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Research article

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A remarkable new genus and species of Euryproctini (Hymenoptera: Ichneumonidae, Ctenopelmatinae) from Thailand

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Abstract. *Rhytidaphora* Reshchikov & Quicke gen. nov. (type species *Rhytidaphora thailandica* Reshchikov & Quicke gen. et sp. nov.) from Thailand is described and illustrated. It belongs to the tribe Euryproctini of the subfamily Ctenopelmatinae (Hymenoptera, Ichneumonidae) based on the absence of glymma and the subapical notch on the ovipositor. The new taxon differs from all other genera of Euryproctini by the occipital carina being broadly incomplete dorsally, the hypostomal carina joining the occipital carina shortly before the base of the mandible, distinctly pectinate tarsal claws, and immovably fused and strongly sculptured second and third metasomal tergites.

Keywords. Darwin wasps, new genus, new species, parasitoid, Southeast Asia, Oriental Region, Malaise trap, Chae Son, Doi Phu Kha.

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Introduction

The tribe Euryproctini Thomson, 1883, together with eight other tribes, comprise the subfamily Ctenopelmatinae Förster, 1869 (Hymenoptera, Ichneumonidae), one of the most poorly known groups of Darwin wasps (Gauld 1997). The Ctenopelmatinae are well represented in all major biogeographical

regions, occurring from the Arctic to the tropics, and comprising 1616 species in 111 genera, including 265 species and 19 genera of Euryproctini (Reshchikov 2011, 2016; Kasparyan 2016, 2017, 2018, 2020a, 2020b, 2021a, 2021b; Kasparyan *et al.* 2016; Lima & Kumagai 2016; Yu *et al.* 2016, 2018, 2020a, 2020b, 2021a, 2021b; Reshchikov *et al.* 2017a, 2017b, 2017c, 2018, 2019; Reshchikov & van Achterberg 2018; Khalaim *et al.* 2019; Sun *et al.* 2019, 2020, 2021a, 2021b; Li *et al.* 2020; Sheng *et al.* 2020, 2022; Watanabe 2021; Li & Sun 2022), excluding genera we consider belonging to Metopiinae Förster, 1869 (*Bremiella* Dalla Torre, 1901 (Quicke *et al.* 2009) and *Scolomus* Townes & Townes, 1950 (Gauld & Wahl 2006; Araujo *et al.* 2018)).

Members of the Ctenopelmatinae are overwhelmingly endoparasitoids of sawfly larvae. Together with their hosts these wasps display distribution patterns with the highest diversity in the North temperate zone. Their tropical fauna most probably developed from invasions from the Holarctic along mountain ranges (Malaise 1945; Smith 2011; Reshchikov 2015). Thus, 140 species of Euryproctini are recorded from the Holarctic region and only 9 species are known from the Oriental region (Yu *et al.* 2016; Sun *et al.* 2021a).

Here we describe a new genus and species of Euryproctini from Thailand based on recently collected specimens. Its morphology suggests that it is a member of the Euryproctini, where we place it. The tribe can be characterized by the absence of glymma and the subapical notch on the ovipositor. The first character state is broadly derived in the subfamily; however, other tribes have only a few genera with the glymma absent. Thus, euryproctines (except some *Hadrodactylus* Förster, 1869) lack the T2 ridges between the anterior margin and the spiracle, differing from the members of the tribe Ctenopelmatini. Ovipositor structure differs between Euryproctini and Pionini Smith & Shenefelt, 1955; the latter have a needle-like ovipositor without a subapical notch. *Seleucus* Holmgren, 1860, which was recovered by Quicke *et al.* (2009) as a sister group to Euryproctini, also has the ovipositor with the subapical notch and the glymma absent, but the second and third metasomal tergites (T2–3) are exceptionally elongated (Holmgren 1860). Our new genus and the species described here were readily recovered within Euryproctini in our phylogenetic analysis (see discussion). They differ from all other known members of the tribe Euryproctini by the occipital carina being broadly incomplete dorsally, joining the hypostomal carina shortly before the base of the mandible, distinctly pectinate tarsal claws, and immovably fused T2 and T3.

Material and methods

This work is based on material collected by the TIGER project (http://sharkeylab.org/tiger) in Chae Son National Park in Lampang Province in 2007, and by the research group of the third author in Doi Phu Kha National Park, Nan Province in 2020.

Type specimens are deposited at the following collections:

CUMZ = Collection of the Insect Museum, Chulalongkorn University Museum of Natural History, Bangkok, Thailand

QSBG = Queen Sirikit Botanic Garden, Chiang Mai, Thailand

A 407 base pair sequence partial 3'-barcode for the new species was obtained following a failed first sequencing run. GenBank accession numbers and provenances of the taxa included in the analysis are given in Table 1. A molecular dataset of the barcode region of cytochrome oxidase c subunit 1 (CO1) was compiled for a total of 46 species of Ctenopelmatinae, two Tryphoninae Shuckard, 1840, which were used for rooting the tree, plus a species of *Scolomus*, a genus originally placed in Ctenopelmatinae but subsequently transferred to Metopiinae; however, placement of the latter is still uncertain (Bennett *et al.* 2019).

Table 1 (continued on next page). GenBank accession numbers of the taxa examined.

| Species | GenBank accession number | Geographical origin |
|------------------------------------------------|--------------------------------|-------------------------------------------------------------------------------------------------------|
| Absyrtus vicinator (Thunberg, 1822) | MK643008 | Germany: Rhineland-Palatinate, Kreis Ahrweiler, Landskrone |
| Alexeter multicolor (Gravenhorst, 1829) | JF962872 | Finland |
| Barytarbes honestus (Cresson, 1868) | MK959387 | USA: Kentucky, Harrison Co., Silverlake Farm |
| Campodorus ultimus Jussila, 2006 | MN674254 | Canada: Nunavut, Kitikmeot, Cambridge Bay, CHARS Intensive Monitoring Area, near Base Camp |
| Dyspetes rufus (Provancher, 1874) | HM414093 | Canada |
| Euryproctus nemoralis (Geoffroy, 1785) | MK642994 | Germany: Rhineland-Palatinate, Kreis Ahrweiler, Landskrone |
| Euryproctus sentinis Davis, 1897 | MK959423 | USA: Kentucky, Harrison Co., Silverlake Farm |
| Gunomeria sordida (Gravenhorst, 1829) | JF963363 | Austria |
| Hadrodactylus larvatus Kriechbaumer, 1891 | MK643015 | Germany: Bavaria, Niederbayern, Bayerischer National Park |
| Hadrodactylus seldoviae (Ashmead, 1902) | KU496749 | USA: Alaska, Kenai Peninsula, Kenai National Wildlife Refuge, Skilak River at Skilak Lake |
| Hadrodactylus vulneratus (Zetterstedt, 1838) | JF963368 | Finland |
| Himerta sp. | KR933726 | Canada: Alberta, Jasper NP, Highway 16 / 93A Junction |
| Hypamblys albopictus (Gravenhorst, 1829) | KR790876 | Canada: Ontario, Leeds and Grenville, Elizabethtown-Kitley, 4452 Rowsome Rd., Elizabethtown |
| Hypamblys sp. | KR406928 | Canada: Ontario, Georgian Bay Islands National Park, Beausoleil Island, Cedar Spring Campground |
| Lathrolestes nigricollis (Thomson, 1883) | GQ325435 | USA: Alaska |
| Lophyroplectus oblongopunctatus (Hartig, 1838) | KR874312 | Canada: Ontario, Wellington County, Puslinch Township, Concession 11/Hume Rd |
| Megaceria sp. | KY447164 | Australia |
| Mesoleius affinis Brischke, 1892 | JF963569 | Finland: Muhos |
| Mesoleptidea cingulata (Gravenhorst, 1829) | MG354808 | Canada: Ontario, Peterborough |
| Mesoleptidea decens (Cresson, 1868) | MK959443 | USA: Kentucky, Harrison Co., Silverlake Farm |
| Mesoleptidea stalii (Holmgren, 1858) | JF963574 | Finland: Hindsby |
| Mesoleptidea sp. | KR799300 | Canada: Northwest Territories, Nahanni National Park, Nailicho (Virginia Falls) |
| Mesoleptidea sp. | KR928907 | Canada: Alberta, Waterton Lakes NP, Foothills Parkland Region |
| Occapes hinzi Jussila, 1996 | KU373457 | Denmark: NE Greenland, Zackenberg, South of ZERO station |

Table 1 (continued). GenBank accession numbers of the taxa examined.

| Species | GenBank accession number | Geographical origin |
|------------------------------------------------|--------------------------------|-----------------------------------------------------------------------------------------------------|
| Opheltes sp. | MW056298 | |
| Pantorhaestes xanthostomus (Gravenhorst, 1829) | MG349317 | Canada: Ontario, Guelph, Arkell Research Station |
| Phobetes nigriceps (Gravenhorst, 1829) | JF963753 | Finland: Muhos |
| Physotarsus fabioi Gauld, 1997 | HQ548633 | Costa Rica: Guanacaste, Area de Conservación Guanacaste, Sector Pitilla, Bullas |
| Pion sp. | MK642990 | Germany: Rhineland-Palatinate, Kreis Ahrweiler, Landskrone |
| Polyblastus varitarsus (Gravenhorst, 1829) | HM414321 | Canada |
| Priopoda sp. | JF963793 | Russia: Primorsk |
| Rhinotorus sp. | FJ414416 | Canada: Manitoba |
| Rhorus longigena (Thomson, 1883) | MN666112 | Canada: Nunavut, Kitikmeot, Cambridge Bay, CHARS Intensive Monitoring Area, near Base Camp |
| Rhytidiphora thailandica gen. et sp. nov. | OK623371 | Thailand: Nan, Doi Phu Kha National Park |
| Saotis longiventris (Thomson, 1888) | MN683217 | Canada: Nunavut, Kitikmeot, Cambridge Bay, CHARS Intensive Monitoring Area, near Base Camp |
| Scolobates ruficeps Uchida, 1932 | KU753367 | South Korea |
| Scolomus sp. | MK959478 | Chile: Region X PN, Puyehue Antillanca, crater trail, water tank, <i>Notofagus</i> forest |
| Scopesis polita (Holmgren, 1857) | MG497546 | Canada: Yukon Territory, Kluane National Park and Reserve, Auriol Trail |
| Sympherta fucata (Cresson, 1868) | MK959487 | USA: Tennessee, Sevier Co., Great Smoky Mountains National Park, Twin Creeks, GRSM, ATBI Plot |
| Syndipnus lateralis (Gravenhorst, 1829) | MG349607 | Canada: British Columbia, Haida Gwaii, Naikoon Provincial Park, Hwy 16, Tlell |
| Syndipnus sp. | HQ566593 | Canada |
| Syndipnus sp. | MN677648 | Canada: Nunavut, Kitikmeot, Cambridge Bay, CHARS Intensive Monitoring Area, near Base Camp |
| Synodites lineiger (Thomson, 1894) | JF963864 | Finland: Muhos |
| Synomelix albipes (Gravenhorst, 1829) | MG503577 | Canada: Yukon Territory, Kluane National Park and Reserve, Dezadeash River Trail |
| Synomelix faciator Idar, 1983 | JF963865 | Finland: Lieksa |
| Synomelix sp. | KR797773 | Canada: Northwest Territories, Nahanni National Park, Nailicho (Virginia Falls) |
| Trematopygus sp. | JF963903 | Germany |
| Xenoschesis fulvicornis Kriechbaumer, 1891 | MW056248 | |
| Zaplethocornia procurator (Gravenhorst, 1820) | JF963963 | United Kingdom |

Most of the recent DNA extractions were carried out using normal procedures for 96-well plates (Ivanova et al. 2006), and PCR and sequencing reactions were carried out using standard protocols (Hajibabaei et al. 2005). Most sequences were obtained using the LCO-HCO primer pair combination (Folmer et al. 1994: LCO 5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3', HCO 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') or, less often, LepF1-LepR1 (Smith et al. 2005: LepF1 5'-ATT CAA CCA ATC ATA AAG ATA TTG G-3', LepR1 5'-TAA ACT TCT GGA TGT CCA AAA AAT CA-3'). Sequence alignment was carried out manually and was largely trivial as there were no indels. Sequences were analysed using maximum likelihood with the programme RAxML ver. 8.2.X (Stamatakis 2014), using a GTR+G rate model with the three codons as separate data partitions, with 100 replicates with two threads. Trees were visualised using Figtree (ver. 1.4.3) (Rambaut 2016).

The morphological terminology follows Gauld (1991). Images were taken using a Leica M205 C microscope with Montage multifocus, Interactive measurement and fusion optics stereo microscope combined with Leica Application Suite. Metasomal tergites and sternite are abbreviated as T and S, respectively.

Results

Taxonomy

Class Insecta Linnaeus, 1758 Order Hymenoptera Linnaeus, 1758 Superfamily Ichneumonoidea Latreille, 1802 Family Ichneumonidae Latreille, 1802 Subfamily Ctenopelmatinae Förster, 1869 Tribe Euryproctini Thomson, 1883

Rhytidaphora Reshchikov & Quicke gen. nov. urn:lsid:zoobank.org:act:718AE550-9DB0-4AB6-83ED-95549932F36B

Type species

Rhytidaphora thailandica Reshchikov & Quicke gen. et sp. nov. by present designation.

Diagnosis

Rhytidaphora gen. nov. can be distinguished from other genera of Euryproctini by the following combination of character states: lower mandibular tooth much longer than upper (Fig. 1B); occipital carina broadly incomplete dorsally, joining hypostomal carina shortly before base of mandible; occiput with distinct concavity; fore wing without areolet (Fig. 2A); tarsal claws distinctly pectinate (Fig. 2B); T1 dorsal carinae well-developed, continuing as dorsal carinae of T2 (Fig. 2F); S1 very short (0.3 times as long as T1); T2 and T3 immovably fused (Fig. 2D); T1–5 with deep basal and subapical transverse striate impressions (Fig. 2D, F); ovipositor rather short, straight, with subapical, dorsal notch (Fig. 2D).

Etymology

The generic name *Rhytidaphora* derives from Greek "ρυτίδα" – "wrinkle" and "φέρω" – "bear", referring to the sculpture of the metasoma. The gender is feminine.

Description

Measurements. Fore wing length 6.0 mm.

HEAD. Clypeus flat in lateral view (Fig. 2E), its lower margin blunt in its middle and slightly sharp laterally, bulging apically (Fig. 1B). Face rather sparsely setose (Figs 1B, 2E). Anterior tentorial pit rather large (Fig. 1B). Eyes bare (Fig. 2C). Lower mandibular tooth much longer than upper (Fig. 1B). Occipital carina broadly incomplete dorsally, joining hypostomal carina shortly before base of mandible. Occiput with distinct concavity.

Mesosoma. Epomia absent. Notauli shallow and indistinct (Fig. 2C). Mesopleuron sparsely setose, not punctate (Fig. 2C). Epicnemial carina joining anterior margin of mesopleuron (Fig. 2C). Propodeum in lateral profile convexly rounded (Fig. 2E), with carinae complete except for area apicalis, which is absent (fused with area superomedia) (Fig. 1C). Fore wing without areolet (Fig. 2A). Pterostigma receiving vein Rs+2r at its basal 0.35. Vein 2m-cu with a single bulla (Fig. 2A). Hind wing with cu-a receiving Cu1 well below middle. Tarsal claws distinctly pectinate (Fig. 2A). Fore tibia with apical tooth (Fig. 2G–H).

METASOMA. Without obvious punctures but densely finely setose (Fig. 2D, F). T1 as long as broad with strong dorsal longitudinal carina continuing in dorsal carinae of T2 (Fig. 2F). Glymma absent (Fig. 2D). S1 rather short, 0.3 times as long as T1. T2 and T3 immovably fused (Fig. 2D). T1–5 with distinct basal and subapical transverse impressions distinctly striate. Ovipositor very short, straight, with a long, shallow, subapical dorsal notch (Fig. 2D).

Species included

The genus is described as monotypic.

Rhytidaphora thailandica Reshchikov & Quicke gen. et sp. nov. urn:lsid:zoobank.org:act:EC8F8A55-E204-45C5-8750-7D26E24078E1 Figs 1–2

Etymology

The specific name refers to the species distribution.

Type material

Holotype

THAILAND • ♀; Nan Province, Doi Phu Kha National Park; 19°12.3′ N, 101°04′ E; 6 Sep. 2019; Malaise trap 5; W. Atsawasiramanee leg.; DNA voucher code CCDB06324-E02; GenBank accession code OK623371; CUMZ.

Paratype

THAILAND • 1 ♀; Lampang Province, Chae Son National Park, nature trail; 18°50.172′ N, 99°28.38′ E; 507 m a.s.l.; 14–21 Oct. 2007; Malaise trap; B. Kwannui and A. Sukpeng leg., T5315; QSBG.

Description

Female (holotype)

Measurements. Body length 6.0 mm, fore wing length 6.0 mm, antenna length 7.5 mm.

Body. Matt and sparsely setose.

HEAD. Antenna slender, as long as fore wing and with 37 flagellomeres. Scape 1.4 times as long as broad. First flagellomere with prominent basal annellus, $1.6 \times$ as long as 2^{nd} and $1.9 \times$ as long as 3^{rd} . Head narrowed behind eyes. Clypeus 0.4 times as high as wide, separated from face by distinct groove. Anterior tentorial pit rather large (Fig. 1B). Malar space 0.5 times basal mandible width. Inner margins

of eyes (Fig. 1B) almost parallel, scarcely concave near antennal sockets. Lateral ocellus separated from eye margin by 1.2 times its widest diameter. Face matt with dense setiferous punctures (Fig. 1B), with short yellow setosity. Frons with weak curved groove behind antennal sockets; with deep, moderately dense setiferous punctures. Occipital carina broadly incomplete dorsally, joining hypostomal carina shortly before base of mandible. Gena matt, with sparse punctures (Fig. 2E).

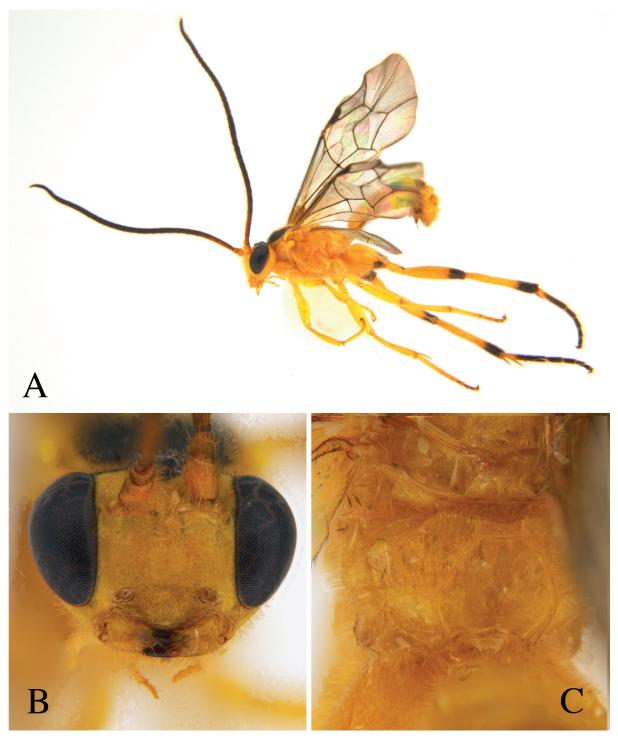


Fig. 1. *Rhytidaphora thailandica* Reshchikov & Quicke gen. et sp. nov., holotype, $\stackrel{\frown}{}$ (CUMZ). **A.** Habitus, in lateral view. **B.** Face **C.** Propodeum.

MESOSOMA. Mesoscutum shining, finely and densely punctate (Fig. 2C). Pronotum with crenulate groove only anteriorly, weakly shiny and with fine, moderately dense puncturation. Mesopleuron weakly shiny, setose and without punctures (Fig. 2E). Scuto-scutellar groove deep with steep posterior margin, triangular and gradually merging with mesoscutum anteriorly. Scutellum strongly convex, matt, without punctures. Juxtacoxal carina absent. Area superomedia and area apicalis fused, hexagonal (Fig. 1C).

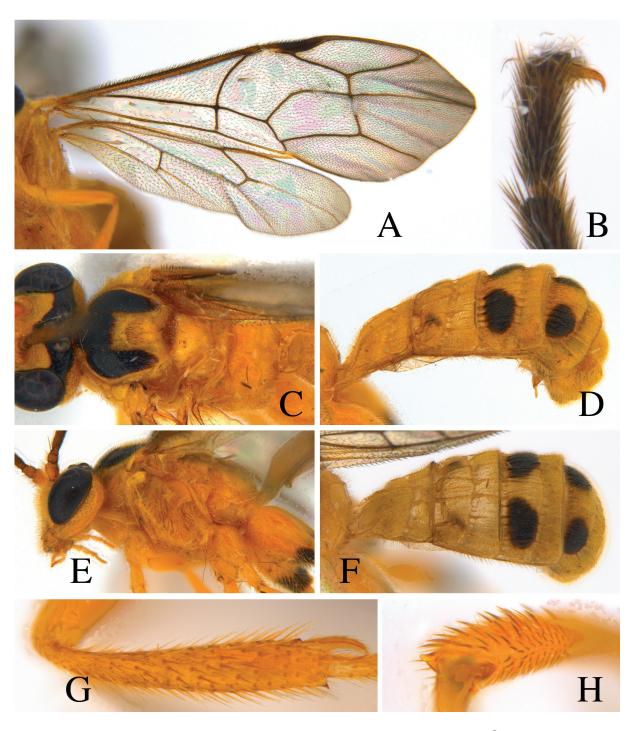


Fig. 2. *Rhytidaphora thailandica* Reshchikov & Quicke gen. et sp. nov., holotype, $\[\bigcirc \]$ (CUMZ). **A.** Wings. **B.** Tarsal claw. **C.** Head and mesosoma dorsally. **D.** Metasoma laterally. **E.** Head and mesosoma laterally. **F.** Metasoma dorsally. **G.** Fore tibia laterally. **H.** Fore tibia distally.

Spiracles almost round. Wings slightly hyaline (Fig. 2A). Fore wing with 1cu-a interstitial. Areolet absent, veins 2m-cu and 2rs-m interstitial. Pterostigma receiving vein Rs+2r at its basal 0.35. 2m-cu with a single, wide bulla anteriorly. Hind wing with cu-a receiving Cu1 well below middle (Fig. 2A). Propodeum smooth with strong lamelliform carination. Area basalis short and wide. Posterior transverse carina absent (Fig. 1C). Claws pectinate (Fig. 2B), fore claw with four teeth, mid- and hind claw with three teeth. Hind femur 4.2 times as long (including trochantellus) as maximally broad. Hind tibia 6.2 times as long as apically broad. First tarsomere of hind leg 8 times as long as broad and 2.5 times as long as second tarsomere.

METASOMA. Without obvious punctures but densely finely setose (Fig. 2D, F). T1 as long as broad, with strong dorsal longitudinal carina continuing in dorsal carinae of T2 (Fig. 2F). Ventro-lateral carinae complete (Fig. 2D). Glymma absent (Fig. 2D). S1 rather short, 0.3 times as long as T1. T2 and T3 immovably fused, second suture deep and crenulate (Fig. 2D, F). T1–5 with distinct basal and subapical transverse impressions distinctly striate (Fig. 2F). Ovipositor sheath very short, sheaths 0.13 times as long as hind tibia. Ovipositor straight, with a long, shallow, subapical dorsal notch (Fig. 2D).

COLORATION. Yellow, except for the following which are marked with black: antenna (dorsally), teeth of mandible, dorsal part of head, pterostigma, hind coxa dorsoapically, hind femur and tibia apically, hind tarsus (except first tarsomere basally), lateral parts of mesoscutum entirely and its anterior medial part, pair of spots on T3 and T4 (Figs 1–2).

Male

Unknown.

Distribution

Thailand.

Molecular analysis

As in the only previous study in which Ctenopelmatinae were relatively well represented (Quicke *et al.* 2009), the molecular analysis did not recover any large ctenopelmatine tribes as monophyletic (Fig. 3). The placement of *Scolomus* within Ctenopelmatinae, even though this genus has been transferred to Metopiinae (Gauld & Wahl 2006), is consistent with the idea that Metopiinae may be derived from within the Ctenopelmatinae (Quicke *et al.* 2009). The Euryproctini as currently constituted were recovered spread across the tree in five separate clades but with low support. Nevertheless, nine of the included euryproctine genera formed a monophyletic grouping (Fig. 3, top) including *Rhytidaphora* gen. nov., and is therefore consistent with the placement of the new genus based on our morphological assessment.

Discussion

Members of Euryproctini can be recognized from other Ctenopelmatinae by the combination of: absence of glymma and of tyloids on the male antenna; the epicnemial carina reaching the anterior margin of the mesopleuron; the groove between metapleuron and propodeum shallow and not U-shaped; the ovipositor with subapical notch; and tarsal claws not pectinate. Otherwise, only *Occapes* Townes, 1970 has pectinate claws within Euryproctini. In our analysis *Rhytidaphora* gen. nov. is readily recovered within Euryproctini (Fig. 3), and actually nested among *Synomelix* Foerster, 1868 species. However, a number of unique character combinations suggest that *Rhytidaphora* is a new genus and not actually a derived species of *Synomelix*. Species of *Synomelix* have the mandibular teeth of equal length (lower teeth longer in *Rhytidaphora*), fore wing with areolet present (absent in *Rhytidaphora*), occipital carina complete. The pectinate tarsal claws can be considered as a possible synapomorphy for *Occapes* and *Rhytidaphora*. In *Syndipnus* Förster, 1868 and the newly described genus, T2 and T3 are immovably

fused (Fig. 2D). This character occurs also in the *Rhorus mesoxanthus* (Gravenhorst, 1829) speciesgroup of the Pionini (Reshchikov *et al.* 2017b) and a few other ichneumonids. The distinctly striate deep transverse impressions of T1–5 (Fig. 2F) is a unique character within Euryproctini and Ctenopelmatinae in general. There are only shallow transverse grooves on T1–3 in *Rhinotorus* Foerster, 1869 (Reshchikov 2016) and *Gilen* Reshchikov & Achterberg, 2018 (Reshchikov & van Achterberg 2018). There is also similarity with the euryproctine genus *Hypsantyx* Pfankuch, 1906, which also has a huge petiolar area on the propodeum (Fig. 2C, F).

Most members of the Euryproctini are koinobiont endoparasitoids of sawflies, mostly Tenthredinidae Latreille, 1802. Some genera are specialised on particular groups of sawflies, e.g., *Hadrodactylus* Förster, 1869 on Selandriinae Thomson, 1871 (Hinz 1961; Idar 1975, 1981), *Hyperallus* Förster, 1869

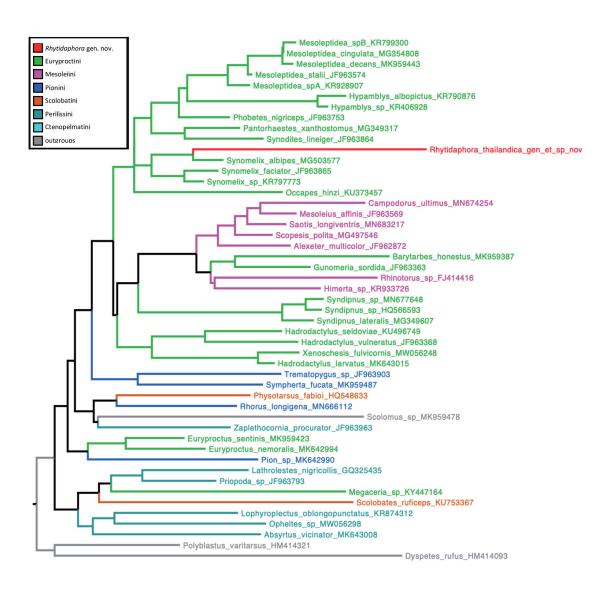


Fig. 3. Maximum likelihood tree based on a 658 base pair segment near the 5', terminus of the CO1 gene. This tree includes the new genus plus at least one representative of each genus of Ctenopelmatinae Förster, 1869 with a DNA barcode, plus two tryphonines as outgroups.

on Heterarthrinae Benson, 1952 (Viereck 1914), and *Synomelix* Förster, 1869 on Nematinae Thomson, 1871 (Brischke 1878; Rudow 1919; Hellén 1961; Idar 1983). Unfortunately, nothing is known about the biology of the newly described genus. Species of *Syndipnus* have a similar structure of T2 and T3 and attack free living nematine sawflies (Nyman *et al.* 2006). Thus, could we expect similar biology in *Rhytidaphora* gen. nov.? Some examined species of *Synomelix* also have a rather thin and short ovipositor, similar to the ovipositor in the new genus. Some species of the perilissine genus *Lathrolestes* Förster, 1869, which attack Heterarthrinae also display this trend (Reshchikov 2015).

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