•	•	**8**
Cantharomyces	***numidicus***		•	•			•	•	•	•		**6**
Cantharomyces	***orientalis***	•	•	•	•	•	•	•	•	•	•	**10**
Cantharomyces	***papillatus***		•									**1**
Cantharomyces	***platystethi***	•	•						•	•	•	**5**
Cantharomyces	***robustus***	•						•	•			**3**
Capillistichus	***tenellus***								•			**1**
Ceratomyces	***pyrenaeus***		•						•			**2**
Chaetarthriomyces	***crassiappendicatus***		•		•			•	•	•	•	**6**
Chaetarthriomyces	***spiralis***		•					•	•			**3**
Chitonomyces	***aculeifer***	•	•		•		•	•	•			**6**
Chitonomyces	***bakeri***								•			**1**
Chitonomyces	***bidessarius***		•	•	•	•		•		•		**6**
Chitonomyces	***bullardii***								•			**1**
Chitonomyces	***elongatus***		•				•		•			**3**
Chitonomyces	***ensifer***		•				•	•	•			**4**
Chitonomyces	***hydropori***			•	•	•		•		•		**5**
Chitonomyces	***iriomotensis***								•			**1**
Chitonomyces	***italicus***	•	•		•		•	•	•			**6**
Chitonomyces	***melanurus***	•	•	•	•	•	•	•	•	•	•	**10**
Chitonomyces	***paradoxus***	•	•	•	•	•	•	•	•	•	•	**10**
Chitonomyces	***spinosus***								•			**1**
Chitonomyces	***tylopus***								•			**1**
Colonomyces	***appendiculatus***				•					•		**2**
Compsomyces	***lestevae***	•	•	•			•	•	•	•	•	**8**
Compsomyces	***verticillatus***		•		•		•		•	•		**5**
Coreomyces	***arcuatus***	•	•					•				**3**
Coreomyces	***corixae***		•	•	•	•	•	•	•			**7**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Coreomyces	***curvatus***						●					**1**
Coreomyces	***elongatus***				●	●	●	●				**4**
Coreomyces	***macropus***		●					●	●			**3**
Corethromyces	***apotomi***			●			●		●			**3**
Corethromyces	***bialowiezensis***		●					●				**2**
Corethromyces	***curtipes***								●			**1**
Corethromyces	***henrotii***	●	●	●			●		●			**5**
Corethromyces	***hernandoi***								●			**1**
Corethromyces	***laminifer***								●			**1**
Corethromyces	***obscuristipes***								●			**1**
Corethromyces	***propinquus***			●					●			**2**
Corethromyces	***sardous***						●					**1**
Corethromyces	***scymbalii***						●					**1**
Corethromyces	***stilici***	●	●		●	●	●	●	●	●		**8**
Corethromyces	***striatus***								●			**1**
Corylophomyces	***peyerimhoffii***			●					●			**2**
Corylophomyces	***sericoderi***								●			**1**
Cryptandromyces	***bibloplecti***	●	●					●	●			**4**
Cryptandromyces	***bryaxidis***		●					●	●			**3**
Cryptandromyces	***cryptophagi***		●									**1**
Cryptandromyces	***danicus***		●									**1**
Cryptandromyces	***elegans***	●	●	●	●	●	●	●	●	●	●	**10**
Cryptandromyces	***euplecti***	●	●	●			●		●			**5**
Cucujomyces	***rotundatus***						●	●	●			**3**
Dimeromyces	***adriaticus***						●		●			**2**
Dimeromyces	***balazucii***			●			●	●	●		●	**5**
Dimeromyces	***catalaunicus***								●			**1**
Dimeromyces	***corynetis***		●	●			●	●	●	●	●	**7**
Dimeromyces	***falcatus***			●			●					**2**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Dimeromyces	***leleupii***						●					**1**
Dimeromyces	***longitarsi***			●				●	●		●	**4**
Dimeromyces	***maginii***						●					**1**
Dimeromyces	***oculatus***		●									**1**
Dimeromyces	***oochroti***						●		●			**2**
Dimeromyces	***rossii***								●			**1**
Dimeromyces	***strongylii***			●					●			**2**
Dimorphomyces	***myrmedoniae***	●	●				●	●	●		●	**6**
Dimorphomyces	***phloeoporae***		●					●		●		**3**
Dimorphomyces	***tuzsonii***			●		●	●		●			**4**
Dioicomyces	***anthici***		●	●		●	●	●	●	●	●	**8**
Dioicomyces	***denticulatus***								●			**1**
Dioicomyces	***italicus***						●		●			**2**
Dioicomyces	***ladoi***								●			**1**
Dioicomyces	***leptalei***								●			**1**
Dioicomyces	***myrmecophilus***		●					●				**2**
Dioicomyces	***spiniger***								●			**1**
Dioicomyces	***umbonatus***								●			**1**
Diphymyces	***kaaistoepi***	●										**1**
Diphymyces	***niger***		●	●			●	●	●	●	●	**7**
Diphymyces	***oryoti***						●					**1**
Diphymyces	***urbasoli***								●			**1**
Diplomyces	***clavifer***						●	●	●	●		**4**
Diplopodomyces	***callipodos***			●			●					**2**
Diplopodomyces	***lusitanipodos***								●			**1**
Dipodomyces	***phloeocharidis***		●					●				**2**
Distolomyces	***forficulae***	●	●				●	●	●			**5**
Ecteinomyces	***trichopterophilus***	●	●		●	●	●	●	●	●	●	**9**
Eucantharomyces	***fennoscandicus***								●			**1**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Eucantharomyces	***franzinii***						●					**1**
Eucantharomyces	***introflexus***								●			**1**
Eucantharomyces	***philorhizicola***								●			**1**
Eucantharomyces	***rugatus***								●			**1**
Eucantharomyces	***singilidis***								●			**1**
Eucantharomyces	***spinosus***								●			**1**
Eucantharomyces	***stammeri***	●		●	●	●						**4**
Euceratomyces	***terrestris***								●			**1**
Euhaplomyces	***ancyrophori***										●	**1**
Eumonoicomyces	***papuanus***							●				**1**
Euphoriomyces	***agathidii***		●		●		●	●	●	●		**6**
Euphoriomyces	***bilateralis***								●			**1**
Euphoriomyces	***enghoffii***		●									**1**
Euphoriomyces	***gillerforsii***		●				●		●	●		**4**
Euphoriomyces	***huggertii***		●					●	●			**3**
Euphoriomyces	***liodivorus***		●				●		●	●	●	**5**
Euphoriomyces	***magnicellulatus***		●					●	●			**3**
Euphoriomyces	***rossii***							●	●			**2**
Euphoriomyces	***smicri***		●									**1**
Euphoriomyces	***unilateralis***		●					●	●			**3**
Eusynaptomyces	***benjaminii***				●			●				**2**
Eusynaptomyces	***cornutus***								●			**1**
Eusynaptomyces	***enochri***		●		●			●	●			**4**
Eusynaptomyces	***hydrobii***		●					●				**2**
Euzodiomyces	***lathrobii***	●	●	●	●	●	●	●	●	●	●	**10**
Haplomyces	***texanus***		●	●			●	●	●	●	●	**7**
Helodiomyces	***elegans***	●	●	●	●	●	●	●	●	●	●	**10**
Herpomyces	***ectobiae***	●	●	●		●		●	●			**6**
Herpomyces	***leurolestis***					●						**1**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Herpomyces	***periplanetae***	●	●	●			●	●	●			**6**
Herpomyces	***shelfordellae***					●		●				**2**
Herpomyces	***stylopygae***	●	●			●		●	●			**5**
Hesperomyces	***coccinelloides***	●	●					●	●			**4**
Hesperomyces	***halyziae***	●										**1**
Hesperomyces	***virescens***	●	●	●	●	●	●	●	●	●	●	**10**
Histeridomyces	***europaeus***						●			●		**2**
Homaromyces	***epieri***						●					**1**
Hydraeomyces	***halipli***	●	●	●	●	●	●	●	●	●	●	**10**
Hydrophilomyces	***aduncus***								●			**1**
Hydrophilomyces	***atroseptatus***		●					●	●			**3**
Hydrophilomyces	***coneglianensis***		●		●	●	●	●	●			**6**
Hydrophilomyces	***deflexus***								●			**1**
Hydrophilomyces	***digitatus***		●	●					●	●		**4**
Hydrophilomyces	***gracilis***	●	●					●				**3**
Hydrophilomyces	***hamatus***	●	●					●			●	**4**
Hydrophilomyces	***limnebii***			●			●	●	●	●		**5**
Hydrophilomyces	***pusillus***							●				**1**
Hydrophilomyces	***riberae***								●			**1**
Idiomyces	***peyritschii***	●	●	●	●	●	●	●	●		●	**9**
Ilyomyces	***mairei***								●			**1**
Kainomyces	***rehmanii***	●						●				**2**
Kainomyces	***alutellae***		●									**1**
Laboulbenia	***agelaeae***						●					**1**
Laboulbenia	***anceps***				●	●	●					**3**
Laboulbenia	***anchomenidii***								●			**1**
Laboulbenia	***argutoris***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***asperata***								●			**1**
Laboulbenia	***atlantica***	●		●				●	●		●	**5**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Laboulbenia	***aubryi***	●	●					●	●		●	**5**
Laboulbenia	***balazucii***			●		●				●		**3**
Laboulbenia	***barbara***			●				●				**2**
Laboulbenia	***benjaminii***	●	●	●				●	●	●	●	**7**
Laboulbenia	***biondii***						●	●				**2**
Laboulbenia	***bolivarii***								●			**1**
Laboulbenia	***broscosomae***						●					**1**
Laboulbenia	***cafii***		●	●			●		●	●	●	**6**
Laboulbenia	***calathi***	●	●	●	●		●	●	●		●	**8**
Laboulbenia	***camponoti***						●		●			**2**
Laboulbenia	***cantabrica***								●			**1**
Laboulbenia	***carelica***							●				**1**
Laboulbenia	***chionophila***								●			**1**
Laboulbenia	***clivinalis***	●	●	●	●		●	●	●		●	**8**
Laboulbenia	***coiffaitii***			●			●		●			**3**
Laboulbenia	***collae***	●	●				●	●	●			**5**
Laboulbenia	***coneglianensis***	●	●	●	●	●	●	●	●	●		**9**
Laboulbenia	***contorta***								●	●		**2**
Laboulbenia	***cornuta***		●			●		●	●			**4**
Laboulbenia	***corylophi***		●		●			●				**3**
Laboulbenia	***cristata***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***curtipes***		●					●	●	●		**4**
Laboulbenia	***deltomeri***								●			**1**
Laboulbenia	***dolicaontis***								●			**1**
Laboulbenia	***dubia***	●		●	●		●	●	●		●	**7**
Laboulbenia	***egens***	●	●	●			●	●	●		●	**7**
Laboulbenia	***elaphri***	●	●	●	●			●		●		**6**
Laboulbenia	***elaphricola***					●		●				**2**
Laboulbenia	***endogaea***			●			●					**2**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Laboulbenia	***epithricis***							●				**1**
Laboulbenia	***etrusca***					●	●	●	●	●		**5**
Laboulbenia	***eubradycelli***	●	●	●	●		●	●	●	●	●	**9**
Laboulbenia	***fasciculata***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***fennica***	●						●	●		●	**4**
Laboulbenia	***filifera***				●		●	●		●		**4**
Laboulbenia	***flagellata***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***formicarum***			●		●			●			**3**
Laboulbenia	***giardii***	●	●	●	●	●	●		●	●	●	**9**
Laboulbenia	***gigantea***				●	●	●					**3**
Laboulbenia	***gracilis***						●					**1**
Laboulbenia	***gridellii***						●					**1**
Laboulbenia	***gyrinicola***	●	●	●		●	●	●	●	●	●	**9**
Laboulbenia	***halophila***								●			**1**
Laboulbenia	***hyalopoda***	●	●							●	●	**4**
Laboulbenia	***inexpectata***		●									**1**
Laboulbenia	***inflata***	●	●	●	●	●	●	●	●		●	**9**
Laboulbenia	***kajanensis***	●	●					●				**3**
Laboulbenia	***lecoareri***	●	●	●	●	●		●			●	**7**
Laboulbenia	***leisti***	●	●	●	●	●		●	●	●	●	**9**
Laboulbenia	***lichtensteinii***		●	●					●		●	**4**
Laboulbenia	***littoralis***	●	●	●			●					**4**
Laboulbenia	***luxurians***		●	●	●	●	●	●	●			**7**
Laboulbenia	***macrotheca***			●	●		●	●	●	●		**6**
Laboulbenia	***maghrebiana***								●			**1**
Laboulbenia	***magrinii***						●					**1**
Laboulbenia	***manubriolata***		●					●			●	**3**
Laboulbenia	***marina***			●					●		●	**3**
Laboulbenia	***melanaria***		●	●		●	●	●	●			**6**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Laboulbenia	***metableti***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***mirabilis***						●					**1**
Laboulbenia	***murmanica***	●	●					●			●	**4**
Laboulbenia	***nana***			●				●	●			**3**
Laboulbenia	***nebriae***			●		●	●	●		●	●	**6**
Laboulbenia	***notiophili***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***olisthopi***		●	●	●		●	●	●			**6**
Laboulbenia	***oodiphila***		●				●	●				**3**
Laboulbenia	***ophoni***	●	●	●	●		●	●	●	●	●	**9**
Laboulbenia	***orientalis italica***				●		●		●			**3**
Laboulbenia	***paludosa***			●								**1**
Laboulbenia	***paradoxa***						●					**1**
Laboulbenia	***parriaudii***		●	●					●			**3**
Laboulbenia	***parvula***				●						●	**2**
Laboulbenia	***pasquetii***			●					●			**2**
Laboulbenia	***patrata***			●			●	●	●			**4**
Laboulbenia	***paupercula***							●				**1**
Laboulbenia	***pedicellata***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***peiroleri***			●			●					**2**
Laboulbenia	***philonthi***	●	●	●	●	●	●	●	●		●	**9**
Laboulbenia	***picardii***		●				●		●			**3**
Laboulbenia	***polyphaga***				●					●		**2**
Laboulbenia	***polystichi***			●	●		●		●		●	**5**
Laboulbenia	***proliferans***			●	●	●	●	●	●			**6**
Laboulbenia	***pseudomasei***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***pygidicola***		●									**1**
Laboulbenia	***quarantenae***	●										**1**
Laboulbenia	***rigida***			●				●				**2**
Laboulbenia	***rossii***								●			**1**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Laboulbenia	***rougetii***	●	●	●	●	●	●	●	●	●	●	**10**
Laboulbenia	***santamariae***						●					**1**
Laboulbenia	***scelophila***						●		●			**2**
Laboulbenia	***siagonae***								●			**1**
Laboulbenia	***slackensis***	●	●	●	●		●	●	●		●	**8**
Laboulbenia	***sphaerii***		●					●	●	●		**4**
Laboulbenia	***stenolophi***	●	●	●	●	●	●	●	●		●	**9**
Laboulbenia	***stilicicola***	●	●	●			●	●	●	●	●	**8**
Laboulbenia	***subterranea***			●	●	●	●	●	●	●	●	**8**
Laboulbenia	***temperei***			●								**1**
Laboulbenia	***tenera***							●				**1**
Laboulbenia	***thaxteri***	●	●	●			●	●	●	●	●	**8**
Laboulbenia	***typhlocharidis***								●			**1**
Laboulbenia	***uncinata***			●				●	●			**3**
Laboulbenia	***vulgaris***	●	●	●	●	●	●	●	●	●	●	**10**
Microsomyces	***psammoechi***		●									**1**
Mimeomyces	***zeelandicus***							●	●		●	**3**
Misgomyces	***dyschirii***	●	●	●	●	●	●	●	●	●	●	**10**
Misgomyces	***reicheiae***			●					●			**2**
Misgomyces	***speluncae***								●			**1**
Monoicomyces	***athetae***		●		●			●		●	●	**5**
Monoicomyces	***balazyi***							●				**1**
Monoicomyces	***bolitocharae***	●	●					●			●	**4**
Monoicomyces	***brachiatus***		●									**1**
Monoicomyces	***britannicus***	●	●	●	●	●	●	●	●	●	●	**10**
Monoicomyces	***crassicaulis***		●									**1**
Monoicomyces	***drusillae***		●				●		●			**3**
Monoicomyces	***focarilei***						●					**1**
Monoicomyces	***fragilis***	●	●	●	●			●	●	●	●	**8**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Monoicomyces	***homalotae***	●	●	●	●	●	●	●	●	●	●	**10**
Monoicomyces	***infuscatus***							●	●			**2**
Monoicomyces	***invisibilis***	●	●	●			●	●	●	●	●	**8**
Monoicomyces	***labiatus***							●	●			**2**
Monoicomyces	***matthiatis***	●	●					●				**3**
Monoicomyces	***myllaenae***		●						●			**2**
Monoicomyces	***nigrescens***	●	●		●		●	●	●	●	●	**8**
Monoicomyces	***oxypodae***								●			**1**
Monoicomyces	***reboleirae***		●									**1**
Monoicomyces	***sanctae-helenae***			●	●		●	●	●			**5**
Monoicomyces	***similis***							●	●	●		**3**
Monoicomyces	***validus***		●									**1**
Monoicomyces	***venetus***						●					**1**
Monoicomyces	***zealandicus***								●	●		**2**
Neohaplomyces	***medonalis***								●			**1**
Parvomyces	***merophysiae***								●			**1**
Peyritschiella	***biformis***	●						●	●	●	●	**5**
Peyritschiella	***dubia***	●			●							**2**
Peyritschiella	***furcifera***		●	●	●	●		●	●	●	●	**8**
Peyritschiella	***geminata***							●				**1**
Peyritschiella	***heinemanniana***	●					●		●			**3**
Peyritschiella	***homalotae***						●					**1**
Peyritschiella	***hybrida***		●						●		●	**3**
Peyritschiella	***nigrescens***		●	●	●		●				●	**5**
Peyritschiella	***oxyteli***	●	●	●	●	●	●	●	●	●	●	**10**
Peyritschiella	***princeps***	●	●	●	●	●	●	●	●	●		**9**
Peyritschiella	***protea***			●	●			●	●	●	●	**6**
Peyritschiella	***subinaequilatera***						●		●			**2**
Peyritschiella	***vulgata***		●	●		●	●	●	●		●	**7**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Phaulomyces	***denticulatus***								●			**1**
Phaulomyces	***ephistemi***									●		**1**
Phaulomyces	***euaestheti***		●		●			●				**3**
Phaulomyces	***mediterraneus***			●			●		●			**3**
Phaulomyces	***octotemni***		●					●	●			**3**
Phaulomyces	***perparvus***							●	●			**2**
Phaulomyces	***ptilii***							●				**1**
Phaulomyces	***simplocariae***	●										**1**
Picardella	***endogaea***			●								**1**
Polyascomyces	***trichophyae***									●	●	**2**
Prolixandromyces	***triandrus***			●		●	●		●			**4**
Pseudozeugandromyces	***tachypori***	●										**1**
Rhachomyces	***anophthalmi***						●					**1**
Rhachomyces	***aphaenopsis***			●								**1**
Rhachomyces	***bucciarellii***						●					**1**
Rhachomyces	***canariensis***	●	●	●	●	●	●	●	●	●	●	**10**
Rhachomyces	***fagniezii***			●			●					**2**
Rhachomyces	***furcatus***	●	●	●	●	●	●	●	●	●	●	**10**
Rhachomyces	***girardii***			●					●			**2**
Rhachomyces	***hypogaeus***						●					**1**
Rhachomyces	***ilerdensis***								●			**1**
Rhachomyces	***lasiophorus***	●	●		●	●	●	●			●	**7**
Rhachomyces	***lavagnei***			●			●		●			**3**
Rhachomyces	***maublancii***			●			●					**2**
Rhachomyces	***orotrechorum***						●					**1**
Rhachomyces	***pacei***						●					**1**
Rhachomyces	***peyerimhoffii***					●						**1**
Rhachomyces	***philonthinus***	●	●	●	●	●	●	●	●	●	●	**10**
Rhachomyces	***pilosellus***	●	●	●	●	●	●	●				**7**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Rhachomyces	***proliferans***					●						**1**
Rhachomyces	***pyrenaeus***								●			**1**
Rhachomyces	***reveilletii***			●								**1**
Rhachomyces	***richardii***			●			●					**2**
Rhachomyces	***richardii***						●					**1**
Rhachomyces	***spadiceus***			●								**1**
Rhachomyces	***speluncalis***							●				**1**
Rhachomyces	***spinosus***	●	●						●			**3**
Rhachomyces	***stipitatus***			●			●		●			**3**
Rhachomyces	***tenenbaumii***	●		●		●	●	●	●			**6**
Rhachomyces	***venetianus***						●					**1**
Rhachomyces	***vignae***						●					**1**
Rhadinomyces	***pallidus***	●	●	●	●	●	●	●	●	●	●	**10**
Rhizopodomyces	***mexicanus***								●			**1**
Rhynchophoromyces	***anacaenae***	●	●	●	●	●	●	●	●	●		**9**
Rhynchophoromyces	***helophori***								●			**1**
Rhynchophoromyces	***rostratus***				●	●						**2**
Rickia	***dendroiuli***	●					●				●	**3**
Rickia	***georgii***							●				**1**
Rickia	***huggertii***		●	●			●			●		**4**
Rickia	***hyperborea***			●							●	**2**
Rickia	***laboulbenioides***	●	●				●		●		●	**5**
Rickia	***lenoirii***			●		●						**2**
Rickia	***nephanis***				●							**1**
Rickia	***pachylaelapis***							●				**1**
Rickia	***peyerimhoffii***	●	●	●	●	●	●	●	●	●	●	**10**
Rickia	***polonica***							●				**1**
Rickia	***proteini***	●	●	●				●				**4**
Rickia	***ptiliidarum***							●				**1**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Rickia	***stellata***							●				**1**
Rickia	***uncigeri***		●		●	●		●				**4**
Rickia	***wasmannii***	●		●	●	●	●	●	●		●	**8**
Rickia	***zanettii***						●		●		●	**3**
Rossiomyces	***falcatus***		●				●	●		●	●	**5**
Scepastocarpus	***peritheciiformis***								●			**1**
Siemaszkoa	***annae***							●				**1**
Siemaszkoa	***fennica***		●				●	●	●	●	●	**6**
Siemaszkoa	***flexa***		●					●				**2**
Siemaszkoa	***ptenidii***	●	●		●			●				**4**
Siemaszkoa	***ramificans***		●					●				**2**
Siemaszkoa	***valida***							●				**1**
Smeringomyces	***anomalus***						●		●			**2**
Sphaleromyces	***lathrobii***		●	●				●	●	●	●	**6**
Stichomyces	***conosomatis***	●	●	●			●	●	●	●	●	**8**
Stigmatomyces	***asteiae***						●		●			**2**
Stigmatomyces	***athyroglossae***						●					**1**
Stigmatomyces	***baeri***					●		●				**2**
Stigmatomyces	***biformis***							●			●	**2**
Stigmatomyces	***borbori***								●			**1**
Stigmatomyces	***brevicollis***			●								**1**
Stigmatomyces	***burdigalensis***	●	●	●							●	**4**
Stigmatomyces	***canzonerii***								●			**1**
Stigmatomyces	***carles-tolrae***								●			**1**
Stigmatomyces	***ceratophorus***							●	●			**2**
Stigmatomyces	***chamaemyiae***			●								**1**
Stigmatomyces	***coeniae***			●								**1**
Stigmatomyces	***constrictus***		●		●		●				●	**4**
Stigmatomyces	***crassicollis***	●	●		●		●	●	●		●	**7**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Stigmatomyces	***dichaetae***						●					**1**
Stigmatomyces	***discocerinae***						●		●			**2**
Stigmatomyces	***divergatus***	●	●					●	●			**4**
Stigmatomyces	***entomophilus***		●	●							●	**3**
Stigmatomyces	***ephydrae***		●	●			●				●	**4**
Stigmatomyces	***euconni***			●								**1**
Stigmatomyces	***geomyzae***		●				●		●		●	**4**
Stigmatomyces	***gracilis***						●					**1**
Stigmatomyces	***hydrelliae***		●	●			●	●	●		●	**6**
Stigmatomyces	***latinus***						●					**1**
Stigmatomyces	***limosinae***	●	●				●	●			●	**5**
Stigmatomyces	***majewskii***		●	●	●						●	**4**
Stigmatomyces	***manicatae***						●		●			**2**
Stigmatomyces	***mantis***						●		●			**2**
Stigmatomyces	***micrandrus***						●	●				**2**
Stigmatomyces	***minilimosinae***	●						●	●			**3**
Stigmatomyces	***oecotheae***						●					**1**
Stigmatomyces	***papuanus***			●			●		●			**3**
Stigmatomyces	***parydrae***								●			**1**
Stigmatomyces	***platensis***	●	●				●	●				**4**
Stigmatomyces	***ptilomyiae***			●			●					**2**
Stigmatomyces	***purpureus***		●	●			●	●	●		●	**6**
Stigmatomyces	***rugosus***			●		●	●		●			**4**
Stigmatomyces	***scaptomyzae***		●	●	●		●	●	●			**6**
Stigmatomyces	***spiralis***			●			●		●			**3**
Stigmatomyces	***succini***				●							**1**
Stigmatomyces	***thoracochaetae***		●									**1**
Stigmatomyces	***trianguliapicalis***						●	●	●		●	**4**
Stigmatomyces	***venetus***				●		●					**2**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Symplectromyces	***vulgaris***	●	●	●	●	●	●	●	●	●	●	**10**
Synandromyces	***sinensis***								●			**1**
Synandromyces	***telephani***							●	●			**2**
Tanmaurkiella	***huggertii***		●									**1**
Tanmaurkiella	***pselaphi***		●									**1**
Tavaresiella	***hebri***		●					●	●			**3**
Tavaresiella	***santamariae***							●	●			**2**
Teratomyces	***actobii***	●	●	●	●	●	●	●	●	●	●	**10**
Teratomyces	***mirificus***					●	●		●			**3**
Teratomyces	***philonthi***	●	●	●	●	●	●	●	●		●	**9**
Teratomyces	***quedianus***					●						**1**
Thripomyces	***italicus***		●				●		●			**3**
Thripomyces	***tessinensis***							●				**1**
Trenomyces	***aquaticus***				●							**1**
Trenomyces	***circinans***				●			●				**2**
Trenomyces	***gibbus***							●				**1**
Trenomyces	***histophthorus***		●	●	●		●	●				**5**
Trenomyces	***thaxteri***				●							**1**
Triceromyces	***balazucii***							●				**1**
Triceromyces	***benjaminii***								●			**1**
Triceromyces	***hebri***								●			**1**
Triceromyces	***hydrometrae***						●		●			**2**
Triceromyces	***poissonii***			●								**1**
Troglomyces	***botryandrus***						●					**1**
Troglomyces	***manfrediae***	●					●		●			**3**
Troglomyces	***pusillus***								●			**1**
Troglomyces	***rossii***						●				●	**2**
Troglomyces	***triandrus***	●	●	●	●				●			**5**
Zeugandromyces	***orientalis***								●			**1**

		Belgium	**Denmark**	France	Germany	Hungary	Italy	Poland	Spain	Sweden	United Kingdom	**No. of Countries**
Zodiomyces	***subseriatus***							●				**1**
Zodiomyces	***vorticellarius***	●	●	●	●	●	●	●	●	●	●	**10**
Total spp. (A)		**118**	**195**	**160**	**108**	**93**	**212**	**215**	**283**	**102**	**119**	
Spp. also in DK (B)		98	195	96	80	63	110	141	132	81	96	
% Similarity spp. in DK (B/A×100)		**83**	100	**60**	**74**	**68**	**52**	**65**	**47**	**79**	**81**	
Ranking		**7**	**4**	**5**	**8**	**10**	**3**	**2**	**1**	**9**	**6**	

Appendix 2 (continued on next 4 pages). Hosts with Laboulbeniomycetes in Denmark (*only from literature, see Table 1; • from H. Enghoff, pers. comm.).

HOST	FUNGUS
Blattodea, Blattidae	
Periplaneta americana	*Herpomyces periplanetae*
Periplaneta australasia	*Herpomyces periplanetae*
Blatella germanica	*Herpomyces ectobiae*
Blatta orientalis	*Herpomyces stylopigae*
Coleoptera, Anthicidae	
Omonadus formicarius	*Dioicomyces anthici*
Coleoptera, Carabidae	
Acupalpus dubius	*Laboulbenia inflata*
	Rhachomyces lasiophorus
Acupalpus exiguus	*Laboulbenia inexpectata* sp. nov.
	Laboulbenia inflata
	Laboulbenia stenolophi
	Rhachomyces lasiophorus
Acupalpus flavicollis	*Laboulbenia inflata*
	Laboulbenia stenolophi
	Rhachomyces lasiophorus
Acupalpus parvulus	*Laboulbenia stenolophi*
Agonum emarginatum	*Laboulbenia flagellata*
Agonum fuliginosum	*Laboulbenia flagellata*
Agonum gracile	*Laboulbenia flagellata*
Agonum marginatum	*Laboulbenia flagellata*
Agonum micans	*Laboulbenia flagellata*
Agonum muelleri	*Laboulbenia flagellata*
Agonum piceum	*Laboulbenia flagellata*
Agonum thoreyi	*Laboulbenia flagellata*
Agonum viduum	*Laboulbenia flagellata*
Amara apricaria	*Laboulbenia ophoni*
Amara municipalis	*Laboulbenia aubryi*
Anchomenus dorsalis	*Laboulbenia flagellata*
Anisodactylus binotatus	*Laboulbenia coneglianensis*
	Laboulbenia flagellata
Anthracus consputus	*Rhachomyces lasiophorus*
Asaphidion curtum	*Laboulbenia thaxteri*
Badister bullatus	*Laboulbenia benjaminii*
Badister dilatatus	*Laboulbenia benjaminii*
Badister dorsiger	*Laboulbenia benjaminii*
Badister lacertosus	*Laboulbenia benjaminii*
Badister peltatus	*Laboulbenia benjaminii*
Badister sodalis	*Laboulbenia benjaminii*
Bembidion aeneum	*Laboulbenia pedicellata*
	Laboulbenia vulgaris
Bembidion assimile	*Laboulbenia curtipes*
	Laboulbenia murmanica
	Laboulbenia pedicellata
	Laboulbenia vulgaris
Bembidion biguttatum	*Laboulbenia pedicellata*
	Laboulbenia vulgaris
Bembidion bruxellense	*Laboulbenia vulgaris*
Bembidion dentellum	*Laboulbenia luxurians*
	Laboulbenia vulgaris
Bembidion doris	*Laboulbenia murmanica*
	Laboulbenia pedicellata
Bembidion femoratum	*Laboulbenia vulgaris*
Bembidion gilvipes	*Laboulbenia pedicellata*
Bembidion guttula	*Laboulbenia pedicellata*
	Laboulbenia vulgaris
Bembidion illigeri	*Laboulbenia pedicellata*
Bembidion lampros	*Laboulbenia vulgaris*
	**Laboulbenia pedicellata*
Bembidion lunulatum	*Laboulbenia pedicellata*
	Laboulbenia vulgaris
Bembidion mannerheimii	*Laboulbenia curtipes*
	Laboulbenia pedicellata
	Laboulbenia vulgaris
Bembidion minimum	*Laboulbenia pedicellata*
Bembidion normannum	*Laboulbenia pedicellata*
Bembidion obtusum	*Laboulbenia vulgaris*
Bembidion quadrimaculatum	*Laboulbenia pedicellata*
Bembidion stephensii	*Laboulbenia vulgaris*
Bembidion tetracolum	*Laboulbenia vulgaris*
Bembidion varium	*Laboulbenia cornuta*
	Laboulbenia curtipes
	Laboulbenia luxurians
	Laboulbenia murmanica
	Laboulbenia pedicellata
Brachinus crepitans	*Laboulbenia rougetii*
Bradycellus caucasicus	*Laboulbenia eubradycelli*
Bradycellus csikii	*Laboulbenia eubradycelli*
Bradycellus harpalinus	*Laboulbenia eubradycelli*
Bradycellus ruficollis	*Laboulbenia eubradycelli*
Bradycellus verbasci	*Laboulbenia eubradycelli*
Calathus cinctus	*Laboulbenia calathi*
Calathus fuscipes	*Laboulbenia calathi*
Calathus melanocephalus	*Laboulbenia calathi*
Calathus micropterus	*Laboulbenia calathi*
Cillenus lateralis	*Laboulbenia lichtensteinii*
Clivina fossor	*Laboulbenia clivinalis*
Demetrias imperialis	*Laboulbenia notiophili*
Diachromus germanus	*Laboulbenia melanaria*
Dicheirotrichus gustavii	*Laboulbenia giardii*
Dyschirius globosus	*Laboulbenia pedicellata*
	Misgomyces dyschirii
Dyschirius salinus	*Misgomyces dyschirii*
Dyschirius tristis	*Laboulbenia pedicellata*
	Misgomyces dyschirii
Elaphropus parvulus	*Laboulbenia egens*
Elaphrus cupreus	*Laboulbenia elaphri*
Epaphius secalis	*Laboulbenia vulgaris*
	Rhachomyces canariensis
Harpalus affinis	*Laboulbenia coneglianensis*
	Laboulbenia flagellata
	Laboulbenia ophoni
Harpalus griseus	*Laboulbenia coneglianensis*
Harpalus latus	*Laboulbenia coneglianensis*
Harpalus rubripes	*Laboulbenia ophoni*
Leistus ferrugineus	*Laboulbenia leisti*
**Leistus terminatus*	*Laboulbenia eubradycelli*?
Loricera pilicornis	*Laboulbenia flagellata*
Nebria brevicollis	*Laboulbenia flagellata*
	**Laboulbenia pseudomasei*?
Notiophilus aestuans	*Laboulbenia notiophili*
Notiophilus biguttatus	*Laboulbenia notiophili*
Notiophilus germinyi	*Laboulbenia notiophili*
Notiophilus palustris	*Laboulbenia notiophili*
Notiophilus rufipes	*Laboulbenia notiophili*
Olisthopus rotundatus	*Laboulbenia olisthopi*
Oodes helopioides	*Laboulbenia oodiphila*
Ophonus melletii	*Laboulbenia ophoni*
Ophonus puncticeps	*Laboulbenia ophoni*
Ophonus rufibarbis	*Laboulbenia ophoni*
Ophonus rupicola	*Laboulbenia ophoni*
Oxypselaphus obscurus	*Laboulbenia flagellata*

HOST	FUNGUS
Paradromius linearis	*Laboulbenia hyalopoda*
	Laboulbenia notiophili
Paranchus albipes	*Laboulbenia collae*
	Laboulbenia flagellata
Patrobus atrorufus	*Laboulbenia fasciculata*
Perigona nigriceps	*Laboulbenia manubriolata*
Philorhizus melanocephalus	*Laboulbenia notiophili*
Philorhizus sigma	*Laboulbenia notiophili*
Platynus assimilis	*Laboulbenia flagellata*
Platynus livens	*Laboulbenia flagellata*
Pogonus chalceus	*Laboulbenia slackensis*
Porotachys bisulcatus	*Laboulbenia picardii*
Pterostichus diligens	*Laboulbenia argutoris*
	Laboulbenia kajanensis
Pterostichus minor	*Laboulbenia pseudomasei*
Pterostichus nigrita	*Laboulbenia pseudomasei*
Pterostichus oblongopunctatus	*Laboulbenia flagellata*
Pterostichus rhaeticus	*Laboulbenia fasciculata*
	Laboulbenia pseudomasei
Pterostichus strenuus	*Laboulbenia argutoris*
Pterostichus vernalis	*Laboulbenia flagellata*
Stenolophus mixtus	*Laboulbenia stenolophi*
Stenolophus teutonus	*Laboulbenia stenolophi*
Syntomus foveatus	*Laboulbenia metableti*
	Rhachomyces spinosus
Syntomus truncatellus	*Laboulbenia metableti*
	Laboulbenia pygidicola
Trechoblemus micros	*Laboulbenia lecoareri*
Trechus obtusus	*Laboulbenia vulgaris*
	Rhachomyces canariensis
Trechus quadristriatus	*Laboulbenia vulgaris*
	Rhachomyces canariensis
Trichocellus cognatus	*Laboulbenia eubradycelli*
Trichocellus placidus	*Laboulbenia eubradycelli*
Coleoptera, Chrysomelidae	
Longitarsus luridus	*Dimeromyces oculatus*
Coleoptera, Ciidae	
Octotemnus glabriculus	*Phaulomyces octotemni*
Coleoptera, Cleridae	
Necrobia ruficollis	*Dimeromyces corynetis*
Coleoptera, Coccinellidae	
Adalia bipunctata	*Hesperomyces virescens*
Stethorus pusillus	*Hesperomyces coccinelloides*
Coleoptera, Corylophidae	
Corylophus cassidoides	*Laboulbenia corylophi*
Coleoptera, Cryptophagidae	
Cryptophagus distinguendus	*Cryptandromyces cryptophagi* sp. nov.
	Rossiomyces falcatus
Coleoptera, Dryopidae	
Dryops auriculatus	*Cantharomyces denigratus*
	Helodiomyces elegans
Dryops griseus	*Helodiomyces elegans*
Dryops luridus	*Cantharomyces denigratus*
	Cantharomyces italicus
	Helodiomyces elegans
Dryops similaris	*Cantharomyces denigratus*
	Cantharomyces italicus

HOST	FUNGUS
	Helodiomyces elegans
Coleoptera, Dytiscidae	
Graptodytes bilineatus	*Chitonomyces aculeifer*
Hygrotus inaequalis	*Chitonomyces bidessarius*
Laccophilus minutus	*Chitonomyces elongatus*
	Chitonomyces ensifer
	Chitonomyces italicus
	Chitonomyces melanurus
	Chitonomyces paradoxus
Coleoptera, Gyrinidae	
Gyrinus caspius	*Laboulbenia gyrinicola*
Gyrinus distinctus	*Laboulbenia gyrinicola*
Gyrinus marinus	*Laboulbenia gyrinicola*
Gyrinus paykulli	*Laboulbenia gyrinicola*
Gyrinus substriatus	*Laboulbenia gyrinicola*
Gyrinus suffriani	*Laboulbenia gyrinicola*
Coleoptera, Haliplidae	
Haliplus apicalis	*Hydraeomyces halipli*
Haliplus immaculatus	*Hydraeomyces halipli*
Haliplus ruficollis	*Chitonomyces aculeifer*
	Hydraeomyces halipli
Coleoptera, Heteroceridae	
Augyles hispidulus	*Botryandromyces heteroceri*
Heterocerus fenestratus	*Botryandromyces heteroceri*
Heterocerus obsoletus	*Botryandromyces heteroceri*
Coleoptera, Hydraenidae	
Hydraena riparia	*Thripomyces italicus*
Limnebius aluta	*Hydrophilomyces atroseptatus*
Ochthebius marinus	*Hydrophilomyces digitatus*
Coleoptera, Hydrochidae	
Hydrochus crenatus	*Autoicomyces aquatilis*
	Autoicomyces humilis
Coleoptera, Hydrophilidae	
Anacaena limbata	*Rhynchophoromyces anacaenae*
Cercyon littoralis	*Hydrophilomyces gracilis*
	Hydrophilomyces hamatus
Cercyon marinus	*Hydrophilomyces gracilis*
Chaetarthria seminulum	*Chaetarthriomyces crassiappendicatus*
	Chaetarthriomyces spiralis
Enochrus coarctatus	*Eusynaptomyces enochri*
Helochares obscurus	*Zodiomyces vorticellarius*
Hydrobius rottenbergii	*Ceratomyces pyrenaeus*
	Eusynaptomyces hydrobii
Laccobius minutus	*Hydrophilomyces coneglianensis*
Coleoptera, Kateretidae	
Brachypterus urticae	*Aphanandromyces audisioi*
Coleoptera, Leiodidae	
Agathidium atrum	*Euphoriomyces unilateralis*
Agathidium convexum	*Euphoriomyces agathidii*
Agathidium laevigatum	*Euphoriomyces agathidii*
Agathidium rotundatum	*Euphoriomyces agathidii*
Agathidium seminulum	*Euphoriomyces unilateralis*
Agathidium varians	*Euphoriomyces agathidii*
Apocatops nigrita	*Asaphomyces cholevae*
Catops coracinus	*Asaphomyces cholevae*
Catops fuliginosus	*Asaphomyces cholevae*

HOST	FUNGUS
Catops morio	*Asaphomyces cholevae*
Catops nigricans	*Asaphomyces cholevae*
Catops nigriclavis	*Asaphomyces cholevae*
Catops picipes	*Asaphomyces cholevae*
Catops tristis	*Asaphomyces cholevae*
Choleva agilis	*Corethromyces henrotii*
Choleva fagniezi	*Corethromyces henrotii*
Choleva jeanneli	*Corethromyces henrotii*
Choleva oblonga	*Corethromyces henrotii*
Colenis immunda	*Euphoriomyces gillerforsii*
Fissocatops westi	*Asaphomyces cholevae*
Hydnobius multistriatus	*Euphoriomyces magnicellulatus*
Hydnobius punctatus	*Euphoriomyces magnicellulatus*
Leiodes badia	*Euphoriomyces liodivorus*
Leiodes calcarata	*Euphoriomyces enghoffii* sp. nov.
	Euphoriomyces liodivorus
Leiodes ciliaris	*Euphoriomyces liodivorus*
Leiodes ferruginea	*Euphoriomyces liodivorus*
Leiodes furva	*Euphoriomyces liodivorus*
Leiodes gallica	*Euphoriomyces liodivorus*
Leiodes longipes	*Euphoriomyces liodivorus*
Leiodes picea	*Euphoriomyces liodivorus*
Leiodes rufipennis	*Euphoriomyces liodivorus*
Leiodes rugosa	*Euphoriomyces enghoffii* sp. nov.
Leiodes triepkei	*Euphoriomyces liodivorus*
Ptomaphagus sericatus	*Diphymyces niger*
Ptomaphagus subvillosus	*Diphymyces niger*
**Ptomaphagus variicornis*	*Diphymyces niger*
Coleoptera, Ptiliidae	
Acrotrichis atomaria	*Ecteinomyces trichopterophilus*
Acrotrichis brevipennis	*Ecteinomyces trichopterophilus*
Acrotrichis cognata	*Ecteinomyces trichopterophilus*
Acrotrichis danica	*Ecteinomyces trichopterophilus*
Acrotrichis fascicularis	*Ecteinomyces trichopterophilus*
Acrotrichis grandicollis	*Ecteinomyces trichopterophilus*
Acrotrichis intermedia	*Ecteinomyces trichopterophilus*
Acrotrichis montandonii	*Ecteinomyces trichopterophilus*
Acrotrichis sitkaensis	*Ecteinomyces trichopterophilus*
Acrotrichis thoracica	*Ecteinomyces trichopterophilus*
Ptenidium fuscicorne	*Siemaszkoa flexa*
	Siemaszkoa ptenidii
Ptenidium intermedium	*Siemaszkoa fennica*
	Siemaszkoa flexa
	Siemaszkoa ptenidii
Ptenidium laevigatum	*Siemaszkoa fennica*
Ptenidium pusillum	*Siemaszkoa fennica*
	Siemaszkoa flexa
	Siemaszkoa ptenidii
Ptenidium turgidum	*Siemaszkoa fennica*
	Siemaszkoa ramificans
Smicrus filicornis	*Euphoriomyces smicri* sp. nov.
Coleoptera, Silvanidae	
Psammoecus bipunctatus	*Microsomyces psammoeci*
Coleoptera, Sphaeriusidae	
Sphaerius acaroides	*Laboulbenia sphaerii*
Coleoptera, Staphylinidae	
Acrotona aterrima	*Monoicomyces britannicus*
Acrotona fungi	*Monoicomyces britannicus*
Acrotona pseudotenera	*Monoicomyces britannicus*
Acrulia inflata	*Euphoriomyces huggertii*
Aleochara grisea	*Monoicomyces validus* sp. nov.

HOST	FUNGUS
Aloconota gregaria	*Monoicomyces homalotae*
Aloconota sulcifrons	*Monoicomyces britannicus*
Anotylus inustus	*Monoicomyces invisibilis*
Anotylus rugifrons	*Peyritschiella oxyteli* comb. nov.
Anotylus rugosus	*Peyritschiella oxyteli* comb. nov.
Anotylus sculpturatus	*Monoicomyces invisibilis*
Aploderus caesus	*Cantharomyces aploderi*
Astenus gracilis	*Camptomyces europaeus*
	Compsomyces verticillatus
Atheta castanoptera	*Monoicomyces homalotae*
Atheta graminicola	*Monoicomyces homalotae*
Atheta longicornis	*Monoicomyces britannicus*
Atheta melanocera	*Monoicomyces homalotae*
Atheta pallidicornis	*Monoicomyces homalotae*
Atheta picipes	*Monoicomyces athetae*
Atheta sodalis	*Monoicomyces brachiatus* sp. nov.
Atheta triangulum	*Monoicomyces homalotae*
Atheta vestita	*Monoicomyces validus*
Atheta volans	*Monoicomyces britannicus*
Bibloplectus ambiguus	*Cryptandromyces bibloplecti*
	Cryptandromyces euplecti
Bibloporus minutus	*Bordea denotata*
Bisnius cephalotes	*Peyritschiella princeps*
Bisnius fimetarius	*Rhachomyces philonthinus*
Bisnius parcus	*Peyritschiella princeps*
Bisnius sordidus	*Peyritschiella princeps*
Bisnius subuliformis	*Peyritschiella princeps*
Bledius diota	*Haplomyces texanus*
Bledius dissimilis	*Haplomyces texanus*
Bledius femoralis	*Haplomyces texanus*
Bledius fergussoni	*Laboulbenia parriaudii*
Bledius furcatus	*Haplomyces texanus*
Bledius gallicus	*Haplomyces texanus*
Bledius longulus	*Haplomyces texanus*
Bledius occidentalis	*Haplomyces texanus*
Bledius opacus	*Haplomyces texanus*
Bledius pallipes	*Haplomyces texanus*
Bledius terebrans	*Cantharomyces papillatus* sp. nov.
Bledius tricornis	*Haplomyces texanus*
Bolitochara obliqua	*Monoicomyces bolitocharae*
Brachygluta fossulata	*Cryptandromyces elegans*
Brachygluta helferi	*Cryptandromyces elegans*
Bryaxis bulbifer	*Cryptandromyces bryaxidis*
Bryaxis puncticollis	*Cryptandromyces bryaxidis*
Cafius xantholoma	*Laboulbenia littoralis*
Carpelimus bilineatus	*Cantharomyces orientalis*
Carpelimus corticinus	*Cantharomyces orientalis*
Carpelimus elongatulus	*Cantharomyces orientalis*
Carpelimus erichsoni	*Cantharomyces orientalis*
Carpelimus foveolatus	*Cantharomyces orientalis*
Deleaster dichrous	*Idiomyces peyritschii*
Dilacra luteipes	*Monoicomyces nigrescens*
Dilacra vilis	*Dimorphomyces myrmedoniae*
Dinaraea aequata	*Monoicomyces fragilis*
Dinaraea angustula	*Monoicomyces fragilis*
Drusilla canaliculata	*Monoicomyces drusillae*
Erichsonius cinerascens	*Teratomyces actobii*
Euaesthetus ruficapillus	*Phaulomyces euaestheti*
Euconnus wetterhallii	*Cryptandromyces danicus* sp. nov.
	**Stigmatomyces euconni*?
Euplectus kirbii	*Cryptandromyces euplecti*
Gabrius breviventer	*Teratomyces philonthi*
Geostiba circellaris	*Monoicomyces homalotae*
	Monoicomyces validus sp. nov.
Gnypeta carbonaria	*Monoicomyces reboleirae* sp. nov.
Gyrohypnus angustatus	*Kainomyces isomali*

HOST	FUNGUS
Lathrobium brunnipes	*Euzodiomyces lathrobii*
	Rhadinomyces pallidus
Lathrobium elongatum	*Euzodiomyces lathrobii*
Lathrobium fulvipenne	*Rhachomyces pilosellus*
	Rhadinomyces pallidus
Lathrobium geminum	*Euzodiomyces lathrobii*
	Rhachomyces pilosellus
	Rhadinomyces pallidus
Lathrobium impressum	*Euzodiomyces lathrobii*
Lathrobium lineatocolle	*Euzodiomyces lathrobii*
Lathrobium longulum	*Euzodiomyces lathrobii*
Lesteva pubescens	*Compsomyces lestevae*
Lesteva sicula	*Compsomyces lestevae*
Myllaena elongata	*Monoicomyces myllaenae*
Myrmecocephalus concinnus	*Amorphomyces ventricosus* sp. nov.
Ocalea concolor	*Monoicomyces fragilis*
Ocalea picata	*Monoicomyces fragilis*
Ocalea rivularis	*Monoicomyces fragilis*
Ocyusa picina	*Monoicomyces brachiatus* sp. nov.
Omalium riparium	*Rickia huggertii*
Othius angustus	*Rhachomyces furcatus*
Othius punctulatus	*Rhachomyces furcatus*
Othius subuliformis	*Rhachomyces furcatus*
Oxypoda elongatula	*Monoicomyces crassicaulis* sp. nov.
Oxytelus fulvipes	*Monoicomyces invisibilis*
Paederus riparius	*Laboulbenia cristata*
Philonthus coprophilus	*Peyritschiella furcifera*
	Rhachomyces philonthinus
Philonthus cruentatus	*Rhachomyces philonthinus*
Philonthus debilis	*Peyritschiella furcifera*
	Peyritschiella nigrescens
Philonthus discoideus	*Peyritschiella furcifera*
	Peyritschiella hybrida
	Peyritschiella nigrescens
Philonthus fumarius	*Rhachomyces philonthinus*
Philonthus marginatus	*Rhachomyces philonthinus*
Philonthus parvicornis	*Rhachomyces philonthinus*
Philonthus politus	*Peyritschiella princeps*
Philonthus quisquiliarius	*Peyritschiella nigrescens*
	Peyritschiella vulgata
Philonthus rectangulus	*Peyritschiella furcifera*
Philonthus salinus	*Laboulbenia philonthi*
Philonthus umbratilis	*Peyritschiella furcifera*
Philonthus varians	*Rhachomyces philonthinus*
Phloeocharis subtilissima	*Dipodomyces phloeocharidis*
Phloeopora testacea	*Dimorphomyces phloeoporae*
	**Peyritschiella protea*?
Platystethus arenarius	*Monoicomyces invisibilis*
	Monoicomyces matthiatis
Platystethus cornutus	*Cantharomyces platystethi*
Platystethus nodifrons	*Cantharomyces platystethi*
Proteinus laevigatus	*Rickia proteini*
Pselaphus heisei	*Tanmaurkiella huggertii* gen. et sp. nov.
	Tanmaurkiella pselaphi gen. et sp. nov.
Quedius boopoides	*Symplectromyces vulgaris*
Quedius cinctus	*Symplectromyces vulgaris*
Quedius fuliginosus	*Symplectromyces vulgaris*
Quedius longicornis	*Symplectromyces vulgaris*
Quedius maurorufus	*Symplectromyces vulgaris*
Quedius mesomelinus	*Symplectromyces vulgaris*
Quedius persimilis	*Symplectromyces vulgaris*
Quedius semiobscurus	*Symplectromyces vulgaris*
Quedius truncicola	*Symplectromyces vulgaris*
Quedius umbrinus	*Symplectromyces vulgaris*
Quedius xanthopus	*Symplectromyces vulgaris*
Remus sericeus	*Laboulbenia cafii*
Rugilus rufipes	*Corethromyces stilici*
	Laboulbenia stilicicola
Scaphisoma agaricinum	*Rickia peyerimhoffii*
Scaphisoma assimile	*Rickia peyerimhoffii*
Schistoglossa aubei	*Monoicomyces homalotae*
Sepedophilus immaculatus	*Stichomyces conosomatis*
Sepedophilus nigripennis	*Stichomyces conosomatis*
Sepedophilus pedicularius	*Stichomyces conosomatis*
Sepedophilus testaceus	*Stichomyces conosomatis*
Stenichnus collaris	*Acompsomyces stenichni*
Syntomium aeneum	*Cantharomyces elongatus*
Tetartopeus quadratus	*Rhadinomyces pallidus*
Tetartopeus terminatus	*Rhadinomyces pallidus*
	Sphaleromyces lathrobii
Thinodromus arcuatus	*Cantharomyces numidicus*
Tychus niger	*Cryptandromyces bibloplecti*
Coleoptera, Tenebrionidae	
Myrmechixenus subterraneus	*Dioicomyces myrmecophilus*
Dermaptera, Forficulidae	
Forficula auricularia	*Distolomyces forficulae*
Diptera, Chloropidae	
Elachiptera brevipennis	*Stigmatomyces constrictus*
Diptera, Drosophilidae	
Drosophila cf. *bifasciata*	*Stigmatomyces majewskii*
Drosophila funebris	*Stigmatomyces entomophilus*
Drosophila obscura	*Stigmatomyces majewskii*
Scaptomyza pallida	*Stigmatomyces scaptomyzae*
Diptera, Ephydridae	
Hydrellia griseola	*Stigmatomyces hydrelliae*
**Hydrellia maura*	*Stigmatomyces hydrelliae*
Scatella stagnalis	*Stigmatomyces purpureus*
Diptera, Nycteribiidae	
*Indet.	*Arthrorhynchus nycteribiae*
Diptera, Opomyzidae	
Geomyza balachowskyi	*Stigmatomyces geomyzae*
Geomyza tripunctata	*Stigmatomyces geomyzae*
Diptera, Sphaeroceridae	
Copromyza stercoraria	*Stigmatomyces burdigalensis*
Crumomyia fimetarii	*Stigmatomyces burdigalensis*
Crumomyia glabrifrons	*Stigmatomyces burdigalensis*
**Crumomyia notabilis*	*Stigmatomyces burdigalensis*
Crumomyia pedestris	*Stigmatomyces burdigalensis*
Leptocera fontinalis	*Stigmatomyces crassicollis*
Pullimosina vulgesta	*Stigmatomyces platensis*
Spelobia cf. *luteilabris*	*Stigmatomyces crassicollis*
Spelobia clunipes	*Stigmatomyces divergatus*
Spelobia luteilabris	*Stigmatomyces crassicollis*
	Stigmatomyces divergatus
Spelobia palmata/talparum	*Stigmatomyces divergatus*
	Stigmatomyces limosinae
Spelobia rufilabris	*Stigmatomyces crassicollis*
Thoracochaeta brachystoma	*Stigmatomyces thoracochaetae* sp. nov.
Heteroptera, Corixidae	
Sigara distincta	*Coreomyces corixae*
	Coreomyces macropus

HOST	FUNGUS
Sigara falleni	*Coreomyces macropus*
Sigara limitata	*Coreomyces arcuatus*
	Coreomyces corixae
	Coreomyces macropus
Sigara scotti	*Coreomyces macropus*
Sigara semistriata	*Coreomyces corixae*
	Coreomyces macropus
Heteroptera, Hebridae	
Hebrus ruficeps	*Tavaresiella hebri*

HOST	FUNGUS
Julida, Julidae	
**Archiboreoiulus pallidus*	*Troglomyces triandrus*
**•Cylindroiulus latestriatus*	*Rickia laboulbenioides*
**•Cylindroiulus punctatus*	*Rickia laboulbenioides*
**•Unciger foetidus*	*Rickia uncigeri*
Phthiraptera, Menoponidae	
Amyrsidea perdicis	*Trenomyces histophthorus*
Menopon gallinae	*Trenomyces histophthorus*
Menopon pallens	*Trenomyces histophthorus*

Appendix 3. Pictures of selected collecting sites.

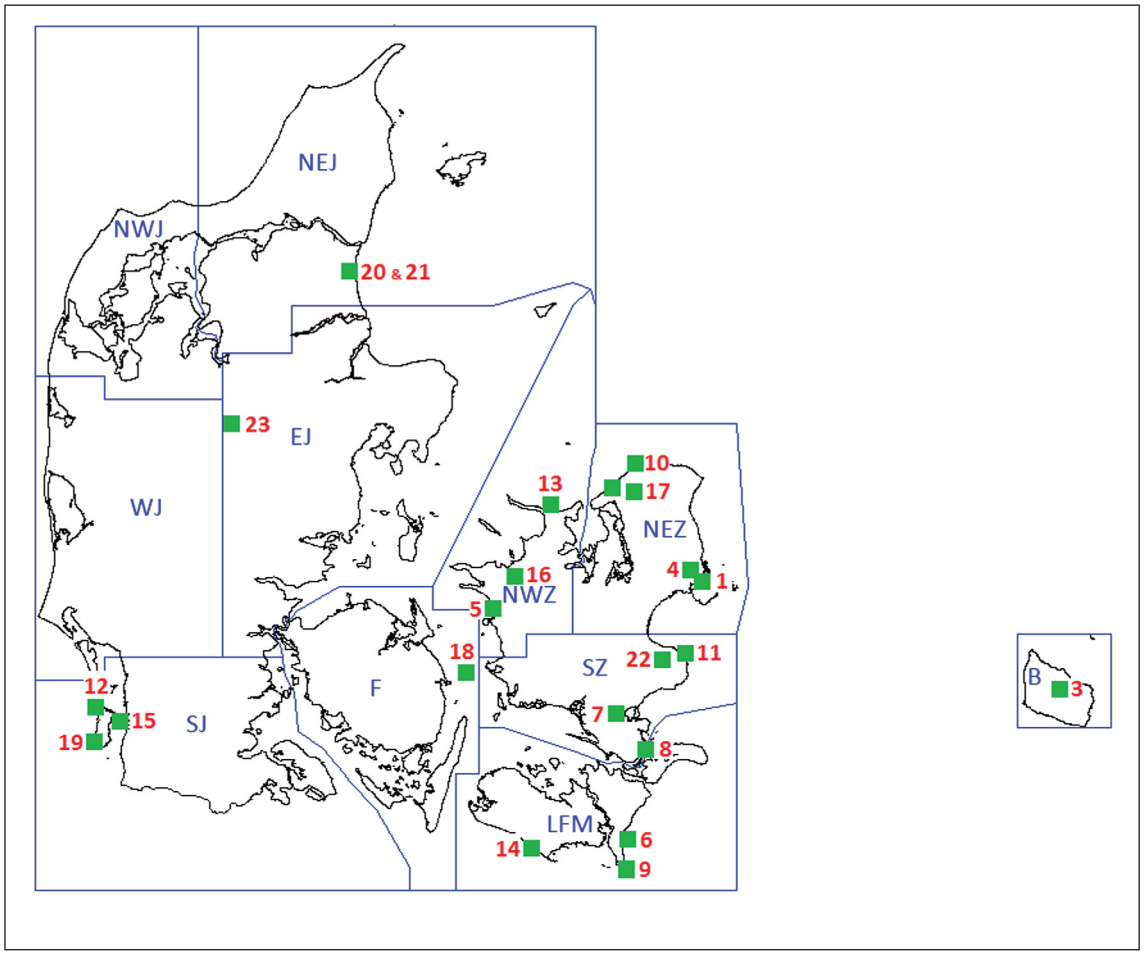

Fig. 96. Location of habitat pictures. **1**. Amager Fælled (Fig. 97A). **2**. Asserbo Plantage (Fig. 97B). **3**. Bastemose (Fig. 97C). **4**. Nordøst for Bispebjerg Station (Fig. 97D). **5**. Bjerge Sydstrand (Fig. 97E). **6**. Bøtø Plantage (Fig. 98A). **7**. Bårse (Fig. 98B). **8**. Gammel Kalvehave (Fig. 98C). **9**. Gedser Odde (Fig. 98D). **10**. Heatherhill (Fig. 98E). **11**. Holtug Kalkbrud (Fig. 99A). **12**. Juvre (Fig. 99B). **13**. Klintebjerg ved Klint (Fig. 99C). **14**. Rødbyhavn (Fig. 99D). **15**. Rømødæmningen (Fig. 99E). **16**. Nordbredden af Skarresø (Fig. 100A). **17**. Skærød (Fig. 100B). **18**. Sprogø (Fig. 100C). **19**. Sønderstrand på Rømø (Fig. 100D). **20**–**21**. Tofte Skov (Bøgebakken & Engskoven) (Fig. 100E–F). **22**. Tryggevælde Å ved Varpelev (Fig. 101A). **23**. Serup Skov (Fig. 101B).

Fig. 97 (next page)**. A**. Amager Fælled in early spring with JP and his two helpers looking for infected hosts. In this lush, sun-exposed temporary freshwater pond ***Helodiomyces elegans***, ***Cantharomyces denigratus*** and ***C. italicus*** (all. on *Dryops similaris*), ***Ceratomyces pyrenaeus*** and ***Eusynaptomyces hydrobii*** (both on *Hydrobius rottenbergii*), and ***Chitonomyces aculeifer*** on *Graptodytes bilineatus* were found. In the more dry area, ***Laboulbenia eubradycelli*** (on *Bradycellus verbasci*), ***L. pedicellata*** (on *Bembidion biguttatum*), and ***Monoicomyces homalotae*** (on *Atheta melanocera*) were sifted from wet flood debris with many mice-tracks. (Photograph: Andrea Schomann). **B**. The old light open pine forest in Asserbo Plantage is an unusual habitat in Denmark. From sifting moss and coniferous litter around the pine trees, and leaves underneath sun-exposed heather bushes ***Rhachomyces spinosus*** (on *Syntomus foveatus*), ***Laboulbenia eubradycelli*** (on *Bradycellus ruficollis*), ***L. inflata*** (on *Acupalpus flavicollis*), ***L. notiophili*** (on *Notiophilus palustris*), and perhaps most notable ***Camptomyces europaeus*** (on *Astenus gracilis*) were found. **C**. In the central part of Denmark's only rocky island, Bornholm, the old peat bog Bastemose is located. In the very wet sun-exposed sphagnum moss the rare ***Laboulbenia oodiphila*** (on *Oodes helopioides*) was collected. (Photograph: Andrea Schomann). **D**. The site "Nordøst for Bispebjerg Station" is one of the many urban ruderal areas that has been shown to contain a very interesting invertebrate fauna and therefore also some exciting Laboulbeniales. From sifting dry moss and leaf litter on this sun-exposed abandoned railway area ***Symplectromyces vulgaris*** (on *Quedius semiobscurus*), ***Laboulbenia aubryi*** (on *Amara municipalis*), ***L. eubradycelli*** (on *Bradycellus verbasci*), ***L. metableti*** (on *Syntomus foveatus*), and ***L. notiophili*** (on *Notiophilus rufipes*) were discovered. (Photograph: Jan Pedersen). **E**. Bjerge Sydstrand is a typical Danish sandy beach and the type locality of ***Stigmatomyces thoracochaetae*** (on *Thoracochaeta brachystoma*). This new species was found by sifting damp rotten seaweed (like shown on upper right picture where JP has skilled assistance). In the same piles of seaweed ***Hydrophilomyces gracilis*** (on *Cercyon littoralis*), ***Laboulbenia vulgaris*** Peyr. (on *Bembidion obtusum*), ***Peyritschiella oxyteli*** (on *Anotylus rugosus*), and ***Rickia huggertii*** (on *Omalium riparium*) also occurred. (Photograph: Andrea Schomann).


A
B
C
D
E

Fig. 98 (next page)**. A**. Bøtø Plantage is a relatively young pine forest that until recently was a commercial plantation. Now, however, it has been bought by a Danish nature foundation, which aims to do as much for Danish biodiversity as possible. This, among other things, meant that large parts of the plantation have been thinned to increase sun exposure, as shown in the picture here. The experienced collector in the picture is Henning Liljehult, who unfortunately did not catch any infected hosts in this situation. By sifting slightly damp moss and leaves around tree trunks ***Laboulbenia argutoris*** (on *Pterostichus diligens*), ***L. eubradycelli*** (on *Bradycellus harpalinus*), ***L. metableti*** (on *Syntomus foveatus*), and ***Cryptandromyces elegans*** on (*Brachygluta fossulata*) were collected. (Photograph Jan Pedersen). **B**. This shallow pond in a gravel pit near Bårse turned out to accommodate some very exciting Laboulbeniales which were all found by sifting very wet moss and plant debris along the sun-exposed shore. Most notable was the finding of ***Tavaresiella hebri*** (on *Hebrus ruficeps*), but also ***Zodiomyces vorticellarius*** (on *Helochares obscurus*) and ***Hydrophilomyces coneglianensis*** (on *Laccobius minutus*) could be found. (Photograph: Andrea Schomann). **C**. The locality Gammel Kalvehave does not look like much but has been shown to contain a very high species diversity of Laboulbeniales, with no less than 27 species found so far. All specimens were found either by sifting semi-fresh debris from the reeds standing in brackish water (immediately behind JP) – or by sifting the old mouldy garden compost in the foreground. Here it is first and foremost the finding of ***Kainomyces isomali*** (on *Gyrohypnus angustatus*) that should be highlighted, as this species was not known from Europe before. Of the other Laboulbeniales species, the following should also be mentioned: ***Euzodiomyces lathrobii*** (on *Lathrobium longulum*), ***Siemaszkoa fennica*** (on *Ptenidium laevigatum*), ***S. ptenidii*** (on *Ptenidium fuscicorne*), ***Symplectromyces vulgaris*** (on *Quedius mesomelinus*), ***Misgomyces dyschirii*** (on *Dyschirius globosus*), ***Ecteinomyces trichopterophilus*** (on *Acrotrichis montandonii*), ***Laboulbenia argutoris*** (on *Pterostichus diligens* and *P. strenuus*), ***L. clivinalis*** (on *Clivina fossor*), ***L. coneglianensis*** (on *Anisodactylus binotatus*), ***L. curtipes*** (on *Bembidion assimile* and *B. varium*), ***L. eubradycelli*** (on *Trichocellus placidus*), ***L. fasciculata*** (on *Patrobus atrorufus* and *Pterostichus rhaeticus*), ***L. flagellata*** (on *Agonum fuliginosum*, *A. thoreyi*, *Oxypselaphus obscurus* and *Pterostichus vernalis*), ***L. littoralis*** (on *Cafius xantholoma*), ***L. luxurians*** (on *Bembidion varium*), ***L. metableti*** (on *Syntomus foveatus*), ***L. murmanica*** (on *Bembidion assimile*), ***L. pedicellata*** (on *Bembidion assimile*, *B. mannerheimii* and *Dyschirius globosus*), ***L. vulgaris*** (on *Bembidion guttula* and *B. tetracolum*), ***Distolomyces forficulae*** (on *Forficula auricularia*), ***Peyritschiella furcifera*** (on *Philonthus debilis*), ***P. nigrescens*** (on *Philonthus debilis*), ***P. oxyteli*** (on *Anotylus rugosus*), ***Cantharomyces orientalis*** (on *Carpelimus corticinus*, *C. elongatulus* and *C. foveolatus*), ***Monoicomyces britannicus*** (on *Acrotona pseudotenera* and *Atheta longicornis*), and ***M. fragilis*** (on *Dinaraea angustula* and *Ocalea picata*). (Photograph: Andrea Schomann). **D**. Gedser Odde, the southernmost point in Denmark, where ***Laboulbenia lecoareri*** (on *Trechoblemus micros*), ***L. metableti*** (on *Syntomus foveatus*), ***L. vulgaris*** (on *Bembidion bruxellense*), ***Peyritschiella vulgata*** (on *Philonthus quisquiliarius*), and ***Monoicomyces validus*** (on *Aleochara grisea*) were collected by sifting rotten seaweed at the base of the coastal soft clay cliff. (Photograph: Andrea Schomann). **E**. The heath land of Heatherhill contains some very exciting old peat bog water holes (can be seen on the right in the picture). By netting in the dense vegetation in the shallows of these sun-exposed water holes ***Autoicomyces aquatilis*** and ***A. humilis*** (on *Hydrochus crenatus*), ***Eusynaptomyces enochri*** (on *Enochrus coarctatus*), ***Zodiomyces vorticellarius*** (on *Helochares obscurus*), ***Chitonomyces bidessarius*** (on *Hygrotus inaequalis*), and ***Hydraeomyces halipli*** (on *Haliplus ruficollis*) were found. (Photograph: Andrea Schomann).

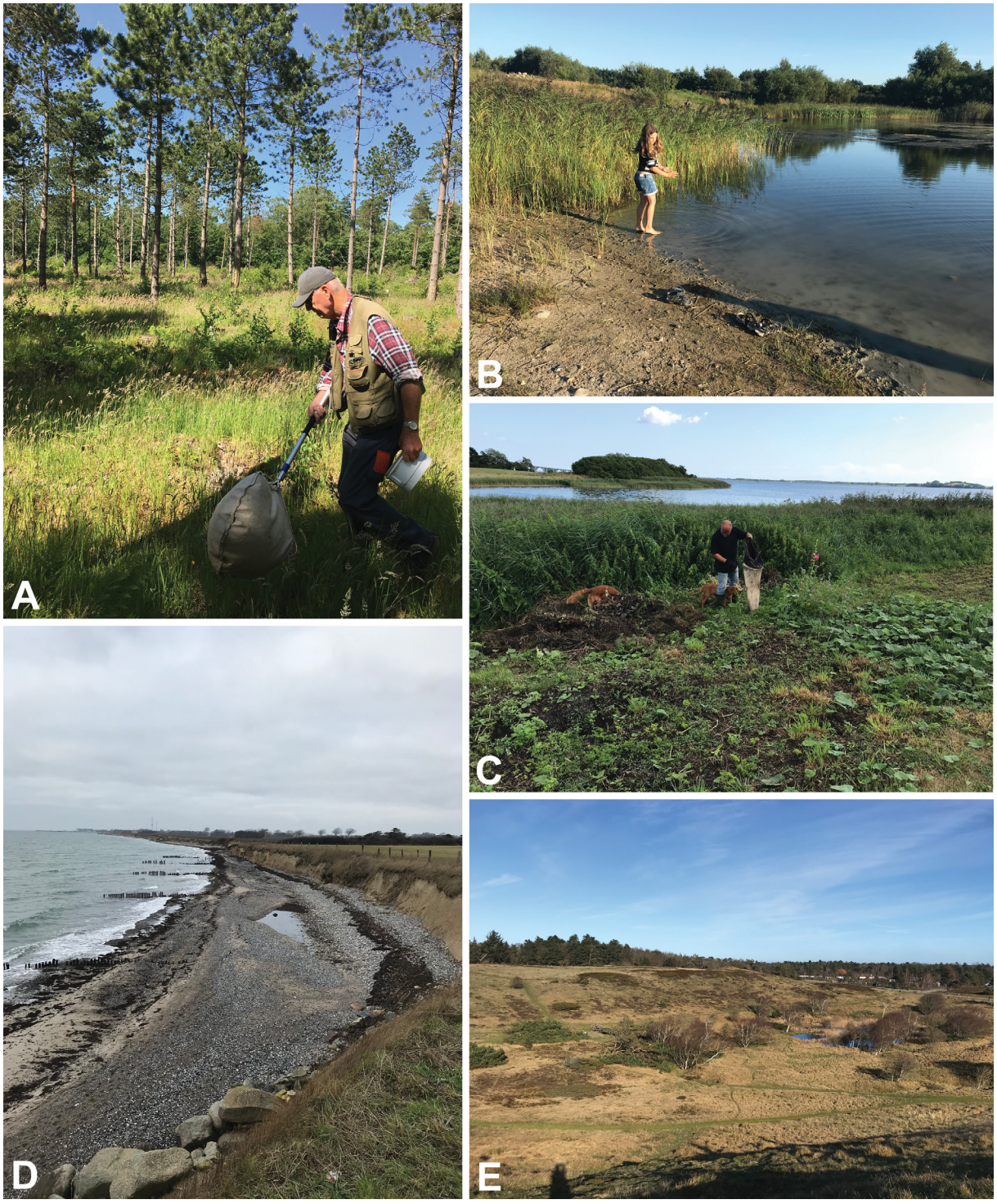
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Fig. 99 (next page)**. A**. The disused "Holtug Kalkbrud" is an old limestone quarry where the small water ponds (visible in the middle of the picture) completely dry out and leave a lot of plant debris behind. By sifting this debris ***Teratomyces philonthi*** (on *Gabrius breviventer*), ***Laboulbenia flagellata*** (on *Anchomenus dorsalis*), ***L. leisti*** (on *Leistus ferrugineus*), ***Cantharomyces orientalis*** (on *Carpelimus bilineatus* and *C. corticinus*), and ***Monoicomyces homalotae*** (on *Atheta graminicola*) can be found. (Photograph: Andrea Schomann). **B**. By sifting this semi-fresh flood debris on the dike at Juvre in the northern part of the island Rømø in the Wadden Sea, the extremely rare ***Corethromyces bialowiezensis*** (on *Tachyporus chrysomelinus*) very surprisingly was found, and also ***Monoicomyces invisibilis*** (on *Platystethus alutaceus*) was among the species found here. The sifting of flood debris immediately after severe autumn and winter storms with large floods as a result, has proven to be extremely effective in finding large amounts of invertebrates. The picture shows evidence of no less than three such incidents, in the form of well-separated belts of flood debris consisting of large amounts of plant material on the dike. Henning Liljehult is seen here a little irresolute about where to start on a 3-kilometer-long belt of debris. (Photograph: Jan Pedersen). **C**. "Klintebjerg ved Klint" is a sun-exposed, sandy grazed meadow with small shallow ponds where ***Zodiomyces vorticellarius*** (on *Helochares obscurus*) and ***Chitonomyces paradoxus*** (on *Laccophilus minutus*) can be found. In cow and deer dung on the pasture ***Rhachomyces philonthinus*** (on *Philonthus varians*), ***Laboulbenia argutoris*** (on *Pterostichus strenuus*) and ***Monoicomyces britannicus*** (on *Atheta longicornis*) are found. (Photograph: Andrea Schomann). **D**. The area around the now disused railway terrain in Rødbyhavn is one of the most exciting habitats in Denmark, as for many years a completely unique flora and fauna has proved to be present. Thus, more than 30 thermophilic invertebrate species new to the Danish fauna have been found at this site. This fact is primarily due to the southern location in Denmark and a habitat type which is quite unique to Danish conditions, most of all reminiscent of the conditions on rocky or sandy pastures in Central Europe. Among other things, it is the only known Danish locality for ***Laboulbenia egens*** (on *Elaphropus parvulus*) which, like ***Rhachomyces canariensis*** (on *Trechus obtusus*), ***Ecteinomyces trichopterophilus*** (on *Acrotrichis* spp.), ***Laboulbenia calathi*** (on *Calathus melanocephalus*), ***L. eubradycelli*** (on *Bradycellus caucasicus* and *Bradycellus csikii*), ***L. olisthopi*** (on *Olisthopus rotundatus*), and ***L. pedicellata*** (on *Bembidion illigeri*), was found by sifting extremely sun-exposed dry moss and lichens on gravel. In the seed-heads of wild carrots ***Laboulbenia ophoni*** (on *Ophonus puncticeps*) was found. (Photograph: Jan Pedersen). **E**. View from part of the Wadden Sea as seen from "Rømødæmningen", where ***Laboulbenia giardii*** (on *Dicheirotrichus gustavii*) was found by sifting the seaweed at the foot of the dam. (Photograph: Andrea Schomann).

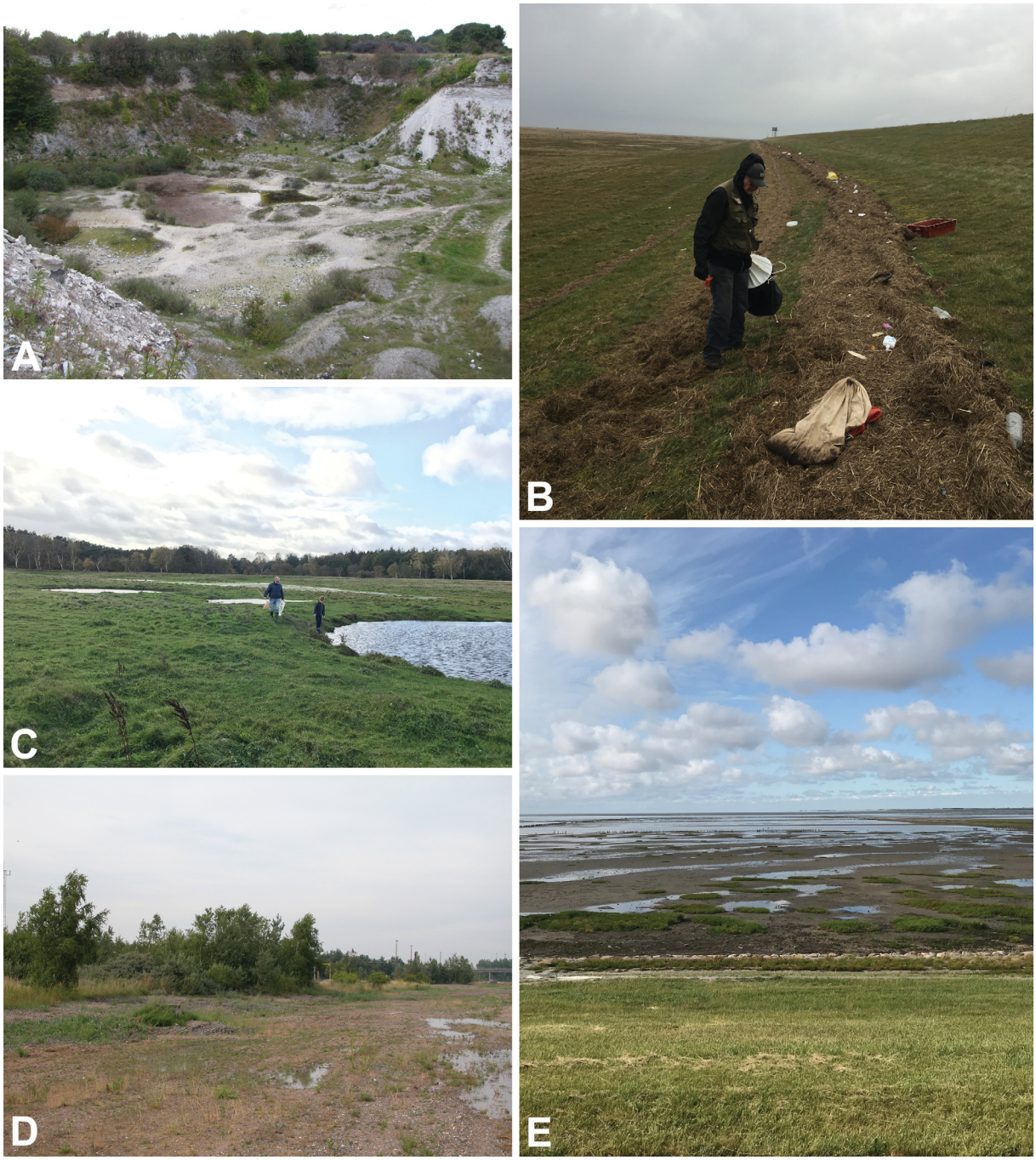
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Fig. 100 (next page)**. A**. "Nordbredden af Skarresø" is a sun-exposed grazed meadow and the type locality of ***Euphoriomyces smicri*** (on *Smicrus filicornis*), which was sifted from the semi-dry, mouldy and rotten straw that can be seen on the upper left corner of the picture, together with ***Rhachomyces philonthinus*** (on *Philonthus varians*), ***Laboulbenia flagellata*** (on *Agonum muelleri*, *Oxypselaphus obscurus*, and *Pterostichus vernalis*), ***L. vulgaris*** (on *Bembidion biguttatum*), and ***Peyritschiella oxyteli*** (on *Anotylus rugosus*). JP is seen here (to the right) in good company. (Photograph: Andrea Schomann). **B**. In this glorious pile of horse manure close to the small village Skærød JP found ***Peyritschiella hybrida*** (on *Philonthus discoideus*) which so far is the only one known Danish locality for this species. Also, ***Siemaszkoa fennica*** (on *Ptenidium pusillum*), ***Ecteinomyces trichopterophilus*** (on *Acrotrichis grandicollis*), and ***Dioicomyces anthici*** (on *Omonadus formicarius*) were sifted from the same fermenting warm and mouldy horse dung heap. (Photograph: Andrea Schomann). **C**. The small island of Sprogø between Zealand and Funen surprisingly housed an unknown species of laboulbeniales and thus became the type locality of ***Monoicomyces validus*** Santam. sp. nov. (on *Atheta vestita*). It was sifted from rotten seaweed on the stony seashore together with ***Laboulbenia giardii*** (on *Dicheirotrichus gustavii*), ***L. littoralis*** (on *Cafius xantholoma*) and ***L. pedicellata*** (on *Bembidion normannum*). Under stones on sandy ground in the intertidal zone ***Laboulbenia lichtensteinii*** (on *Cillenus lateralis*) was found. (Photograph: Andrea Schomann). **D**. "Sønderstrand på Rømø" is often exposed to major floods several times a year, and by sifting semi-fresh flood debris in this dune area ***Laboulbenia argutoris*** (on *Pterostichus diligens*), ***L. eubradycelli*** (on *Bradycellus harpalinus*), ***L. flagellata*** (on *Agonum marginatum*), ***L. lichtensteinii*** (on *Cillenus lateralis*), ***L. vulgaris*** (on *Bembidion assimile*), and ***Haplomyces texanus*** (on *Bledius diota*) were found. (Photograph: Andrea Schomann). **E**. Tofte Skov is one of the few localities in Denmark where there is almost untouched nature with many different habitats. As can be seen here in the picture (taken at "Bøgebakken" in Tofte Skov) nature is allowed to unfold completely on its own terms. By sifting bark and fungi from old beech trees ***Siemaszkoa ramificans*** (on *Ptenidium turgidum*) and ***Stichomyces conosomatis*** (on *Sepedophilus testaceus*) were collected, and by sifting leaf litter and moss in the forest floor or using pitfall traps ***Rhachomyces furcatus*** (on *Othius subuliformis*), ***Laboulbenia eubradycelli*** (on *Bradycellus harpalinus* and *B. csikii*), ***L. flagellata*** (on *Platynus assimilis* and *Agonum fuliginosum*), ***L. notiophili*** (on *Notiophilus biguttatus*, *N. germinyi* and *N. palustris*), and ***Corethromyces stilici*** Thaxt. (on *Rugilus rufipes*) were found. Most notable was the finding of ***Monoicomyces drusillae*** (on *Drusilla canaliculata*) in a pitfall trap. So far it is the only known locality in Denmark for this species. (Photograph: Andrea Schomann). **F**. In the light-open untouched forest swamps in Tofte Skov, such as here in "Engskoven", ***Rhachomyces canariensis*** and ***Laboulbenia vulgaris*** (on *Epaphius secalis* and *Trechus obtusus*) can be found by sifting moist leaf litter and moss. In the open water surfaces ***Helodiomyces elegans*** (on *Dryops auriculatus*) can be found. (Photograph: Andrea Schomann).


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Fig. 101 (next page)**. A**. The contours of the small river Tryggevælde Å near Varpelev can just accurately be seen here after the water has risen from heavy rain in the winter. The water body in the upper left part of the picture is a completely flooded meadow which has created a lot of flood debris along the shore, as seen in the lower right. From sifting this debris ***Compsomyces lestevae*** (on *Lesteva sicula*), ***Idiomyces peyritschii*** (on *Deleaster dichrous*), ***Misgomyces dyschirii*** (on *Dyschirius globosus*), ***Laboulbenia clivinalis*** (on *Clivina fossor*), ***L. corylophi*** (on *Corylophus cassidoides*), ***L. eubradycelli*** (on *Trichocellus placidus*), ***L. inflata***. (on *Acupalpus exiguus* and *A. flavicollis*), ***L. lecoareri*** (on *Trechoblemus micros*), ***L. luxurians*** (on *Bembidion varium*), ***L. murmanica*** (on *Bembidion biguttatum*), ***L. notiophili*** (on *Paradromius longiceps*, *Philorhizus melanocephalus* and *Ph. sigma*), ***L. pedicellata*** (on *Bembidion gilvipes*, *B. guttula* and *Dyschirius globosus*), ***Corethromyces stilici*** (on *Rugilus rufipes*), ***Peyritschiella oxyteli*** (on *Anotylus rugosus*), ***Cantharomyces orientalis*** (on *Carpelimus bilineatus*, *C. corticinus* and *C. elongatulus*), ***Monoicomyces britannicus*** (on *Atheta volans*), ***M. crassicaulis*** (on *Oxypoda elongatula*), and ***M. homalotae*** (on *Aloconota gregaria* and *Atheta graminicola*) were found. (Photograph: Andrea Schomann). **B**. From sifting the moist moss and debris in and around the *Carex paniculata* tussocks in this sun-exposed spring near Serup Skov ***Symplectromyces vulgaris*** (on *Quedius maurorufus*), ***Ecteinomyces trichopterophilus*** (on *Acrotrichis* spp.), ***Laboulbenia eubradycelli*** (on *Trichocellus placidus*) and ***Peyritschiella oxyteli*** (on *Anotylus rugifrons*) were found. But it should first and foremost be the very exciting finding of ***Tanmaurkiella huggertii*** (on *Pselaphus heisei*) that accentuates the type locality of this very rare species found together with the above-mentioned species. (Photograph: Jan Pedersen).


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Appendix 4. Macro photographs of insects with fungi.

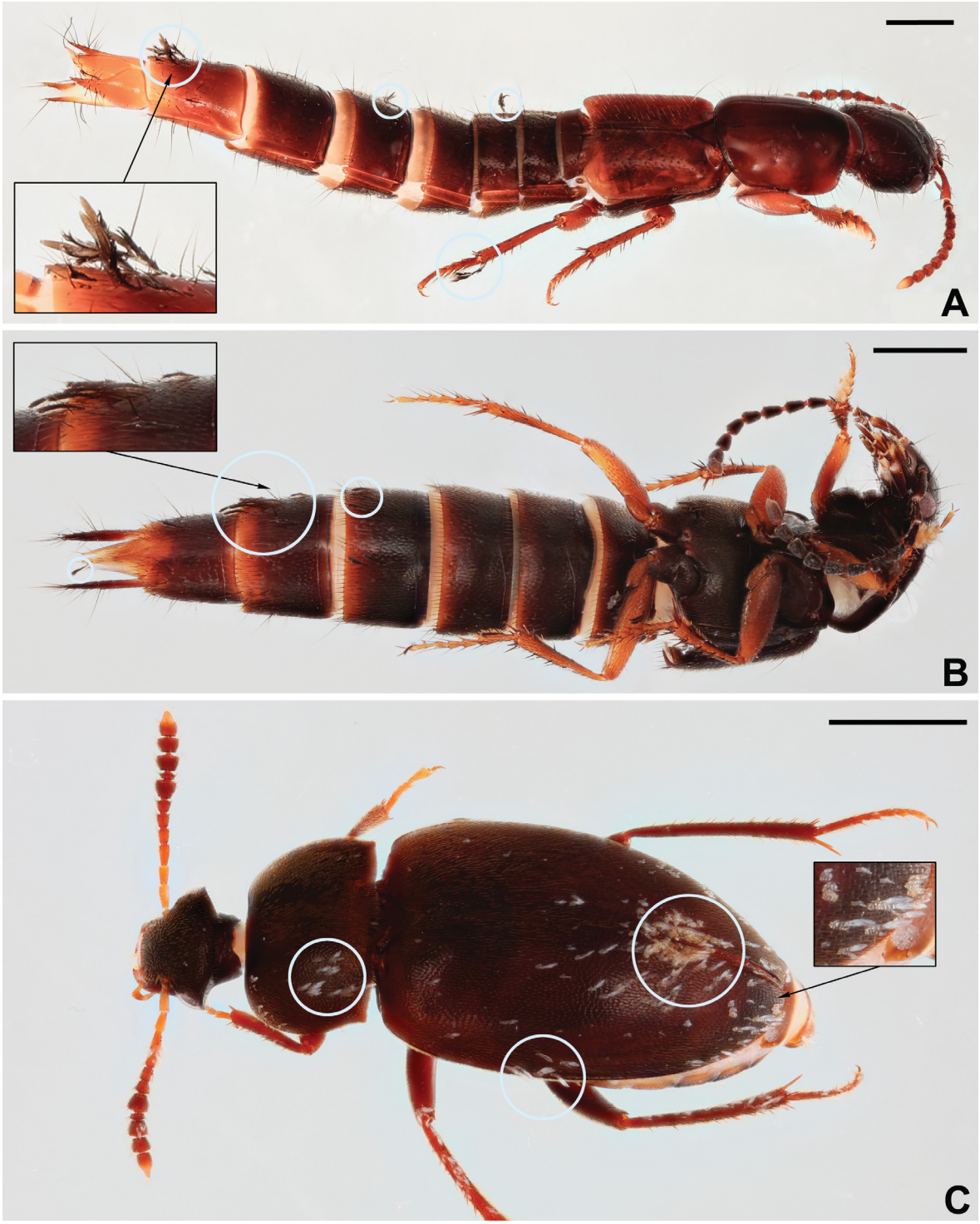

Fig. 102. Habitus of hosts with fungi. Some thalli are zoomed in, and others are encircled. **A**. *Othius punctulatus* with thalli of ***Rhachomyces furcatus***. **B**. *Philonthus fumarius* with thalli of ***Rhachomyces philonthinus*** on the ventral side of the last 4 abdominal segments and a few on the left hind leg. **C**. *Catops tristis* heavily infested with ***Asaphomyces cholevae*** all over the body, even on the ventral side this specimen has just as many thalli. Scale bars: 1 mm. (Photos: Aslak Kappel Hansen).

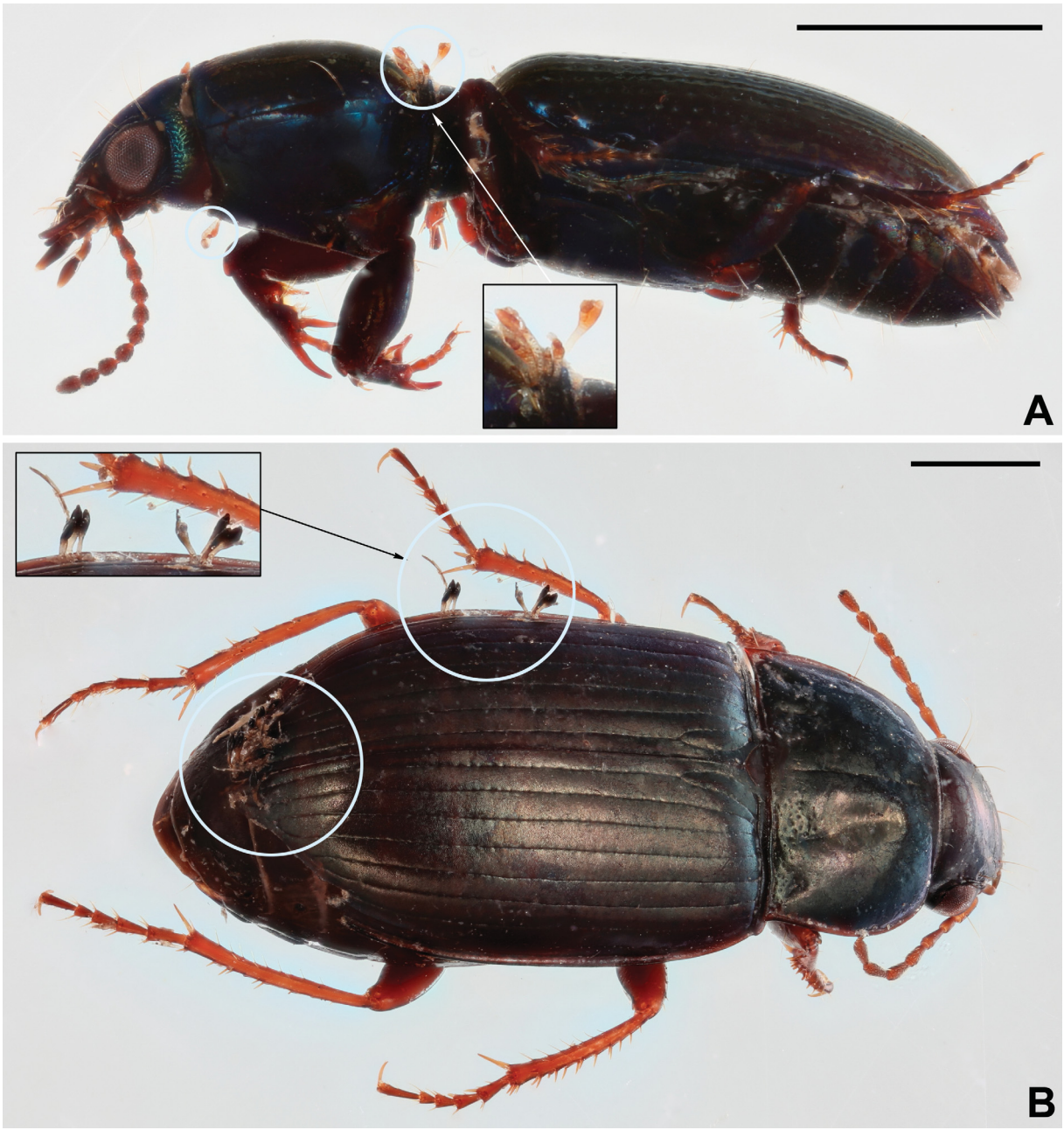

Fig. 103. Habitus of hosts with fungi. Some thalli are zoomed in, and others are encircled. **A**. *Dyschirius salinus* with thalli of ***Misgomyces dyschirii*** on various parts of the pronotum. **B**. *Amara municipalis* with a few mature thalli of ***Laboulbenia aubryi*** on left side of the elytra and many immature on the elytral apices. Scale bars: 1 mm. (Photos: Aslak Kappel Hansen).

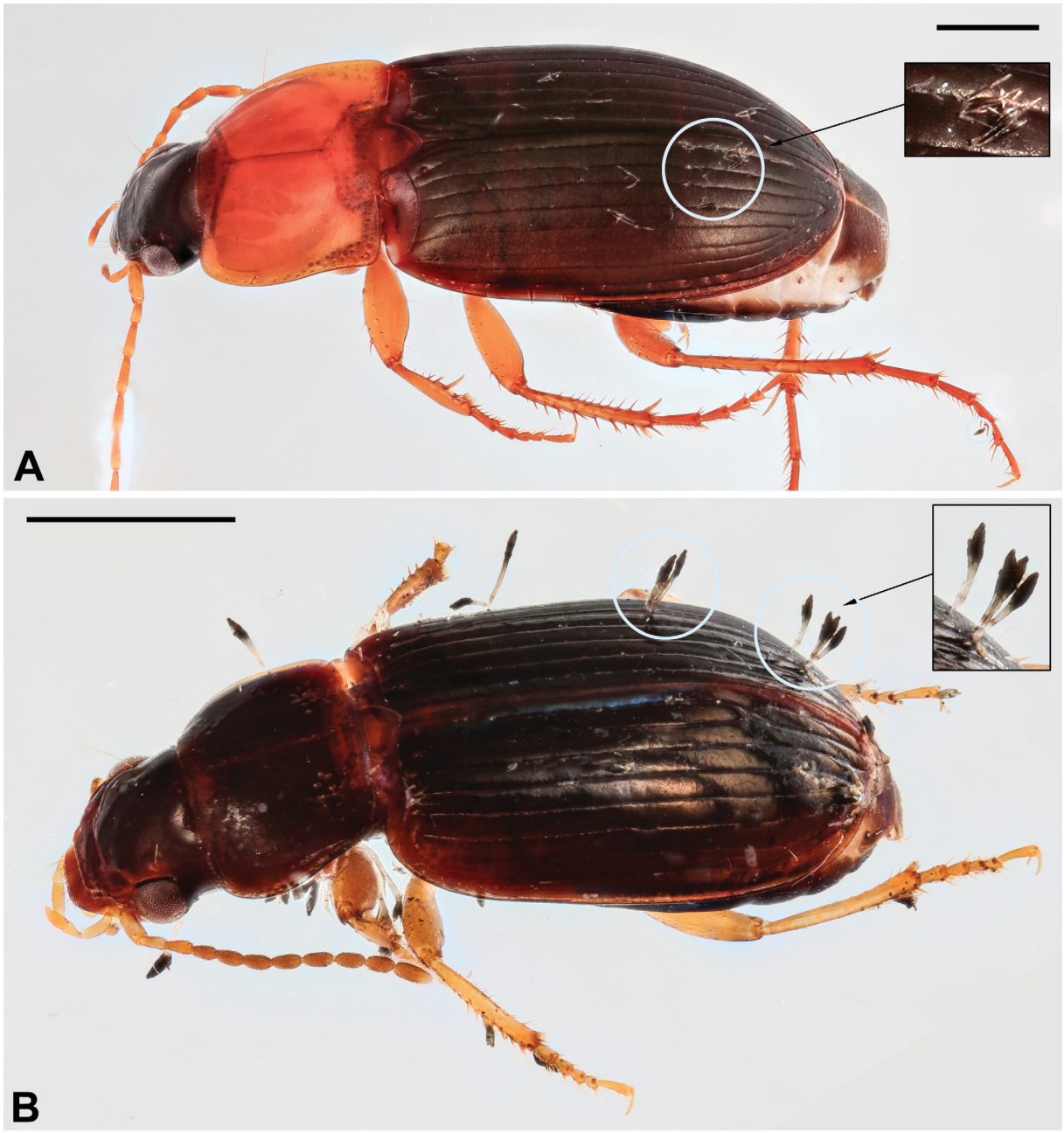

Fig. 104. Habitus of hosts with fungi. Some thalli are zoomed in, and others are encircled. **A**. *Calathus melanocephalus* with mature and immature thalli of ***Laboulbenia calathi*** on dorsal side of the elytra. **B**. *Bradycellus csikii* with thalli of ***Laboulbenia eubradycelli*** on various parts of the body. Scale bars: 1 mm. (Photos: Aslak Kappel Hansen).

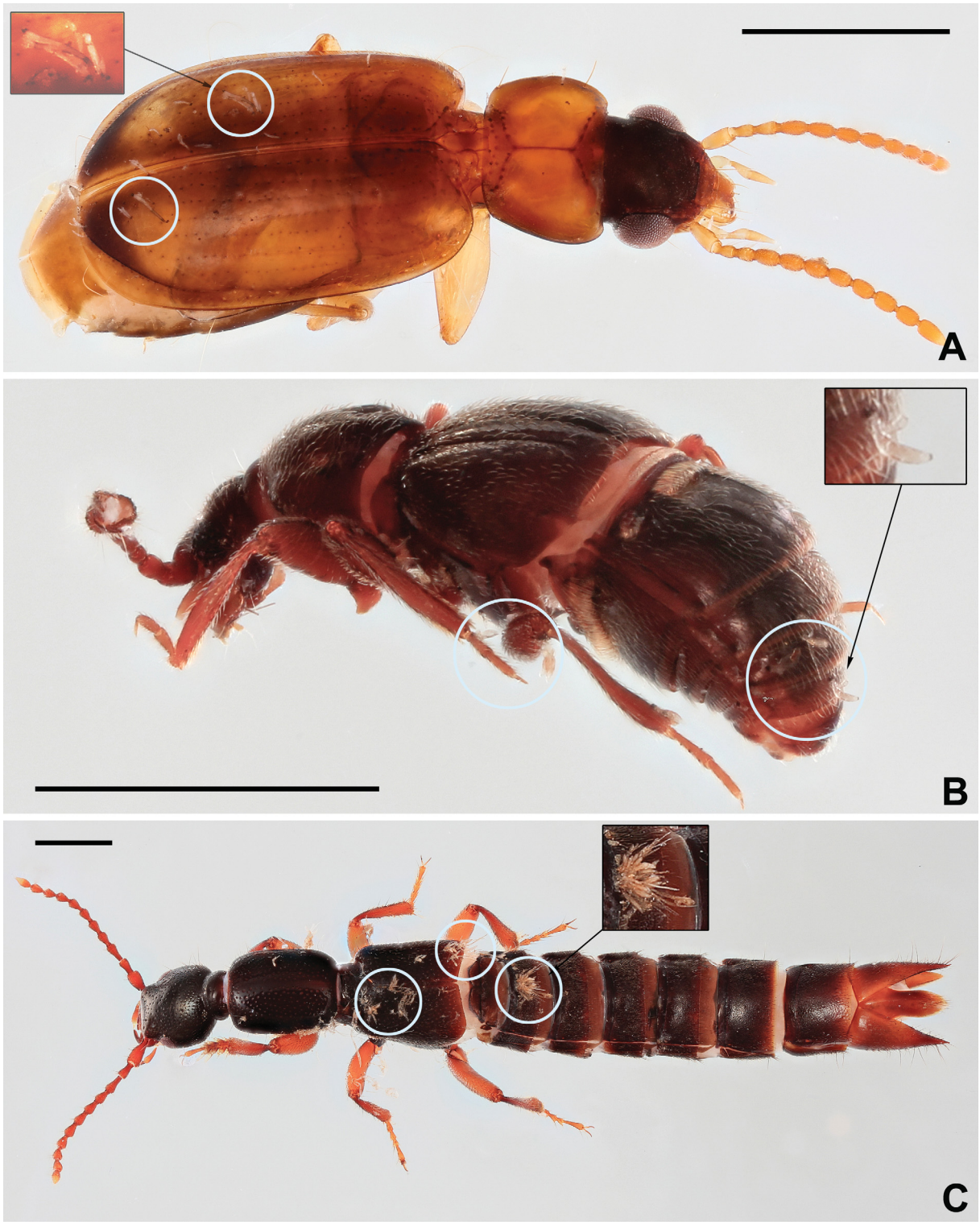

Fig. 105. Habitus of hosts with fungi. Some thalli are zoomed in, and others are encircled. **A**. *Perigona nigriceps* with thalli of ***Laboulbenia manubriolata*** on dorsal side of the elytra. **B**. *Brachygluta fossulata* with a few thalli of ***Cryptandromyces elegans*** on the apex of the abdominal segments, on the hind coxa and the tip of the left hind tibia. **C**. *Lathrobium brunnipes* with thalli of ***Rhadinomyces pallidus*** on various parts of the body. Scale bars: 1 mm. (Photos: Aslak Kappel Hansen).

Fig. 106. Habitus of hosts with fungi. Some thalli are zoomed in, and others are encircled. **A**. *Corylophus cassidoides* with four thalli of ***Laboulbenia corylophi*** on the apex of the elytra. **B**. *Spelobia palmata* with three thalli of ***Stigmatomyces divergatus*** on the left middle coxa. Scale bars: 1 mm. (Photos: Aslak Kappel Hansen).

Fig. 107. Habitus of hosts with fungi. Some thalli are zoomed in, and others are encircled. **A**. *Carpelimus corticinus* with thalli of ***Cantharomyces orientalis*** on various parts of the body. **B**. *Oxypoda elongatula* with thalli of ***Monoicomyces crassicaulis*** on the ventral side of the last abdominal segment. Scale bars: 1 mm. (Photos: Aslak Kappel Hansen).