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Research article

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**New records of *Philopterus* (Ischnocera: Philopteridae)
from Acrocephalidae and Locustellidae, with description of
one new species from Regulidae**

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Abstract. One species of the louse genus *Philopterus* Nitzsch, 1818 is redescribed and illustrated: *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus luscinius* (Quoy & Gaimard, 1830), *A. melanopogon* (Temminck, 1823), *A. scirpaceus* (Hermann, 1804), *A. schoenobaenus* (Linnaeus, 1758), *Iduna aedon rufescens* Stegmann, 1929, *I. rama* (Sykes, 1832), *Locustella* sp. and *L. ochotensis* (von Middendorff, 1853). *Philopterus acrocephalus* represents the first species of the *Philopterus*-complex recorded in the family Locustellidae Bonaparte, 1854. *Philopterus gustafssoni* sp. nov. is described ex *Regulus regulus* (Linnaeus, 1758), *R. regulus regulus* (Linnaeus, 1758), *R. regulus azoricus* Seebohm, 1883, *R. regulus buturlini* von Loudon, 1911, *R. regulus sanctaemariae* Vaurie, 1954, *R. regulus tristis* Pleske, 1892 and *R. ignicapillus* (Temminck, 1820). Descriptions of both species are amended with genetic data, DNA sequences of mitochondrial cytochrome oxidase I, nuclear *hyp* and *TMEDE6*; concatenated sequences are compared to the morphologically nearest species with genetic data available, *Philopterus citrinellae* (Schrank, 1776) and *Philopterus fringillae* (Scopoli, 1772). Holotype of *Philopterus reguli* (Denny, 1842) is pronounced to be a straggler, determination of other known material from Regulidae is changed for *Philopterus gustafssoni* sp. nov.

Keywords. Chewing lice, Passeriformes, reed warblers, kinglets.

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Introduction

In the past, the taxonomy of chewing lice passed through several periods during which different species definitions were applied. One of them was the approach that the lice in each host-louse association constitute separate species, regardless of morphological similarity to species known from other host species. This approach was applied assuming automatically that the lice are so host-specific that an eventual host switching is practically impossible. Nowadays we know that lice actually can switch hosts (e.g., Sychra *et al.* 2014a) and also that the phylogenies of lice do not always match with those of their hosts (Johnson *et al.* 2002). However, from time to time we are still obliged to come to terms with the inheritance of this period. This is also the case with the *Philopterus*-complex (obvious in Fedorenko 1987; Złotorzycka 1964), of which no thorough taxonomic revision was made since that time.

Within the *Philopterus*-complex, one of the groups concerned are *Philopterus* Nitzsch, 1818 species occurring in reed-warblers (Acrocephalidae Salvin, 1882) and kinglets (Regulidae Vigers, 1825). To date, four records of *Philopterus* species from the family Acrocephalidae have been published (Table 1) and practically no description of the any of them can be considered as complete. They are either based on a single sex only (Carriker 1949; Złotorzycka 1964) or their relevance may be disputable as the presented diagnostic features are, in our view, tentative and not sufficient to separate new species (Mey 1983). Therefore, we are confident to provide here a more detailed redescription of *Ph. acrocephalus* Carriker, 1949, based on examination of both museum specimens (including the female holotype) and our freshly collected material. In addition, we also provide the first record of this species in the family Locustellidae Bonaparte, 1854. The other *Philopterus* species described from Acrocephalidae are probably synonyms of *Ph. acrocephalus*, but we do not suggest the synonymization here because the type material for comparison is lacking.

Concerning kinglets (Regulidae), the only species known from this host family is *Philopterus reguli* (Denny, 1842), so far recorded only in goldcrest, *Regulus regulus regulus* (Linnaeus, 1758). After examination of the holotype deposited in the Natural History Museum, London, United Kingdom (NHML), we noticed that this specimen is different from any other *Philopterus* material known from

Table 1. To date described species of *Philopterus* complex from the family Acrocephalidae.

Species	Type host	Type locality
<i>Philopterus acrocephalus</i> Carriker, 1949	<i>Acrocephalus luscinius</i> (Quoy & Gaimard, 1830)	Guam
<i>Philopterus mirificus</i> (Złotorzycka, 1964)	<i>Acrocephalus palustris</i> (Bechstein, 1798)	Poland
<i>Philopterus necopinatus</i> (Złotorzycka, 1964)	<i>Acrocephalus schoenobaenus</i> (Linnaeus, 1758)	Poland
<i>Philopterus fedorenkoae</i> (Mey, 1983)	<i>Acrocephalus arundinaceus</i> <i>arundiceus</i> (Linnaeus, 1758)	Turkmenistan

this family. Therefore, we consider the holotype to be a straggler and *Ph. reguli* to be an invalid name. We here describe the other by us examined material as a new species, *Philopterus gustafssoni* sp. nov. Because our work chronologically follows those of Złotorzycka & Lucińska (1976) which put *Philopterus* from both Acrocephalidae and Regulidae in one species group (see below), we hereby refer to both these groups together.

In our study, we managed to gather DNA sequences of one mitochondrial and two nuclear markers from both *Ph. acrocephalus* and *Ph. gustafssoni* sp. nov. Therefore, we supply the redescrptions with genetic data as well.

Material and methods

The type material of *Philopterus acrocephalus* is represented by a single female, which is furthermore rather aged with some morphological characteristics hardly visible. Therefore, the redescription of this species was based mainly on material collected from moustached warbler, *Acrocephalus melanopogon* (Temminck, 1823) in Gbelce (Slovakia), Letea (Romania) and Nea Agathoupoli (Greece). Examined birds originated from dense reed (*Phragmites australis* (Cav.) Trin. ex Steud.) growths where the moustached warbler is relatively common; in the case of Gbelce it is the only breeding site in Slovakia and the northernmost one in the species' range (Trnka & Capek 2002).

To confirm the identity of *Ph. acrocephalus*, the holotype, from *Acrocephalus luscinius* (Quoy & Gaimard, 1830), mounted on slides in Canada balsam and deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), was used (Fig. 1). For further comparison and confirmation of new host-lice associations, museum material from *Acrocephalus melanopogon*, *Acrocephalus schoenobaenus* (Linnaeus, 1758) and *Iduna aedon* Stegmann, 1929, mounted on slides in Canada balsam and deposited in the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZIN), was used. In addition, we also examined one specimen of *Philopterus* sp. from *A. schoenobaenus* mounted on slide and deposited in the USNM, one specimen from *I. aedon*, mounted on slide and deposited in the ZIN and three nymphs from *Acrocephalus palustris* (Bechstein, 1798) deposited in the collection of J. Złotorzycka in the Museum of Natural History, University of Wrocław, Wrocław, Poland (MNHW). All these lice could not be determined at the species level. The three nymphs are currently the only representatives of *Philopterus* from Acrocephalidae preserved in Złotorzycka's collection, the rest has to be considered as lost.

For the morphological part of the description of *Ph. gustafssoni* sp. nov. we used material collected from *Regulus regulus regulus* in coniferous forests at the various locations in the Czech Republic. Furthermore, some more specimens of *Ph. gustafssoni* sp. nov. were obtained in field work targeted mainly on Fringillidae Leach, 1820 in Moravske Kninice (Czechia). We also morphologically examined

museum material from Złotorzycka's collection (MNHW). Since this material was stored inappropriately for DNA preservation, for the genetic analyses we used material collected on the Azores, Portugal. After DNA extraction, the vouchers were also mounted on slides and examined morphologically.

In order to collect material, birds were captured alive, examined, deloused as described in Sychra *et al.* (2009) and subsequently released. Identifications of birds were based on Svensson *et al.* (2009) but their taxonomy follows Clements *et al.* (2018). The mounted slides will be deposited in the Moravian Museum, Brno, Czechia (MMBC) and the “Grigore Antipa” National Museum of Natural History (MGAB), Bucharest, Romania. The examined museum material will be returned to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZIN) and the Museum of Natural History, University of Wrocław, Wrocław, Poland (MNHW). For determination of identity of *Philopterus reguli* and description of *Philopterus gustafssoni* sp. nov., material deposited in the Natural History Museum, London, United Kingdom (NHML) was used. Additional material, which was not mounted on slides, is deposited in the personal collection of Oldrich Sychra at the University of Veterinary and Pharmaceutical Sciences, Brno, Czechia (UVPS).

The terminology, dimensions taken and chaetotaxy of head and body follow Najer *et al.* (2016). Leg chaetotaxy follows Gustafsson *et al.* (2019). To draw the figures, the following procedure was followed: drawings were made with (1) a CX21FS1 light wide-field upright microscope (Olympus, Tokyo, Japan) fitted with a drawing tube; after drawing, the illustrations were edited using Adobe Illustrator CS6 on a tablet PTZ-930 (Wacom, China); or (2) a Nikon Eclipse TI-E inverted light microscope (Nikon, Tokyo, Japan) fitted with an Andor Clara camera (Oxon, United Kingdom); background photos for the drawings were taken using NIS Elements 4.50.00 LO (Nikon, Tokyo, Japan); after drawing, the illustrations were edited using GIMP (available on <https://www.gimp.org>, downloaded in October 2018) on an Intuos 3 PTZ-1230 tablet (Wacom, China). All dimensions are given in millimeters and were taken using an optical scale in the light microscope, between the same points as explained in Najer *et al.* (2016) and shown in Figs 2–3. The nomenclature of setae presented by Gustafsson & Bush (2017) for the *Brueelia* complex was partially applied here for setae that were not assessed in Najer *et al.* (2016). This concerns in particular the abdominal setae, with the difference that *psps* (postspiracular principal setae) and *tps* (tergal posterior setae) could not be distinguished in *Philopterus* from Acrocephalidae and Regulidae, so they are counted together and presented as *tcs* (tergo-central setae) in this paper. *Aps* (accessory postspiracular setae) are missing in all the specimens examined, so they are not further mentioned. The abbreviations used for the other setae groups are shown in Fig. 3: *ps* = paratergal seta; *ss* = sutural seta; *sts* = sternal seta. In addition, the presence of the *ats* (= anterior tergal seta), introduced by Cicchino & Castro (1996), is also assessed. In the head chaetotaxy the *pts* = posttemporal seta is added, which was not visible in material studied by Najer *et al.* (2016). The *ms* = mental setae were not mentioned in any previous *Philopterus*-related literature but we observed them in all examined specimens, so we introduce the term here. The *pos* = postocular seta is named “preocular” by Gustafsson & Bush (2017), however, it is placed behind the eye, not in front of it. Therefore we rename it here, keeping for it the same abbreviation. In the thoracic chaetotaxy, we introduce term pterothoracic lateral seta (*ptls*) for the group of setae placed in the lateral corner of pterothorax (Fig. 3).

For the genetic analyses, DNA was extracted using a commercial Quigen Blood and Tissue kit. The set of extracts was amplified with the polymerase chain reaction (PCR) using primers commonly used for amplification of the mitochondrial cytochrome oxidase I (*COI*, primers COI-L6625 and COI-H7005) gene and the primers presented by Sweet *et al.* (2014) for the nuclear loci *hyp* (BR50-181L and BR50-621R) and *TMEDE6* (BR69-190F and BR69-432R). These first PCRs were set up in 25 µl, using 3 µl of DNA extract, and run at the INHS in PTC-100 Peltier Thermal Cycler (MJ Research, Waltham, MA) using the following protocol: denaturation at 94°C for 2 minutes, then cycles of denaturation at 94°C for

30 s, annealing at 46°C for 30 s, extension at 72°C for 30 s, repeated 35 times and a final extension step at 72°C for 7 minutes. In a few samples, in which some marker did not amplify, the reaction was repeated in 50 µl volume; if the reaction still did not proceed, the volume of DNA extract was increased from 3 to 5 µl (and dH₂O reduced to 16 µl). After PCR, the samples were purified with Gel/PCR DNA Fragments Extraction Kit (Geneaid, Taiwan) according to the standard protocol and subsequently sequenced by the commercial service of Macrogen, Amsterdam, The Netherlands. The obtained respective sequences of the *COI*, *hyp* and *TMEDE6* genes were aligned in Geneious 9.1.8 (Kearse *et al.* 2012). In order to assess genetic divergence of the obtained sequences and other taxa examined by us, net average interspecific *p*-distances between *Ph. acrocephalus*, *Ph. gustafssoni* sp. nov. and their two probably nearest relatives (Najer, unpublished results) – *Philopterus citrinellae* (Schrank, 1776) and *Philopterus fringillae* (Scopoli, 1772) – were computed in MEGA 7.0.14 (Kumar *et al.* 2016) using four datasets: *COI* (379 bp), *hyp* (386 bp), *TMEDE6* (220 bp), and the concatenated sequences of all three fragments (985 bp).

Abbreviations

Leg chaetotaxy

<i>a</i>	=	anterior seta
<i>c</i>	=	coxa
<i>d</i>	=	dorsal seta
<i>dm</i>	=	distal marginal seta
<i>f</i>	=	femur
<i>p</i>	=	posterior seta
<i>t</i>	=	trochanter
<i>v</i>	=	ventral seta

Sclerites

<i>sgp</i>	=	subgenital plate
<i>svs</i>	=	subvulvar sclerite
<i>vs VIII</i>	=	vestigial sternite VIII

Setae

<i>ads</i>	=	anterior dorsal seta
<i>as</i>	=	anterior seta
<i>ats</i>	=	anterior tergal seta
<i>avs</i>	=	anterior ventral seta
<i>dsms</i>	=	dorsal submarginal seta
<i>mds</i>	=	mandibular seta
<i>ms</i>	=	mental seta
<i>mts</i>	=	marginal temporal seta
<i>os</i>	=	ocular seta
<i>pas</i>	=	preantennal seta
<i>pcs</i>	=	preconal seta
<i>plts</i>	=	setae on lateral part of pterothorax
<i>pns</i>	=	postnodal seta
<i>pos</i>	=	postocular seta
<i>pps</i>	=	pronotal post-spiracular seta
<i>ps</i>	=	paratergal seta
<i>pths</i>	=	pterothoracic seta
<i>ptls</i>	=	pterothoracic lateral seta
<i>pts</i>	=	posttemporal seta
<i>s</i>	=	sensillus

<i>ss</i>	=	sutural seta
<i>sts</i>	=	sternal seta
<i>tcs</i>	=	tergocentral seta
<i>vsms</i>	=	ventral submarginal seta

Body parts

ADP	=	dorsal anterior preantennal plate
EM	=	endomere
MM	=	mesomere

Measurements

ADPL	=	anterior dorsal plate length
ADPW	=	anterior dorsal plate width
AL	=	length of abdomen
ANW	=	anterior notch width
APLL	=	anterior dorsal plate lateral length
AW	=	maximal width of abdomen
EWG	=	external width of genital chamber
GL	=	male genitalia length
GW	=	male genitalia width
HL	=	head length
IWG	=	internal width of genital chamber
PAL	=	preantennal length
PAW	=	preantennal width
PMCL	=	premarginal carina length
POL	=	postantennal length
PTL	=	pterothorax length
PTW	=	pterothorax width
PW	=	prothorax width
TL	=	total length
TPVL	=	tergal plate V length
TRL	=	trabecula length
TRW	=	trabecula width
TW	=	temporal width
SGPW	=	subgenital plate width

Institutions acronyms

MGAB	=	“Grigore Antipa” National Museum of Natural History, Bucharest, Romania
MMBC	=	Moravian Museum, Brno, Czechia
MNHW	=	Museum of Natural History, University of Wrocław, Wrocław, Poland
NHML	=	Natural History Museum, London, United Kingdom
USNM	=	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
UVPS	=	personal collection of Oldrich Sychra at the University of Veterinary and Pharmaceutical Sciences, Brno, Czechia (UVPS)
ZIN	=	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

Results

All 28 examined *A. melanopogon* (11 in 2008, 9 in 2009 and 8 in 2016) caught at Gbelce were parasitized by *Ph. acrocephalus* (100% prevalence). Altogether 158 lice (44 males, 52 females and 62 nymphs) were collected at this location. At Nea Agathoupoli, only two of the 10 birds (prevalence 20%) were

parasitized and together three lice (one male, one female, one nymph) were gathered. Concerning *Ph. gustafssoni* sp. nov., 16 out of 54 examined *R. regulus* (30%) and two of seven *R. ignicapillus* (Temminck, 1820) (29%) were parasitized by this species (19 females, 15 males, 63 nymphs and 1 female and 4 nymphs were found, respectively).

Order Phthiraptera Haeckel, 1896
 Suborder Ischnocera Kellogg, 1896
 Family Philopteridae Burmeister, 1838
Philopterus complex (*sensu* Mey 2004)

Genus *Philopterus* Nitzsch, 1818

Type species: *Philopterus ocellatus* (Scopoli, 1764).

Remarks

Until now, all *Philopterus* known from both Acrocephalidae and Regulidae were included in so called “*reguli*” species group. This species group was established by Złotorzycka & Lucińska (1976), but their description of the group is very general. It uses formulations which do not enable identification of this group without extensive comparison of large series of material (e.g., “mostly trapezoidal” or “mostly shaped differently than in another groups”). Besides *Ph. reguli*, the authors place in this group also *Philopterus rubeculae* (Denny, 1842), *Philopterus capillatus* (Złotorzycka, 1964), *Philopterus desertus* (Złotorzycka, 1964), *Philopterus pallescens* (Denny, 1842), *Philopterus rutteri* (Kellogg, 1899), *Philopterus modularis* (Denny, 1842), *Philopterus emiliae* Balat, 1955, *Philopterus mirificus* (Złotorzycka, 1964) and *Philopterus necopinatus* (Złotorzycka, 1964, the two latter species being known from *Acrocephalus* J.A. Naumann & J.F. Naumann, 1811). In the end of the description they declare identity of the whole group as questionable.

Mey (1983) claims that diagnostic features of this group should be shape of head and anterior dorsal plate, pleural chaetotaxy of abdominal segment IV, chaetotaxy of pronotum and “characteristic features of male genitalia” (without being more concrete). However, in any of these characteristics he does not describe how should they look like to be diagnostic for the species group. He places to this group only *Ph. reguli*, *Ph. pallescens* and *Ph. rutteri*. For *Ph. modularis* and seven other species (*Ph. emiliae*, *Ph. rubeculae*, *Ph. capillatus*, *Ph. desertus*, *Ph. davuricae* Fedorenko & Volkov, 1977, *Ph. markevichi* Fedorenko & Volkov, 1977 and *Ph. mugimaki* Fedorenko & Volkov, 1977), he newly established the *modularis* species group; however, he does not provide further description of this group. Concerning *Philopterus fedorenkoae* (Mey, 1983), *Ph. mirificus* and *Ph. necopinatus*, he states that their relationship to the *reguli* species group cannot be resolved until examination of more material.

We examined the holotype of *Philopterus reguli* (NHML). This specimen is morphologically different (e.g., in shape of head, shape of dorsal preantennal head plate, thoracic and abdominal chaetotaxy, shape of subgenital plate) from all other examined *Philopterus* from Regulidae. Therefore, we hereby pronounce it to be a straggler and below we describe the species infesting Regulidae as a new species, *Philopterus gustafssoni* sp. nov. We also examined the material on which Złotorzycka & Lucińska (1976) based description of “*reguli*” species group. All these specimens (see below) are in fact *Ph. gustafssoni* sp. nov., so if the species group exists, it should be rather named *gustafssoni* species group. Concerning other species of the group, the types of *Ph. mirificus* and *Ph. necopinatus* are lost (Jaloszynski *et al.* 2014), so we could not assess morphological similarity of these two species and *Ph. gustafssoni* sp. nov. We tried to contact Eberhard Mey in order to get information about type material of *Ph. fedorenkoae* and specification of “*reguli*” (now *gustafssoni*) species group diagnosis, but without any success. Figures accompanying description of *Ph. fedorenkoae* (Mey 1983) show that this species differs from

Ph. gustafssoni sp. nov. in several features (e.g., shape of head and dorsal head plate, pronotal chaetotaxy, shape of male subgenital plate), so it does not belong to the species group regardless it exists or not. We can also state that all by us examined *Philopterus* from *Acrocephalus* warblers (including those which might be *Ph. fedorenkoae*, see below) are clearly different from *Ph. gustafssoni* sp. nov. (see below) and do not form one species group. In other figures provided by Mey (1988), *Ph. pallescens*, *Ph. rutteri*, *Philopterus hercynicus* (Mey, 1988) and *Philopterus peripariphilus* (Mey, 1988) show similar head shape, anterior dorsal plate shape and pronotal chaetotaxy (with more than one pair of pronotal setae) as *Ph. gustafssoni* sp. nov. This paper, however, does not contain illustrations of male genitalia (except *Ph. hercynicus*) and subgenital plates. Therefore, we cannot resolve justification of this species group without extensive revision of *Philopterus* from Paridae Vigors, 1825. This revision is currently ongoing and it will be presented in a separate article, so hereby we only state that *Ph. acrocephalus* does not belong to this species group.

***Philopterus acrocephalus* Carriker, 1949**

Figs 1–5, 8A–B; Tables 2–5

Material examined

Holotype

USA • ♀ (Fig. 1); Marianas, Guam Island; 4 Jun. 1945; R.H. Baker leg.; ex *Acrocephalus luscinius luscinius*; USNM No. 58960.

Other material

SLOVAKIA • 1 ♂, 1 ♀; Nitra Region, Nove Zamky District, Gbelce; 47°52'N, 18°30'E; 19 Apr. 2009; T. Najer & O. Sychra leg.; ex *Acrocephalus melanopogon*; MMBC SK21 • 1 ♂, 1 ♀; same collection data as for preceding; MMBC SK22 • 1 ♂, 1 ♀; same collection data as for preceding; MMBC SK23 • 1 ♂, 1 ♀; same collection data as for preceding; MMBC SK24 • 1 ♂ (Fig. 8A), 1 ♀ (Fig. 8B); same collection data as for preceding; MMBC SK25.

ROMANIA • 1 ♀; Tulcea County, Letea; 45°20'N, 29°32'E; 9 Apr. 2011; C. Adam leg.; same host as for preceding; MGAB ISC 317 • 1 ♀; same collection data as for preceding; MGAB ISC 318 • 1 ♀; same collection data as for preceding; MGAB ISC 319 • 1 ♂; same collection data as for preceding; MGAB ISC 320 • 1 ♂; same collection data as for preceding; MGAB ISC 321 • 1 ♂; same collection data as for preceding; MGAB ISC 322.

AZERBAIJAN • 3 ♂♂, 2 ♀♀; 18 Apr. 1937; A. Ivanov leg.; same host as for preceding; ZIN • 1 ♂, 4 ♀♀; 24 Apr. 1937; same collector and host as for preceding; ZIN.

RUSSIA • 1 ♂, 1 ♀; Korsakovo; 3 Aug. 1947; Lyubin leg., same host as for preceding; ZIN I 65 • 1 ♂, 1 ♀; Astrakhan Oblast, Astrakhan State Nature Reserve; 9 Aug. 1946; ex *Acrocephalus schoenobaenus*; ZIN I-8 • 1 ♀; same collection data as for preceding; 14 Aug. 1946; ZIN I 12/7 • 1 ♂; Amur Oblast, Tambovka on Amur District; 26 Jul. 1939; D.I. Blagoveshtchensky leg.; ex *Iduna aedon rufescens*; ZIN I216 • 2 ♀♀, 3 ♂♂; same collection data as for preceding; 29 Jul. 1939; ZIN I277 • 1 ♀, 1 ♂; same collection data as for preceding; 3 Aug. 1939; ZIN I341.

AUSTRIA • 1 subad. ♀; Burgenland, Neusiedl am See; 18 Sep. 1960; F. Balat leg.; ex *Acrocephalus melanopogon*; MMBC No. 1229.

TAJIKISTAN • 4 ♀♀; Khatlon Region, Qurgonteppa; 29 May 1932; ex *Iduna rama*; ZIN I250/353 • 2 ♀♀; Districts of Republican Subordination, Gissar Range; 23 Apr. 1934; ex *Locustella* sp.; ZIN A-129.

COUNTRY UNKNOWN • 1 ♂; 8 May 1909; A. Derzhavin leg.; ex *Locustella ochotensis*; ZIN.

Additional collected material

SLOVAKIA • 18 ♂♂, 21 ♀♀, 27 ♀♀; Nitra Region, Nove Zamky District, Gbelce; 47°52'N, 18°30'E; 12 Apr.–3 May 2008; I. Literak, M. Capek & O. Sychra leg.; ex *Acrocephalus melanopogon*; UVPS • 12 ♂♂, 6 ♀♀, 18 ♀♀; same collection data and host as for preceding; 18 Apr.–1 May 2009; T. Najer, I. Literak, M. Capek & O. Sychra leg.; UVPS • 11 ♂♂, 20 ♀♀, 16 ♀♀; same collection data and host as for preceding; 18–21 Apr. 2016; T. Najer, T. Judak, L. Oslejskova & O. Sychra leg.; UVPS.

GREECE • 1 ♂, 1 ♀, 1 ♀; Pieria, Central Macedonia Region, Nea Agathoupoli; 40°27'N, 22°34'E; 14 Dec. 2013; A. Diakou leg.; same host as for preceding; UVPS.



Fig. 1. *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus luscinius*: female holotype (USNM No. 58960), dorsal view. Scale bar: 0.1 mm.

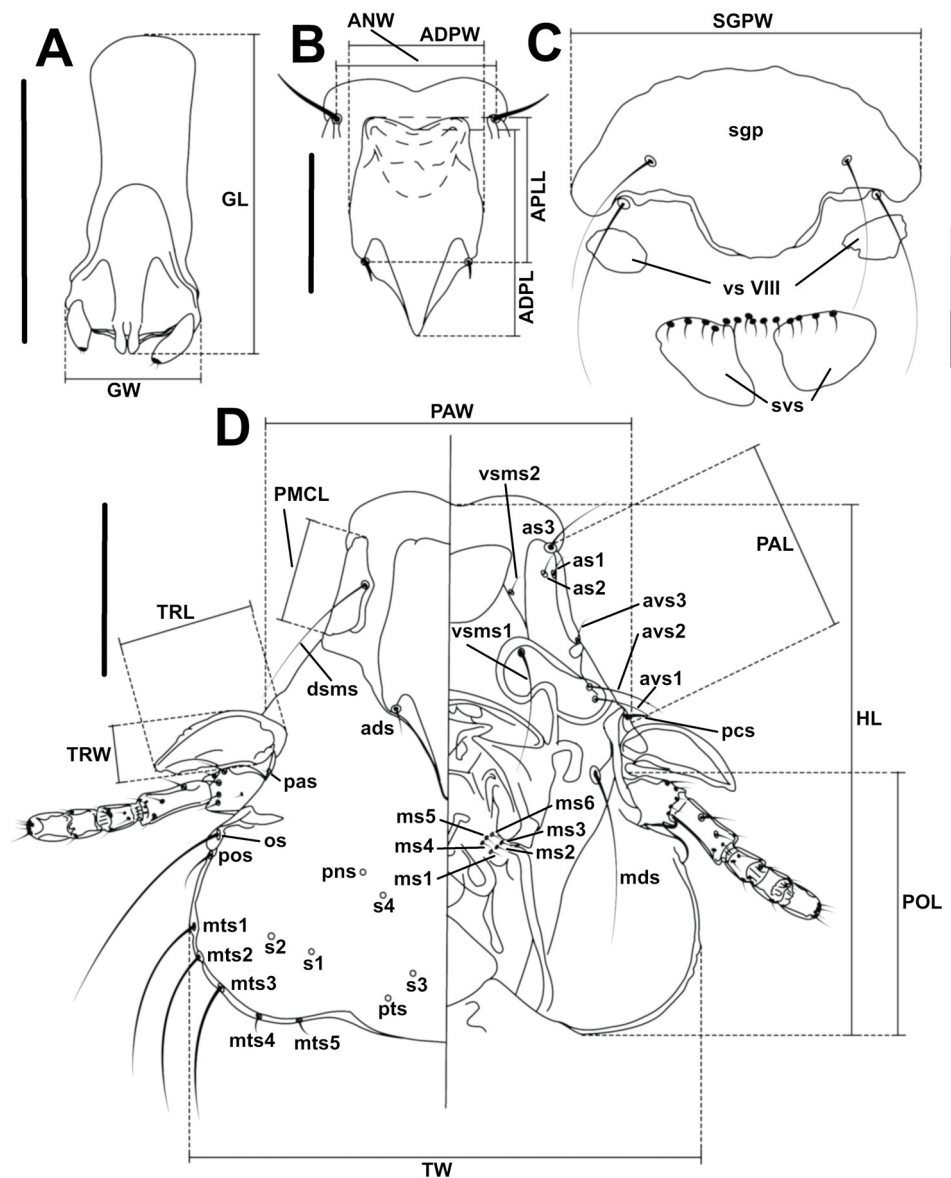


Fig. 2. *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus melanopogon* (SK25 in MMBC): points of measurements and nomenclature of sclerites and setae. **A.** Male genitalia, ventral view. **B.** Male dorsal preantennal plate (ADP), dorsal view. **C.** Female subgenital plate and ventral terminalia, ventral view. **D.** Male head, dorsal and ventral views. Abbreviations: sclerites: *sgp* – subgenital plate; *svv* – subvulvar sclerite; *vs VIII* – vestigial sternite VIII; setae: *ads* – anterior dorsal seta; *as* – anterior seta; *avs* – anterior ventral seta; *dsms* – dorsal submarginal seta; *mds* – mandibular seta; *ms* – mental seta; *mts* – marginal temporal seta; *os* – ocular seta; *pas* – preantennal seta; *pcs* – preconal seta; *pos* – postocular seta; *pns* – postnodal seta; *pts* – posttemporal seta; *s* – sensillus; *vsms* – ventral submarginal seta. Measurements: ADPL – anterior dorsal plate length; APLL – anterior dorsal plate lateral length; ADPW – anterior dorsal plate width; ANW – anterior notch width; GL – male genitalia length; GW – male genitalia width; HL – head length; PAL – preantennal length; PAW – preantennal width; PMCL – premarginal carina length; POL – postantennal length; TRW – trabecula width; TRW – trabecula length; TW – temporal width; SGPW – subgenital plate width. Scale bars: 0.1 mm.

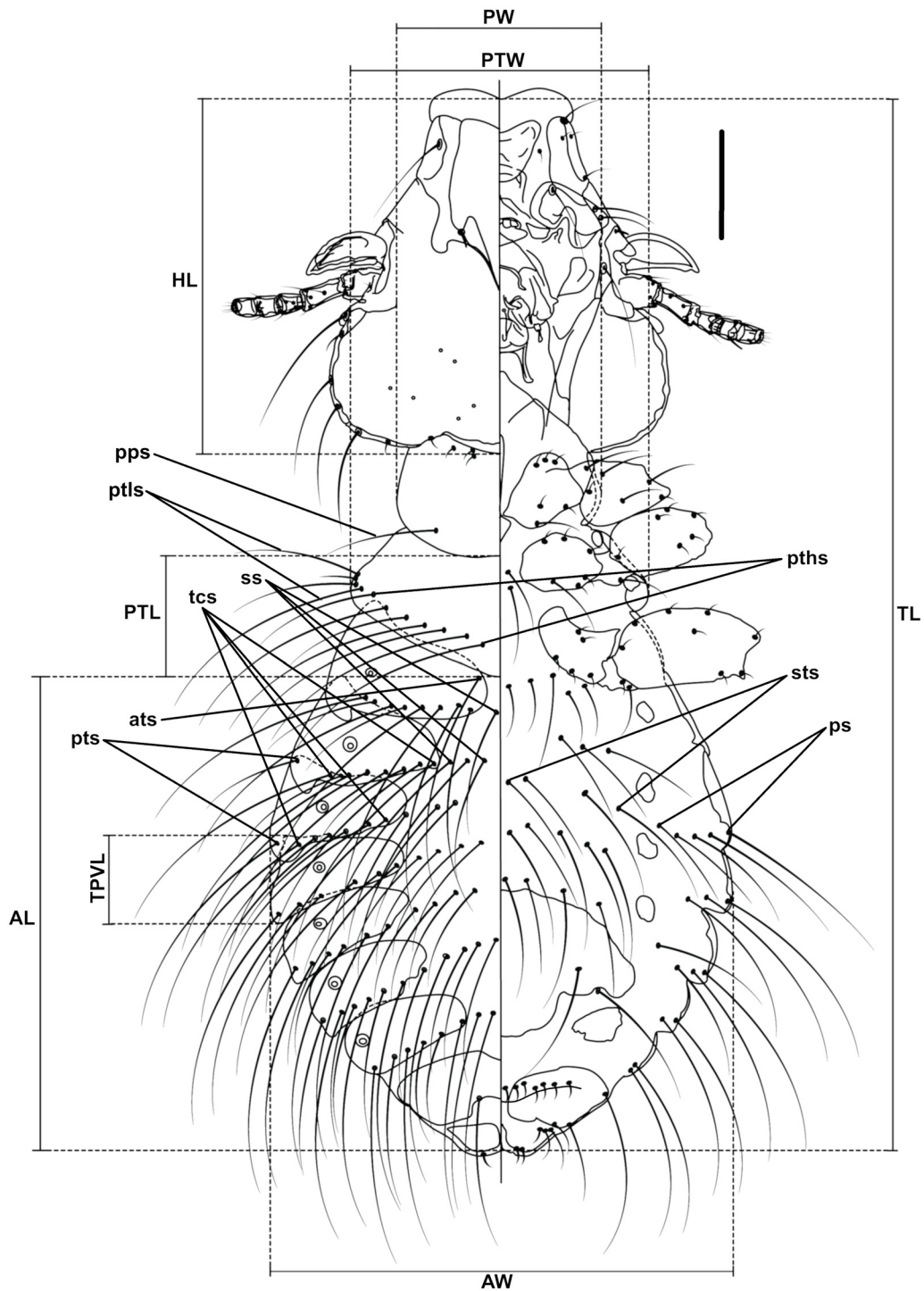


Fig. 3. *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus melanopogon* (SK25 in MMBC): female habitus showing points of measurements and nomenclature of abdominal setae, dorsal and ventral views. Abbreviations: setae: *ats* – anterior tergal seta; *ps* – paratergal seta; *pps* – pronotal post-spiracular seta; *pths* – pterothoracic seta; *ptls* – pterothoracic lateral seta; *ss* – sutural seta; *sts* – sternal seta; *tcs* – tergocentral seta. Measurements: AL – length of abdomen; AW – maximal width of abdomen; HL – head length; PTL – pterothorax length; PW – prothorax width; PTW – pterothorax width; TL – total length; TPVL – tergal plate V length. Scale bars: 0.1 mm.

Not determinable material

In addition to the examined material of *Ph. acrocephalus*, we examined the following specimens. They were noticeably different from *Ph. acrocephalus* but could not be determined because of a lack of available material of other species for comparison.

CZECHIA • 6 ♂♂; Highlands Region, Jihlava District, Jihlava; 25 Aug. 1958; F. Balat leg.; ex *Acrocephalus scirpaceus*; MMBC No. 1387.

POLAND • 3 ♂♂; Warmian-Masurian Voivodeship, Braniewo County, Pasleka; 19 Aug. 1963; Busse leg.; ex *Acrocephalus palustris*; labeled as *Docophorus mirificus*; MNHW 8/i/4–6.

EGYPT • 1 ♀; Bahiq; 7 Oct. 1966; ex *Acrocephalus schoenobaenus*; labeled as *Philoferus necopinatus*; USNM.

AUSTRIA • 1 subad. ♂; Burgenland, Neusiedl am See; 17 Sep. 1960; F. Balat leg.; ex *Acrocephalus scirpaceus*; MMBC No. 1232.

COUNTRY UNKNOWN • 1 ♂, 2 ♂♂; 25 May 1931; ex *Iduna aedon*; ZIN 1463.

Description

Both sexes

Head as in Fig. 4C, slightly longer than wide, with frons slightly concave, preantennal region with slightly concave lateral margin approximately the same length as the postantennal margin. Hyaline margin enlarged, wider than frons. Dorsal anterior preantennal plate (ADP) as in Fig. 4B, with slightly centrally indented anterior margin and straight or slightly concave anterior part of lateral margin. Posterolateral margin of ADP straight or slightly concave, but not sclerotized and therefore almost not apparent, the sclerotization of ADP forming 1 wide, large central and 2 small lateral triangular projections with straight margin, the indentations between the central and lateral projections about the same size as the lateral projections, sharply angled (Fig. 4B). Ventral anterior plate as in Fig. 4C, with lateral and posterior margins continuously merging into 1 rounded postero-lateral margin. Prothorax as in Fig. 4A, E, with 1 long postero-lateral *pps* on each side and 3 short thorn-like setae on each side of its anterior margin. Prosternum narrow and elongated, mesosternum rhombic. In place of metasternum 2 medium-long setae on each side. Pterothorax with 5–6 long setae (*pths*) on each side. Pterothorax with lateral margins straight, reaching approximately to the same level as spiracles on segment II. Tergopleurites II–IX all with long most lateral seta, tergo-central setae (*tcs*) generally very long, mostly overreaching length of 3 abdominal segments, sutural setae (*ss*) medium-long, about the length of 2 abdominal segments. Leg chaetotaxy as in Fig. 5, measurements as in Table 3.

Male

Habitus as in Fig. 4A, head as in Fig. 4C. Lateral parts of pterothorax with 4 separate setae (*ptls*) on each side, 1 medium-long (1st, counting from the most lateral), 2 short (2nd–3rd) and 1 long (4th). Thoracic and abdominal chaetotaxy as in Fig. 4A and Table 2. Sternal setae (*sts*) on segments II–III short, on segments IV–VI medium long, shorter or approximately the same length as *ss*. Subgenital plate of rectangular shape, as in Fig. 4A, with rounded anterior margin, with only slight indentations on both lateral sides. Posterior margin of central part of subgenital plate not clear, 2 (median long and lateral medium-long) setae at the level of anterior lateral indentation and 1 medium-long seta at the level of posterior lateral indentation on each side. Genitalia as in Fig. 4D, basal apodeme long and quadrangular, lateral margins concave, anterior margin rounded. Parameres elongated, length about ½ of width of basal plate, overreaching the mesosome, kidney-shaped, clearly separated from the basal plate, with 2 sensillae on each side of posterior margin. Mesosome consisting of 2 fingerlike parts, which are parallel

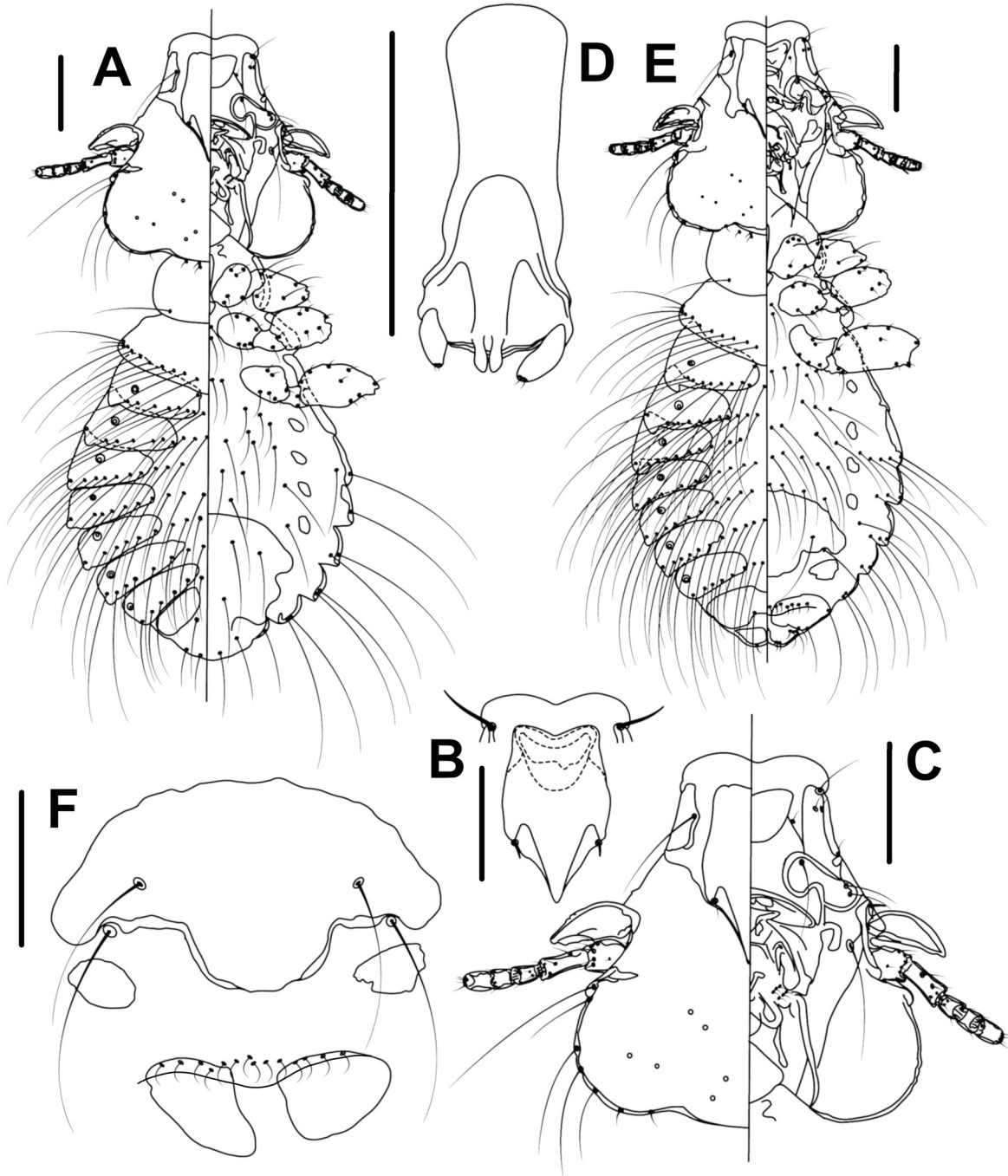


Fig. 4. *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus melanopogon* (SK25 in MMBC). A. Male habitus, dorsal and ventral views. B. Male dorsal anterior plate (ADP), dorsal view. C. Male head, dorsal and ventral views. D. Male genitalia, ventral view. E. Female habitus, dorsal and ventral views. F. Female subgenital plate, vulval margin and ventral terminalia, ventral view. Scale bars: 0.1 mm.

to each other, proximally fused with basal plate, with bulbous distal part and bluntly pointed postero-medial end.

Female

Habitus as in Fig. 4E. Lateral part of pterothorax with 3 separate setae (*ptls*), 1st and 3rd counting from the most lateral medium-long, the 2nd short. Thoracic and abdominal chaetotaxy as in Fig. 4E and Table 2. Sternal setae (*sts*) on segment II short, on the other segments medium-long, on segments III–IV shorter, on segments V–VI about the same length as *ss*, the most median VI *sts* longer than the others. Subgenital plate (Fig. 4F) with rounded anterior margin, concave posteriolateral margins and rounded central part of posterior margin. Postero-lateral parts of subgenital plate separated as vestigial sternites VIII (Fig. 4F). Two long lateral setae on each side, 1 in area of original sternite VII, 1 behind the posterior margin of lateral sternite VII. Subvulval sclerites, associated chaetotaxy and vulval margin as in Fig. 4F. Inner genital sclerites missing, the area where the vulval margin is visible in other *Philopterus* species with a row of 7 short slender setae on each side.

Hosts

Type host

Acrocephalus luscinius (Quoy & Gaimard, 1830).

Other hosts

Acrocephalus melanopogon (Temminck, 1823), *Acrocephalus scirpaceus* (Hermann, 1804), *Acrocephalus schoenobaenus* (Linnaeus, 1758) – from these three hosts, some *Philopterus* species are described, but it is not definitely confirmed that they are synonyms of *Ph. acrocephalus*. Therefore, we cannot exclude that material examined by us represents new host records. *Iduna aedon rufescens* Stegmann, 1929 – new host record, *Iduna rama* (Sykes, 1832) – new host record, *Locustella* sp. – new host record, *Locustella ochotensis* (von Middendorff, 1853) – new host record.

Distribution

Type locality

USA, Guam Island.

Other published locations

Czechia (Balat *in* Hudec 1983); Hungary (Vas *et al.* 2012a); Greece, Nea Agathoupoli (Diakou *et al.* 2017). Always mentioned as *Philopterus* sp. ex *A. melanopogon*, considered to be *Ph. acrocephalus* according to host association.

Newly reported locations

Slovakia, Gbelce; Romania, Letea; Greece, Nea Agathoupoli; Azerbaijan without further specification; Russia, Astrakhan State Nature Reserve; Russia, Korsakov; Russia, Tambovka in Amur District; Tajikistan, Gissar Range; Tajikistan, Qurgonteppa; Austria, Neusiedl am See.

Remarks

Because the holotype is rather old and not all its morphological features are clearly visible, were used specimens of *A. melanopogon* collected in Slovakia for the drawings. The genitalia of the male used to draw all male figures differ in appearance from the other examined males due to the slide-mounting process. The mesosome of these male genitalia is bent upwards, so the shape is not clearly visible. For this reason, for the figure of the male genitalia, we used the mesosome of another specimen, the genitalia of which are otherwise the same as those of the mainly drawn specimen. Specimens of *Ph. acrocephalus* from Azerbaijan have a relatively more narrow central posterior projection of the ADP; in other ways, the morphological features are the same as in the other examined material. In general, the relative

Table 2. Abdominal chaetotaxy for *Philopterus acrocephalus* Carriker, 1949 and *Philopterus gustafssoni* sp. nov. Numbers in parentheses are modes. Sternal code: l – long seta. Letters in parentheses under sternal code refer to missing setae in some specimens.

Abdominal chaetotaxy male <i>Philopterus acrocephalus</i>					
Segment	Paratergal	Tergocentral	Sutural	Sternal number	Sternal code
II	0	5–8 (6)	0–1 (1)	2–5 (3)	III(II)–(II)II
III	1	5–8 (7)	0–4 (3)	3–6 (3)	III(I)–(III)III
IV	3–6 (4)	5–7 (7)	1–5 (4)	3–5 (5)	III(II)–(II)III
V	3–6 (5)	5–7 (5)	2–5 (4)	2–5 (4)	III(I)–(III)II
VI	3–5 (3)	4–7 (6)	2–6 (4)	2–5 (4)	II(III)–(III)II
VII	2–5 (3)	3–7 (6)	1–3 (2)		
VIII	1–3 (3)	3–6 (3)	1–2 (1)		
IX+X		0–2 (2)			

Abdominal chaetotaxy female <i>Philopterus acrocephalus</i>					
Segment	Paratergal	Tergocentral	Sutural	Sternal number	Sternal code
II	0	5–10 (8)	1–2 (1)	1–4 (3)	II(II)–(III)I
III	1	5–11 (7)	2–4 (3)	2–6 (4)	III(III)–(III)II
IV	2–7 (5)	3–12 (6)	2–6 (4)	2–7 (3)	II(III)–(III)II
V	4–7 (5)	3–11 (5)	2–5 (4)	3–6 (4)	III(III)–(II)III
VI	3–6 (4)	3–9 (5)	3–5 (5)	1–5 (4)	II(III)–(III)I
VII	2–5 (3)	3–8 (6)	3–4 (4)		
VIII	2–3 (3)	2–6 (5)	1–2 (1)		
IX+X		1–2 (2)			

Abdominal chaetotaxy male <i>Philopterus gustafssoni</i> sp. nov.					
Segment	Paratergal	Tergocentral	Sutural	Sternal number	Sternal code
II	0	6–9 (8)	0–3 (2)	3–8 (5)	IIII(III)–(IIII)III
III	0–2 (1)	5–9 (7)	1–6 (3)	5–10 (5)	IIII(IIII)–(IIII)IIII
IV	1–9 (3)	5–10 (7)	2–8 (7)	5–10 (9)	IIII(IIII)–(IIII)IIII
V	2–8 (5)	4–9 (7)	4–9 (6)	5–12 (8)	IIIIII(III)–(IIII)IIII
VI	2–8 (4)	6–8 (6)	5–8 (7)	5–10 (8)	IIII(IIII)–(III)IIII
VII	0–6 (4)	4–7 (7)	4–6 (5)		
VIII	1–6 (2)	2–5 (3)	0–2 (0)		
IX+X		0–1 (1)			

Abdominal chaetotaxy female <i>Philopterus gustafssoni</i> sp. nov.					
Segment	Paratergal	Tergocentral	Sutural	Sternal number	Sternal code
II	0	6–11 (8)	1–5 (4)	3–8 (6)	III(IIII)–(III)III
III	0–2 (1)	6–10 (9)	4–8 (4)	4–12 (9)	III(IIII)–(IIII)IIII
IV	1–7 (3)	5–9 (7)	6–12 (9)	7–13 (8)	IIIIII(III)–(IIII)IIII
V	1–6 (3)	5–8 (8)	4–11 (10)	5–11 (11)	IIII(IIII)–(IIII)IIII
VI	1–8 (4)	5–9 (6)	5–11 (9)	4–12 (8)	IIII(IIII)–(IIII)IIII
VII	2–4 (3)	6–9 (6)	4–10 (5)		
VIII	1–4 (3)	2–7 (3)	0–5 (3)		
IX+X		0–1 (1)			

size of lateral and posterior ADP projections shows the largest variability of all the morphological characteristics.

Genetic diversity

Two specimens of *Ph. acrocephalus* from *Acrocephalus melanopogon* were genetically analysed, in which all three examined genes (mitochondrial *COI*, nuclear *hyp* and *TMEDE6*) amplified. Since both examined specimens were from the same host species, their sequences also showed 100% identity in all three genes and the concatenated sequences as well (Table 4). The three other species for genetic comparison, *Ph. gustafssoni* sp. nov. (net interspecific *p*-distances 23.1% for *COI*, 1.6% for *hyp*, 0.8% for *TMEDE6* and 9.7% for the concatenated sequences), *Ph. fringillae* (24.5% for *COI*, 1.8% for *hyp*, 1.4% for *TMEDE6* and 10.5% for the concatenated sequences) and *Ph. citrinellae* (19.8% for *COI*, 1.8% for *hyp*, 1.2% for *TMEDE6* and 8.6% for the concatenated sequences) were chosen because their net interspecific *p*-distances from *Ph. acrocephalus* were the shortest from all by us sequenced *Philopterus* samples (Najer, unpublished results). More details about these distances are given in Table 5.

Philopterus fedorenkoae (Mey, 1983)

Material examined

CZECHIA • 1 ♀; S Moravian Region, Breclav District, pond Nesyt; 22 May 1948; F. Balat leg.; ex *Acrocephalus arundinaceus*; MMBC No. 29 • 4 ♀♀, 1 ♂, 1 ♂; S Moravian Region, Breclav District, Lednice, Mlynsky pond; 8 May 1948; F. Balat leg.; same host as for preceding; labeled as *Philopterus*

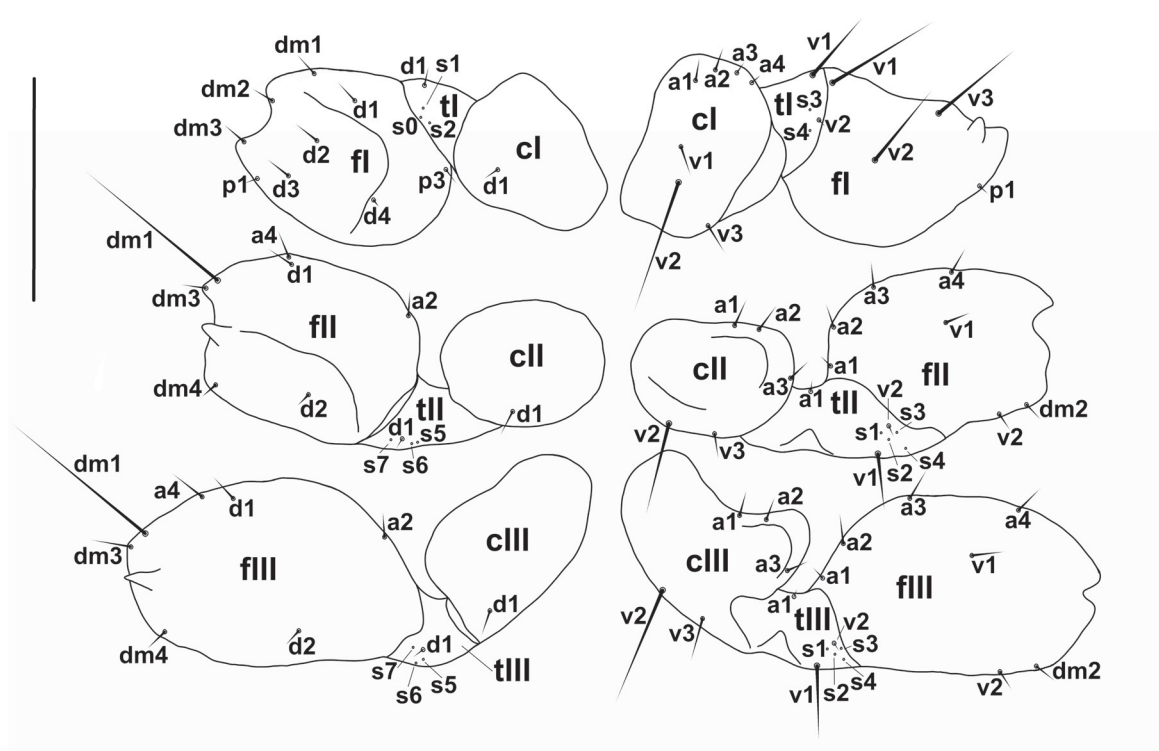


Fig. 5. *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus melanopogon* (SK25 in MMBC): nomenclature of male leg chaetotaxy, dorsal and ventral views. Abbreviations: *c* – coxa; *t* – trochanter; *f* – femur; *dm* – distal marginal seta; *d* – dorsal seta; *a* – anterior seta; *p* – posterior seta; *s* – sensillus; *v* – ventral seta. Scale bar: 0.1 mm.

Table 3. Measurements of *Philopterus acrocephalus* Carriker, 1949 and *Philopterus gustafssoni* sp. nov. Ranges with mean values in parentheses. Abbreviations: *pas* – preantennal seta; *pcs* – preconal seta; *dsms* – dorsal submarginal seta; *as3* – third anterior seta; ADPL – anterior dorsal plate length; APLL – anterior dorsal plate lateral length; ADPW – anterior dorsal plate width; ANW – anterior notch width; AW – maximal width of abdomen; AL – length of abdomen; GL – male genitalia length; GW – male genitalia width; HL – head length; EWG – external width of genital chamber; IWG – internal width of genital chamber; PAL – preantennal length; PAW – preantennal width; PMCL – premarginal carina length; POL – postantennal length; PTW – pterothorax width; PTL – pterothorax length; PW – prothorax width; SGPW – subgenital plate width; TL – total length; TPVL – tergal plate V length; TRL – trabecula length; TRW – trabecula width; TW – temporal width.

	<i>Philopterus acrocephalus</i>		<i>Philopterus gustafssoni</i> sp. nov.	
	Male	Female	Male	Female
<i>pas</i>	0.0038–0.0100 (0.0065)	0.0038–0.0775 (0.0104)	0.0550–0.1500 (0.0969)	0.0500–0.1325 (0.0884)
<i>pcs</i>	0.0100–0.0175 (0.0126)	0.0075–0.0175 (0.0144)	0.0250–0.1100 (0.0766)	0.0300–0.1425 (0.0820)
<i>dsms</i>	0.0975–0.1575 (0.1219)	0.0770–0.1600 (0.1216)	0.0700–0.2625 (0.1540)	0.1000–0.3500 (0.1892)
<i>as3</i>	0.0475–0.0750 (0.0637)	0.0500–0.1100 (0.0709)	0.0450–0.0725 (0.0558)	0.0500–0.0750 (0.0631)
ADPL	0.1975–0.2275 (0.2169)	0.1230–0.2500 (0.2231)	0.1800–0.2250 (0.2041)	0.2250–0.3225 (0.2442)
APLL	0.1300–0.1600 (0.1463)	0.1510–0.1738 (0.1643)	0.1050–0.1975 (0.1439)	0.1175–0.1800 (0.1568)
ADPW	0.1270–0.1375 (0.1328)	0.1290–0.1600 (0.1489)	0.1050–0.1375 (0.1194)	0.1225–0.1575 (0.1379)
ANW	0.1300–0.1750 (0.1633)	0.1610–0.1975 (0.1803)	0.0725–0.1225 (0.1005)	0.0900–0.1800 (0.1175)
AW	0.5525–0.6063 (0.5887)	0.5480–0.8650 (0.6774)	0.5200–0.7800 (0.6583)	0.1525–0.9150 (0.7352)
AL	0.5450–0.6225 (0.5911)	0.6350–0.8425 (0.7307)	0.5900–0.9000 (0.7539)	0.1925–1.1000 (0.8927)
GL	0.1600–0.2500 (0.2202)		0.1950–0.2550 (0.2218)	
GW	0.0550–0.0863 (0.0759)		0.0475–0.0900 (0.0782)	
HL	0.4288–0.4938 (0.4593)	0.0750–0.5400 (0.4635)	0.4200–0.5000 (0.4505)	0.4600–0.6200 (0.5240)
EWG		0.0813–0.1870 (0.0960)		0.0650–0.0925 (0.0786)
IWG		0.0500–0.4020 (0.0962)		0.0325–0.0500 (0.0443)
PAL	0.1425–0.1650 (0.1570)	0.1550–0.1775 (0.1676)	0.1725–0.2050 (0.1925)	0.1925–0.2250 (0.2144)
PAW	0.2650–0.3350 (0.3036)	0.2980–0.3625 (0.3381)	0.3050–0.3600 (0.3377)	0.3425–0.5000 (0.3925)
PMCL	0.0875–0.1125 (0.0946)	0.0770–0.1500 (0.1026)	0.0900–0.1225 (0.1036)	0.1050–0.1325 (0.1159)
POL	0.2050–0.2900 (0.2320)	0.1950–0.3275 (0.2553)	0.2025–0.2600 (0.2420)	0.2675–0.3100 (0.2867)
PTW	0.3725–0.4363 (0.3950)	0.3590–0.4775 (0.4327)	0.1200–0.1925 (0.1641)	0.1700–0.2225 (0.1958)
PTL	0.1410–0.1750 (0.1551)	0.1525–0.1850 (0.1696)	0.3500–0.4700 (0.4186)	0.4100–0.5400 (0.4819)
PW	0.2600–0.3225 (0.2778)	0.2370–0.3225 (0.2941)	0.1225–0.1950 (0.1480)	0.1250–0.1950 (0.1641)
SGPW		0.2850–0.3938 (0.3536)	0.1425–0.2700 (0.2109)	0.2300–0.4100 (0.3284)
TL	1.2575–1.4330 (1.3571)	1.4120–1.6825 (1.5623)	1.2500–1.6875 (1.5000)	1.5750–2.1625 (1.8250)
TPVL	0.0750–0.1225 (0.0957)	0.0930–0.1350 (0.1188)	0.1625–0.2500 (0.2069)	0.1825–0.2800 (0.2279)
TRL	0.0975–0.1190 (0.1105)	0.0985–0.1275 (0.1173)	0.0750–0.1225 (0.0955)	0.0700–0.1250 (0.1036)
TRW	0.0400–0.0500 (0.0443)	0.0430–0.0725 (0.0495)	0.0325–0.0425 (0.0380)	0.0300–0.0500 (0.0427)
TW	0.4300–0.4588 (0.4404)	0.4040–0.5175 (0.4846)	0.4200–0.5100 (0.4677)	0.1275–0.5600 (0.5013)

subflavescens; MMBC No. 62, 63, 64 • 3 ♀♀, 1 ♂; S Moravian Region, Hodonin District, Hodoninske ponds; 24 Apr. 1949; F. Balat leg.; same host as for preceding; MMBC No. 1410.

SLOVAKIA • 1 ♀; Bratislava Region, Malacky District, Jakobov; 1 Sep. 1978; F. Balat leg.; ex *Acrocephalus arundinaceus*; MMBC No. 1501.

Hosts

Type host

Acrocephalus arundinaceus arundinaceus (Linnaeus, 1758).

Distribution

Type locality

Turkmenistan, Kurtlinskoe vodokhranilishche.

Other published location

Romania (Adam & Sandor 2004), Grindul Chituc.

Newly reported locations

Czechia, pond Nesyt, Mlynsky pond, Hodoninske ponds; Slovakia, Jakobov.

Remarks

The description published by Mey (1983), in our view, contains enough morphological characters for determination of this species. We examined material from Balat's collection (MMBC), which in all morphological features corresponds to this description. Even after several attempts to contact E. Mey and the National Academy of Sciences of Ukraine (where it should be stored), we did not get any information about the type material. Therefore, we could not compare our own examined specimens to the type material and cannot verify identity of the species for 100%.

Philoferus reguli (Denny, 1842)

Material examined

Holotype

[UNITED KINGDOM] • ♀; H. Denny leg.; ex *Regulus regulus*; NHML NHMUK010710741, ecat. 8192226.

Misidentified material

The following additional specimens deposited in NHML are designated as *Ph. reguli* but in fact they represent some other Ischnocerans not belonging to *Philoferus* complex:

Ex *Troglodytes troglodytes* (Linnaeus, 1758) (labeled as *Troglodytes vulgaris*): 1 ♂, collected in 1911 without further specification, other collecting data unknown, NHML NHMUK010646434, ecat. 7988337 • 1 ♂; collected in 1914 without further specification, other collecting data unknown; NHML NHMUK010646435, ecat. 7994159 • 1 ♀; same collection data as for preceding; NHML NHMUK010646436, ecat. 7996801.

Hosts

Type host

Regulus aurocapillus = *Regulus regulus regulus* (Linnaeus, 1758) – probably it is a straggler from another host.

Distribution**Type locality**

United Kingdom (without further specification).

Other published locations

Ex *Regulus regulus* – Azerbaijan (Blagoveshtchensky 1940 – as *Ph. subflavescens*), Bulgaria (Balat 1958), Czechia (Balat 1977), Faroe Islands (Palma & Jensen 2005), Finland (Hackman 1994), France (Seguy 1944), Germany (Mey 2003), Hungary (Vas *et al.* 2012b), Kyrgyzstan (Kravtsova 1998), Poland (Złotorzycka 1964, Złotorzycka & Lucińska 1976), Romania (Bechet 1961), Tajikistan (Blagoveshtchensky 1951 – as *Ph. subflavescens*), Sweden (Ash 1960), Turkey (Dik *et al.* 2017), Ukraine (Fedorenko 1987); Ex *Regulus ignicapillus* – Romania (Negru 1958 and Adam & Sandor 2004).

Remarks

Because the name *Ph. reguli* appeared to belong to morphologically different species than is commonly found on the type host, it is possible that all the published locations actually refer to *Ph. gustafssoni* sp. nov. However, none of the above cited publications refers to any concrete specimen, so we are not able to track them and prove their determination.

***Philopterus gustafssoni* sp. nov.**

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Figs 6–8C, D, Tables 2–5

Morphological diagnosis

Based on descriptions and illustrations published by Mey (1988), *Ph. gustafssoni* sp. nov. appears to be closely related to *Ph. pallescens*, *Ph. rutteri*, *Ph. hercynicus* and *Ph. peripariphilus*. With these four species, it shares following morphological characters: (1) broadly triangular head shape with concave frons; (2) trapezoidal anterior dorsal head plate (ADP) with concave anterior margin and heavily sclerotized posterior projection. Anterior part of lateral ADP margin concave, posterior part of lateral ADP margin convex, making all lateral ADP margin S-shaped; (3) three or more pairs of setae on posterior margin of prothorax.

According to what can be seen from the illustrations (Mey 1988), *Ph. gustafssoni* sp. nov. differs from the abovementioned species in the following combination of characters: (1) lateral margin of preantennal head straight or slightly concave in *Ph. gustafssoni* sp. nov. (Fig. 6A, C, E), but noticeably concave in *Ph. pallescens*, *Ph. rutteri*, *Ph. hercynicus* and *Ph. peripariphilus*; (2) frons indented in *Ph. gustafssoni* sp. nov. (Fig. 6A, C, E) and *Ph. hercynicus*, but slightly concave in *Ph. pallescens*, *Ph. rutteri* and *Ph. peripariphilus*; (3) postero-lateral ADP corners broadly triangular with more or less right angles in *Ph. gustafssoni* sp. nov. (Fig. 6A, C, E), but sharp with acute angles in *Ph. pallescens*, *Ph. rutteri*, *Ph. hercynicus* and *Ph. peripariphilus*; (4) posterior ADP projection lingulate, relatively narrow on its base and broad on its apex in *Ph. gustafssoni* sp. nov. (Fig. 6A, C, E), but triangulate with relatively broad base and sharp apex in *Ph. pallescens*, *Ph. rutteri*, *Ph. hercynicus* and *Ph. peripariphilus*; (5) three pairs of setae on posterior margin of prothorax in *Ph. gustafssoni* sp. nov. (Fig. 6A, E) and *Ph. hercynicus*, but more on those of *Ph. pallescens*, *Ph. rutteri* and *Ph. peripariphilus*; (6) three short thorn-like setae on each side of anterior prothorax margin in *Ph. gustafssoni* sp. nov. (Fig. 6A, E, present also in *Ph. acrocephalus*, Fig. 4A, E), but absent in *Ph. pallescens*, *Ph. rutteri*, *Ph. hercynicus* and *Ph. peripariphilus*; (7) ventral head carina with characteristic dark pigmentation in *Ph. gustafssoni* sp. nov. (Fig. 8C–D), but not pigmented in *Ph. pallescens*, *Ph. rutteri*, *Ph. hercynicus* and *Ph. peripariphilus*.

Other body parts than head and prothorax are neither illustrated nor described, so we could not verify how much they differ from *Ph. gustafssoni* sp. nov. We looked for the type material of *Ph. pallescens* and *Ph. rutteri* in the Natural History Museum, London, United Kingdom (BMNH), where a large part of the Denny's (1842) and Kellogg's (1899) collection is placed. We did not find neither specimen of these species nor any *Philopterus* specimens from the type hosts. Type material of *Ph. hercynicus* and *Ph. peripariphilus* should be deposited in the Museum of Natural History Rudolstadt, Germany. We tried to contact Eberhard Mey in order to get more information about this material, but without any success. From Balat's collection (MMBC) we examined one female paratype of *Ph. peripariphilus* and one female from *Periparus ater* (Linnaeus, 1758) labeled as *Ph. pallescens*. Both these specimens correspond to all the characters of each species described by Mey (1988) but we hesitate to assess relevance of these species only on base of one specimen. Hence, we are leaving identity of all the four species unresolved and provide only description of *Ph. gustafssoni* sp. nov.

Etymology

The specific epithet is a patronym in honor of Dr. Daniel R. Gustafsson, for his exceptional contribution to worldwide knowledge of chewing lice and leading of chewing lice frontier research in China.

Material examined

Holotype

CZECHIA • ♂ (Fig. 8C); Moravian-Silesian Region, Frydek-Mistek District, Janovice; 49°37'N, 18°24'E; 19 Mar. 2015; I. Literak leg.; ex *Regulus regulus regulus*; MMBC CZ-OS01.

Paratypes

CZECHIA • 1 ♀; same collection data as for preceding; MMBC CZ-OS01 • 1 ♂, 1 ♀; same collection data as for preceding; MMBC CZ-OS02 • 1 ♂, 1 ♀; same collection data as for preceding; MMBC CZ-OS03 • 1 ♂, 1 ♀; same collection data as for preceding; MMBC CZ-OS04.

Other material

CZECHIA • 18 ♀♀; same collection data as for preceding; MMBC • 13 ♀♀; S Bohemian Region, Jindrichuv Hradec District, Klec; 49°05'N, 14°44'E; 15–16 May 2015; same collector, and host as for preceding; MMBC • 9 ♂♂, 11 ♀♀, 28 ♀♀; Moravian-Silesian Region, Frydek-Mistek District, Lubno; 49°36'N, 18°22'E; 18 Mar. and 15–16 Apr. 2015; same collector and host as for preceding; MMBC • 1 ♀; S Moravian Region, Brno Country District, Skalicka; 49°21'N, 16°30'E; 2 Oct. 2015; same collector and host as for preceding; MMBC • 2 ♂♂, 3 ♀♀, 4 ♀♀; Olomouc Region, Jeseník District, Zuloava; 50°18'N, 17°05'E; 8 and 10 Nov. 2014; same collector and host as for preceding; MMBC • 2 ♀♀, 5 ♀♀; S Moravian Region, Brno Country District, Moravske Kninice; 49°17'N, 16°29'E; 21 Dec. 2009; O. Sychra & I. Literak leg.; same host as for preceding; MMBC • 1 ♀, 4 ♀♀; S Bohemian Region, Jindrichuv Hradec District, Klec; 49°05'N, 14°44'E; 16 May 2015; I. Literak leg.; ex *Regulus ignicapillus*; specimen lost during DNA extraction.

UNITED KINGDOM • 1 ♂, 2 ♀♀, 1 ♀; England, Dorset, Portland Bill, Portland Bird Observatory; 15 Apr. 1975; ex *Regulus ignicapillus*; NHML NHMUK010647797-98, Brit. Mus. 1975-355 • 1 ♂, 2 ♀♀; England, Cumbria, Wasdale; 9 Apr. 1955; ex *Regulus regulus* (labeled as *Regularis regularis*); NHML NHMUK010647799, Brit. Mus. 1955-233 • 1 ♂, 2 ♀♀; England, Lancashire, Southport; 5 Mar. 1961; ex *Regulus regulus*; NHML NHMUK010647803, Brit. Mus. 1961-671 • 1 ♀, 1 ♀; England, Surrey; Oct. 1973; K. M. Barralet; same host as for preceding; NHML NHMUK010647804.

PORTUGAL • 5 ♂♂, 5 ♀♀; Azores, São Miguel Island, Sete Cidades; 37°48'N, 25°12'W; 14–15 Apr. 2013; I. Literak leg.; ex *Regulus regulus azoricus*; MMBC.

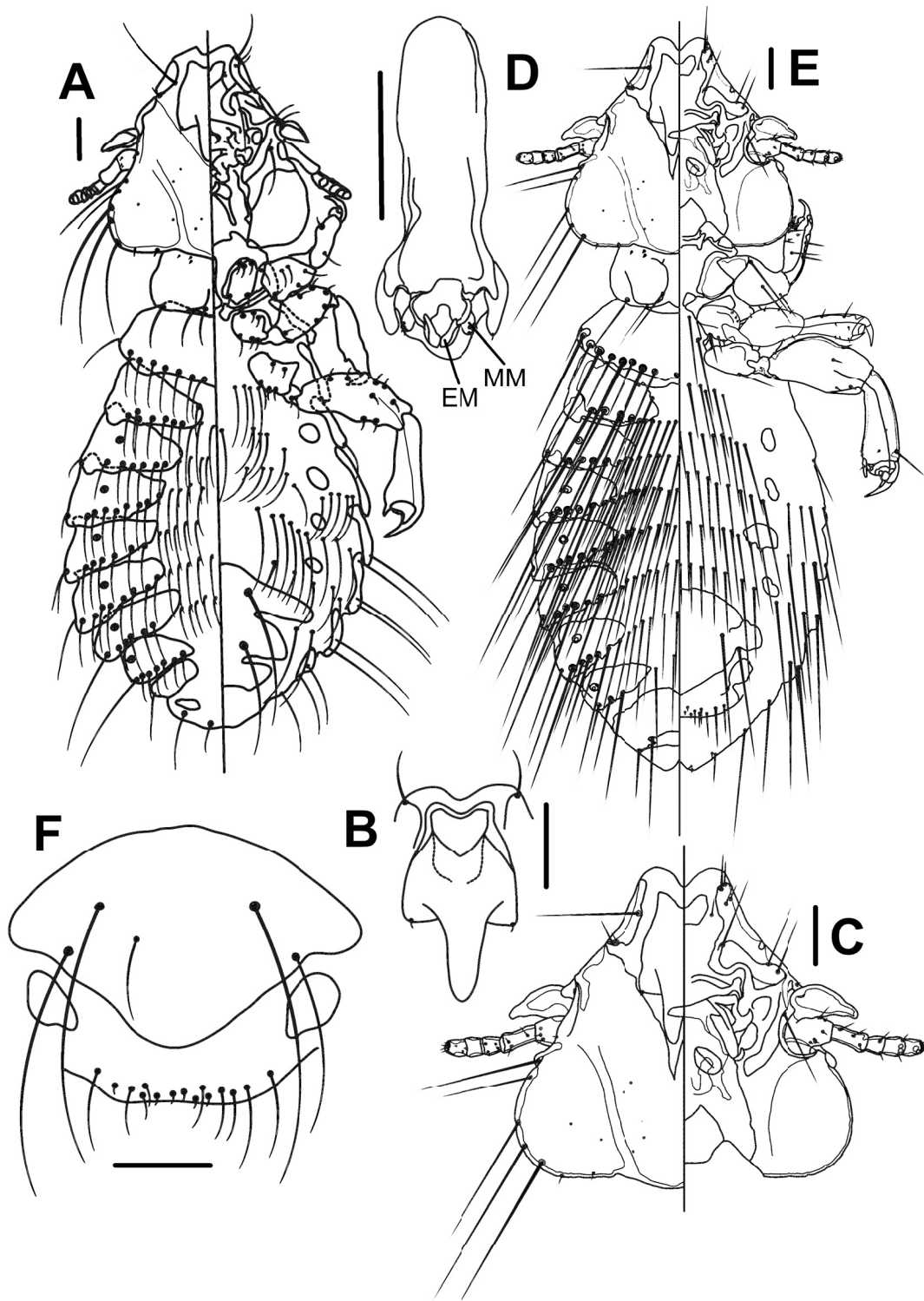


Fig. 6. *Philopterus gustafssoni* sp. nov. ex *Regulus regulus* (MMBC CZ-OS01): **A.** Male habitus, dorsal and ventral views. **B.** Male dorsal anterior plate (ADP), dorsal view. **C.** Female head, dorsal and ventral views. **D.** Male genitalia, ventral view. **E.** Female habitus, dorsal and ventral views. **F.** Female subgenital plate, vulval margin, and ventral terminalia, ventral view. Abbreviations: EM – endomere; MM – mesomere. Scale bars: 0.1 mm.

COUNTRY UNKNOWN • 3 ♂♂, 4 ♀♀, 2 ♂♂; 14 Mar. 1937; A. Ivanov leg.; ex *Regulus regulus*; ZIN • 2 ♂♂, 1 ♀, 4 ♂♂; 16 Mar. 1937; same collector, host and deposit as for preceding • 1 ♂, 2 ♀♀; 14 Apr. 1948; Lyubin leg.; same host as for preceding; ZIN.

POLAND • 1 ♂; Pomeranian Voivodeship, Nowy Dwor Gdanski County, Mierzeja Wislana; 1 Apr. 1966; Busse leg.; same host as for preceding; MNHW 9/a/58 • 1 ♀; same collection data as for preceding; MNHW 9/a/59 • 1 ♀; same location, collector and host as for preceding; 2 Apr. 1966; MNHW 9/a/60 • 1 ♀; same collection data as for preceding; MNHW 9/a/61 • 1 ♂ [labeled as ♀]; same location, collector and host as for preceding; 25 Apr. 1966; MNHW 9/a/62 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1966; MNHW 9/a/63 • 1 ♂; same collection data as for preceding; MNHW 9/a/64 • 1 ♂; same location, collector and host as for preceding; 2 Apr. 1966; MNHW 9/a/65 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1966; MNHW 9/a/66 • 1 ♂; same location, collector and host as for preceding; 4 Apr. 1966; MNHW 9/a/67 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1966; MNHW 9/a/68 • 1 ♀; same location, collector and host as for preceding; 8 Apr. 1966; MNHW 9/a/69 • 1 ♀; same collection data as for preceding; MNHW 9/a/70 • 1 ♂; Pomeranian Voivodeship, Puck County, Hel; 10 Sep. 1962; same collector and host as for preceding; MNHW 9/a/1 • 1 ♂; same location, collector and host as for preceding; 22 Sep. 1962; MNHW 9/a/2 • 1 ♂; same location, collector and host as for preceding; 26 Apr. 1963; MNHW 9/a/5 • 1 ♂; same collection data as for preceding; MNHW 9/a/6 • 1 ♂; same location, collector and host as for preceding; 14 Apr. 1963; MNHW 9/a/7 • 1 ♂; same collection data as for preceding; MNHW 9/a/8 • 1 ♂; same location, collector and host as for preceding; 1 May 1963; MNHW 9/a/9 • 1 ♂; same collection data as for preceding; MNHW 9/a/10 • 1 ♂; same location, collector and host as for preceding; 15 Apr. 1963; MNHW 9/a/11 • 1 ♂; same collection data as for preceding; MNHW 9/a/12 • 1 ♂; same collection data as for preceding; MNHW 9/a/13 • 1 ♀; same location, collector and host as for preceding; 14 Apr. 1963; MNHW 9/a/14 • 1 ♂; same location, collector and host as for preceding; 16 Apr. 1963; MNHW 9/a/15 • 1 ♀; same location, collector and host as for preceding; 27 Apr. 1965; MNHW 9/a/16 • 1 ♀; same collection data as for preceding; MNHW 9/a/17 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1965; MNHW 9/a/18 • 1 ♀; same location, collector and host as for preceding; 20 Apr. 1965; MNHW 9/a/19 • 1 ♀; same location, collector and host as for preceding; 3 Apr. 1965; MNHW 9/a/20 • 1 ♀; same collection data as for preceding; MNHW 9/a/21 • 1 ♀; same collection data as for preceding; MNHW 9/a/22 • 1 ♂; same collection data as for preceding; MNHW 9/a/23 • 1 ♂; same collection data as for preceding; MNHW 9/a/24 • 1 ♂; same collection data as for preceding; MNHW 9/a/25 • 1 ♀; same location, collector and host as for preceding; 17 Apr. 1965; MNHW 9/a/27 • 1 ♂; same collection data as for preceding; MNHW 9/a/28 • 1 ♂; same collection data as for preceding; MNHW 9/a/29 • 1 ♀; same location, collector and host as for preceding; 29 Mar. 1965; MNHW 9/a/30 • 1 ♀; same location, collector and host as for preceding; 25 Mar. 1965; MNHW 9/a/31 • 1 ♂; same location, collector and host as for preceding; 29 Mar. 1965; MNHW 9/a/32 • 1 ♀; same location, collector and host as for preceding; 17 Apr. 1965; MNHW 9/a/35 • 1 ♀; same collection data as for preceding; MNHW 9/a/36 • 1 ♂; same collection data as for preceding; MNHW 9/a/37 • 1 ♂; same collection data as for preceding; MNHW 9/a/38 • 1 ♀; same location, collector and host as for preceding; 3 Apr. 1965; MNHW 9/a/39 • 1 ♂; same location, collector and host as for preceding; 2 Apr. 1965; MNHW 9/a/40 • 1 ♀; same location, collector and host as for preceding; 17 Apr. 1965; MNHW 9/a/43 • 1 ♀; same collection data as for preceding; MNHW 9/a/44 • 1 ♂; same collection data as for preceding; MNHW 9/a/45 • 1 ♀; same collection data as for preceding; MNHW 9/a/47 • 1 ♂; same location, collector and host as for preceding; 3 Apr. 1965; MNHW 9/a/48 • 1 ♂; same collection data as for preceding; MNHW 9/a/49 • 1 ♀; same collection data as for preceding; MNHW 9/a/50 • 1 ♂; same location, collector and host as for preceding; 17 Apr. 1965; MNHW 9/a/53 • 1 ♂; same collection data as for preceding; MNHW 9/a/54 • 1 ♂; same location, collector and host as for preceding; 3 Apr. 1965; MNHW 9/a/55 • 1 ♂; same collection data as for preceding; MNHW 9/a/56 • 1 ♂; same collection data as for preceding; MNHW 9/a/57 • 1 ♂; Pomeranian Voivodeship, Nowy Dwor Gdanski County, Mierzeja Wislana; 1 Apr. 1966, same collector

and host as for preceding; MNHW 9/a/58 • 1 ♀; same collection data as for preceding; MNHW 9/a/59 • 1 ♀; same location, collector and host as for preceding; 2 Apr. 1966; MNHW 9/a/60 • 1 ♀; same collection data as for preceding; MNHW 9/a/61 • 1 ♂; same location, collector and host as for preceding; 25 Apr. 1966; MNHW 9/a/62 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1966; MNHW 9/a/63 • 1 ♂; same location, collector and host as for preceding; 2 Apr. 1966; MNHW 9/a/65 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1966; MNHW 9/a/66 • 1 ♂; same location, collector and host as for preceding; 4 Apr. 1966; MNHW 9/a/67 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1966; MNHW 9/a/68 • 1 ♀; same location, collector and host as for preceding; 8 Apr. 1966; MNHW 9/a/69 • 1 ♀; same collection data as for preceding; MNHW 9/a/70 • 1 ♂; Pomeranian Voivodeship, Puck County, Hel; 25 Apr. 1969; same collector and host as for preceding; MNHW 9/a/73 • 1 ♂; same collection data as for preceding; MNHW 9/a/74 • 1 ♀; same location, collector and host as for preceding; 21 Apr. 1969; MNHW 9/a/75 • 1 ♀; same collection data as for preceding; MNHW 9/a/77(2) • 1 ♂; same location, collector and host as for preceding; 25 Apr. 1969; MNHW 9/a/78(2) • 1 ♂; same collection data as for preceding; MNHW 9/a/79(2) • 1 ♂; same collection data as for preceding; MNHW 9/a/80(2) • 1 ♂; same location, collector and host as for preceding; 17 Apr. 1969; MNHW 9/a/82(3) • 1 ♂; same collection data as for preceding; MNHW 9/a/84 • 1 ♀; same collection data as for preceding; MNHW 9/a/86 • 1 ♂; same collection data as for preceding; MNHW 9/a/88(1) • 1 ♂; same location, collector and host as for preceding; 21 Apr. 1969; MNHW 9/a/100(2) • 1 ♂; same collection data as for preceding; MNHW 9/a/100(2) [the same label as preceding] • 1 ♂; same collection data as for preceding; MNHW 9/a/108(1) • 1 ♂; same collection data as for preceding; MNHW 9/a/109(1) • 1 ♂; same collection data as for preceding; MNHW 9/a/110(4) • 1 ♂; same location, collector and host as for preceding; 14 Apr. 1969; MNHW 9/a/112(2) • 1 ♂; same location, collector and host as for preceding; 17 Apr. 1962; MNHW 9/a/113(2) • 1 ♀; same location, collector and host as for preceding; 21 Apr. 1969; MNHW 9/a/119(2) • 1 ♀; same collection data as for preceding; MNHW 9/a/120(2) • 1 ♀; same location, collector and host as for preceding; 16 Apr. 1969; MNHW 9/a/122(1) • 1 ♂; same collection data as for preceding; MNHW 9/a/129 • 1 ♀; same location, collector and host as for preceding; 21 Apr. 1969; MNHW 9/a/131(4) • 1 ♂; same location, collector and host as for preceding; 31 Apr.[?] 1965; MNHW 9/a/133 • 1 ♀; same location, collector and host as for preceding; 21 Apr. 1969; MNHW 9/a/135(3) • 1 ♂; same collection data as for preceding; MNHW 9/a/136 • 1 ♂; same collection data as for preceding; MNHW 9/a/137(4) • 1 ♂; same collection data as for preceding; MNHW 9/a/157(3) • 1 ♂; same collection data as for preceding; MNHW 9/a/159(3) • 1 ♀; same locality as for preceding; 16 Apr. 1969; Busse leg.; ex *Regulus ignicapillus*; MNHW 9/b/1.

AZERBAIJAN • 1 ♂, 1 ♀; Lankaran District; 10 Mar. 1934; Shtroi leg.; ex *Regulus regulus buturlini*; ZIN I362 • 4 ♂♂; Lankaran District; 14 Mar. 1934; same collector and host as for preceding; labeled as *Philopterus subflavescens* (determined by D.I. Blagoveshtchensky); ZIN I400.

UZBEKISTAN • 1 ♂, 1 ♀; 16 Jan. 1940; ex *Regulus regulus tristis*; ZIN I445-22 • 2 ♀♀; same collection data as for preceding; ZIN I446-23.

Additional material collected

PORTUGAL • 8 ♂♂; Azores, Sao Miguel Island, Nordeste; 18 Apr. 2013; I. Literak leg.; ex *Regulus regulus azoricus*; UVPS • 7 ♂♂, 2 ♀♀, 30 ♂♂; Azores, Sao Miguel Island, Sete Cidades; 37°48'N, 25°12'W; 15 Apr. 2013; same collector and host as for preceding; UVPS • 1 ♀; Azores, Santa Maria Island, Pico Alto; 36°58'N, 25°05'W; 20 Sep. 2013; O. Sychra & I. Literak leg.; ex *Regulus regulus sanctaemariae*; UVPS.

Not determinable material

The following material from Złotorzycka's collection is probably *Ph. gustafssoni* sp. nov., but the species could not be determined because it contained only larvae without any associated adult lice:

POLAND • 1 ♂; Pomeranian Voivodeship, Nowy Dwor Gdanski County, Mierzeja Wislana; 26 Sep. 1965; Busse leg.; ex *Regulus regulus*; MNHW 9/a/26 • 1 ♂; same location, collector and host as for preceding; 30 Sep. 1964; MNHW 9/a/40 • 1 ♂; same collection data as for preceding; MNHW 9/a/41 • 1 ♂; same collection data as for preceding; MNHW 9/a/42 • 1 ♂; same location, collector and host as for preceding; 1 Apr. 1960; MNHW 9/a/64 • 1 ♂; Pomeranian Voivodeship, Nowy Dwor Gdanski County, Skowronki; 3 Sep. 1962; J. Złotorzycka leg.; same host as for preceding; MNHW 9/a/3 • 1 ♂; same location, collector and host as for preceding; 9 Sep. 1962; MNHW 9/a/4.

Description

Both sexes

Head as in Fig. 6C, broadly triangular, at least as wide as long, with frons deeply concave, preantennal region shorter than the postantennal, with straight lateral margin. Hyaline margin slight, not wider than frons, in some specimens barely apparent. Dorsal anterior head preantennal plate (ADP) as in Fig. 6B, with anterior margin centrally deeply indented or concave and straight anterior part of lateral margin. Posterior part of ADP lateral margin convex, so entire ADP (ignoring central posterior projection) trapezoidal with convex lateral margins. Large heavily sclerotized posterior projection protruding from posterior part of ADP, with a base the same width as anterior ADP margin. Postero-lateral corners of ADP broadly triangular, with bases positioned approximately at the level of $\frac{1}{4}$ of length of the central projection, about the same width as the central projection at this level, both postero-lateral ADP angles more or less right, very weakly sclerotized and therefore barely apparent, especially in comparison with

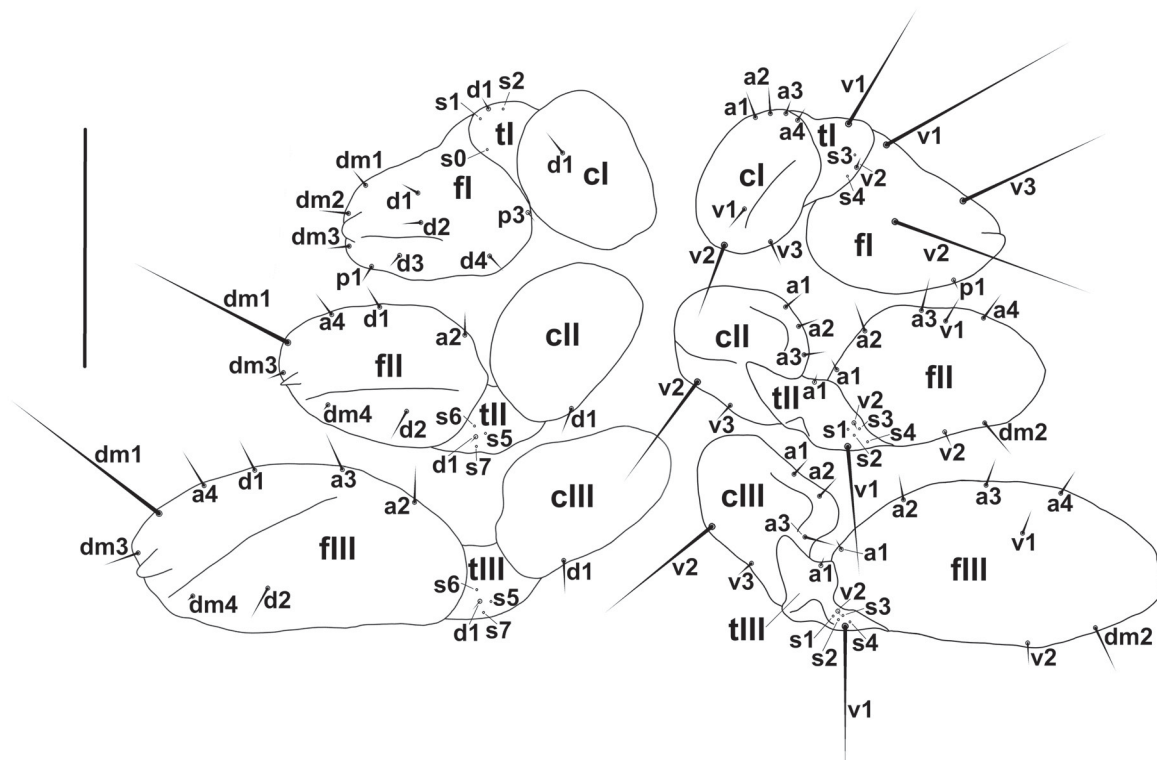


Fig. 7. *Philoaterus gustafssoni* sp. nov. ex *Regulus regulus* (MMBC CZ-OS01): nomenclature of male leg chaetotaxy, dorsal and ventral views. Abbreviations: *c* – coxa; *t* – trochanter; *f* – femur; *dm* – distal marginal seta; *d* – dorsal seta; *a* – anterior seta; *p* – posterior seta; *s* – sensillus; *v* – ventral seta. Scale bar: 0.1 mm.

the central projection. There is no or only a very slight indentation between the ADP postero-lateral corners and the central projection. Ventral anterior plate as in Fig. 6C, lateral quarters of anterior margin straight as well as lateral margins, straight or slightly convex posterior margins converging into one central median point, so the entire posterior ½ of the ventral plate seems a wide triangular jag. Ventral carina darkly pigmented, creating characteristic pied pattern on preantennal head (Fig. 8C–D). Prothorax as in Fig. 6A, E, with 1 medium-long *pps* in each postero-lateral corner, 2 medium-long *pps* on each side of posteriorly convergent central part of posterior margin and 3 short thorn-like setae on each side of its anterior margin. Prosternum elongated and posteriorly fused with anterior part of rhombic mesosternum. In place of metasternum 1–2 medium-long setae on each side. Pterothorax with 10–13 medium-long posterior setae (*mts*) on each side, all of them about the same length. Lateral margins of pterothorax with bulging anterior part, posterior margin with noticeable bulge in places where it overlaps with tergopleurites II on each side. Tergopleurites II–IX with all setae the same length, short or medium-long, never reaching posterior margin of following segment. Leg chaetotaxy as in Fig. 7, measurements as in Table 3.

Male

Habitus as in Fig. 6A, thoracic and abdominal chaetotaxy as in Fig. 6A and Table 2. Sternal setae (*sts*) medium-long on segments II–IV and VI, slightly overreaching posterior margin of following segments, and long on segment V, overreaching anterior margin of subgenital plate. Subgenital plate as in Fig. 6A, with large central anterior bulge, formed from sternites VII–IX, which are fused only in narrow central parts, in most of their width remaining separated by deep lateral indentations. Posterior margin of subgenital plate widely concave, 1 long (reaching to the posterior end of the body) seta on each side of posterior margin of original sternite VII and 1 about the same length (noticeably overreaching posterior body end) on each side of posterior margin of original sternite VIII, all 4 setae placed more or less medio-anteriorly from the median ends of lateral indentations. Genitalia as in Fig. 6D, basal apodeme long with rounded anterior margin fluently flowing into straight lateral margins. Parameres finger-like, clearly separated from the basal plate, relatively short, never overreaching elongated mesosome, never touching each other if turned medianly, either without or with only 1 sensilla on the distal end. Mesomeres (MM in Fig. 6D) and endomeres (EM in Fig. 6D) fully developed, clearly separated from the basal plate. Mesomeres relatively short and wide, with 3 sensillae on each distal end, which reach approximately to the same level as distal end of parameres. Endomeres claviform, with bulbous wider parts distally.

Female

Habitus as in Fig. 6E, head as in Fig. 6C, in general as in male, except following features. Thoracic and abdominal chaetotaxy as in Fig. 6E and Table 2. Sternal setae (*sts*) on all segments long, reaching at least to posterior margin of following segment. Subgenital plate (Fig. 6F) with rounded anterior margin, formed from sternite VII and large triangular central part of sternite VIII, posterior margin of which is composed of 2 posteriorly converging lines and gives the whole plate more or less the appearance of a pie wedge with rounded posterior apex. Lateral parts of sternite VIII separated as vestigial sternites, which are triangular or piriform, placed postero-laterally from the subgenital plate. Subgenital plate with 2 very long setae on each side, 1 placed on the supposed border of original sternites VII and VIII, 1 more anteriorly and medially, placed more or less in center of corresponding half of plate, both reaching always beyond vulval margin. Sometimes, there may be 1 medium-long seta placed on each side on the presumed border of original sternites, medially from the abovementioned long seta. Vulval margin as in Fig. 6F, straight in median part, with both lateral parts flexed anteriorly, fringed by 3–5 medium-long setae in each lateral part and by 6–8 short setae in the median part. Inner genital sclerites missing.

Hosts

Type host

Regulus regulus regulus (Linnaeus, 1758).

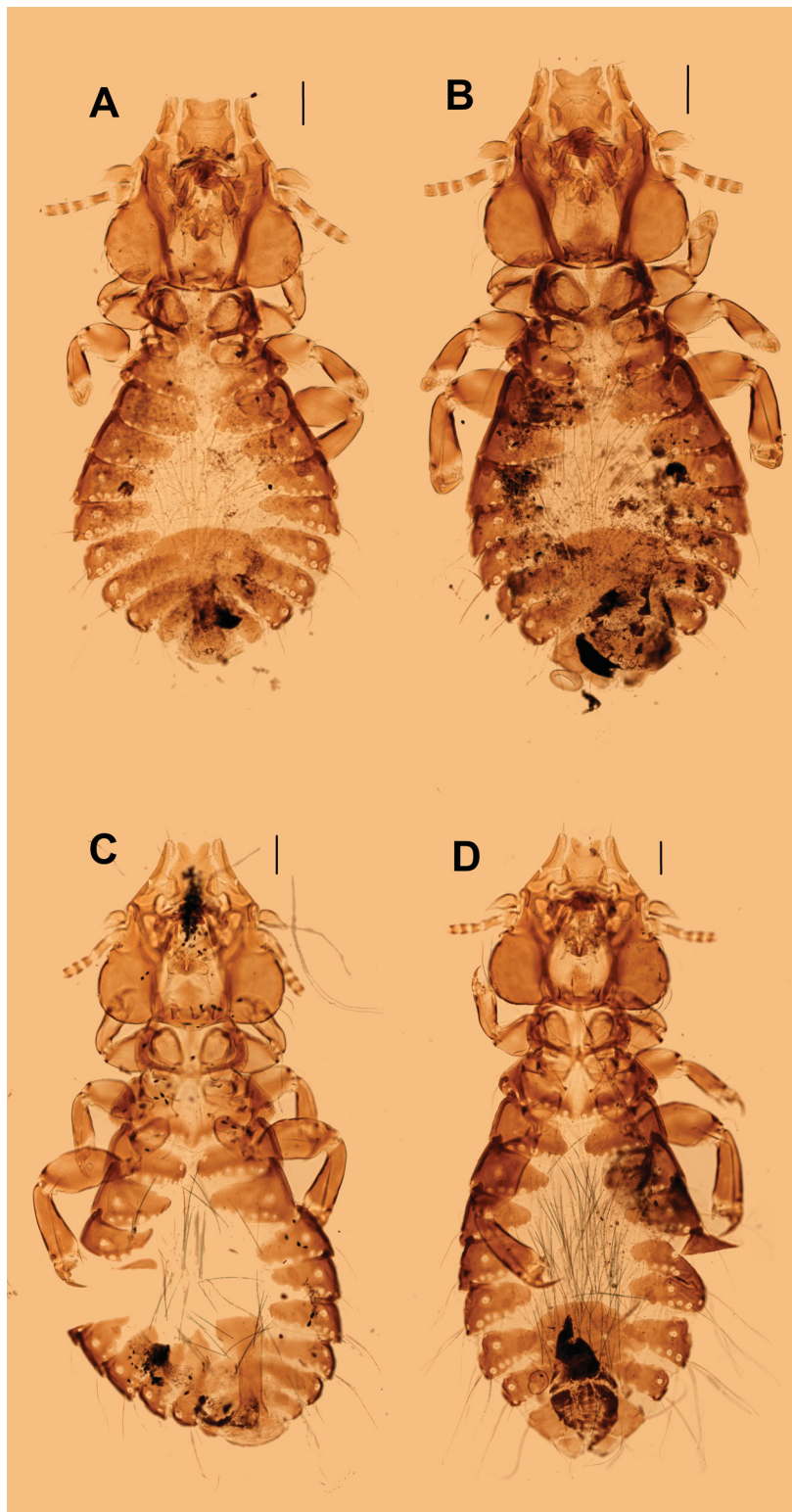


Fig. 8. A–B. *Philopterus acrocephalus* Carriker, 1949 ex *Acrocephalus melanopogon*: A. Herein described and illustrated male (MMBC SK25), dorsal view. B. Herein described and illustrated female (MMBC SK25), dorsal view. – C–D. *Philopterus gustafssoni* sp. nov. ex *Regulus regulus*: C. Holotype (MMBC CZ-OS01), dorsal view. D. Herein described and illustrated female paratype (MMBC CZ-OS01), dorsal view. Scale bars: 0.1 mm.

Table 4. Average intraspecific *p*-distances of examined specimens of *Philopterus acrocephalus* Carriker, 1949, *Philopterus gustafssoni* sp. nov., *Philopterus citrinellae* (Schrank, 1776) and *Philopterus fringillae* (Scopoli, 1772) computed from *COI*, *hyp*, *TMEDE* and concatenated gene sequences.

Species	n	<i>COI</i>	<i>hyp</i>	<i>TMEDE6</i>	concatenated
<i>Philopterus acrocephalus</i>	2	0	0	0	0
<i>Philopterus gustafssoni</i> sp. nov.	4	0.030	0.003	0.003	0.014
<i>Philopterus citrinellae</i>	6	0.063	0	0.004	0.025
<i>Philopterus fringillae</i>	2	0	0.003	0	0.001

Other hosts

Regulus regulus (Linnaeus, 1758), *Regulus regulus azoricus* Seebohm, 1883, *Regulus regulus buturlini* von Loudon, 1911, *Regulus regulus sanctaemariae* Vaurie, 1954, *Regulus regulus tristis* Pleske, 1892, *Regulus ignicapillus* (Temminck, 1820).

Type location

Czechia, Janovice.

Other locations

Czechia, Klec, Lubno, Moravske Kninice, Skalicka, Zulovala; United Kingdom, Portland Bird Observatory, Southport, Surrey, Wasdale; Portugal, Azores, Sao Miguel, Santa Maria; Azerbaijan, Lankaran District; Uzbekistan, specific location unreadable.

Remarks

The odd medium-long seta shown in the left part of the female subgenital plate (Fig. 6F) is not always present. Here it is included in the illustration because it is present in the specimen used for the drawing.

Genetic diversity

Two specimens of *Ph. gustafssoni* sp. nov. from *Regulus regulus regulus* (collected in Czechia), one specimen from *Regulus regulus azoricus* and one specimen from *Regulus ignicapillus* were genetically analysed, providing sequences of all three genes examined. Since samples from two host species (and in the case of goldcrest, *Regulus regulus*, even from its two subspecies) were analysed, the relatively noticeable intraspecific genetic variability in *Ph. gustafssoni* sp. nov. (3.0% for *COI*, 0.3% for *hyp*, 0.3% for *TMEDE6* and 1.4% for the concatenated sequences) was also recorded; for more details and comparison with intraspecific variability of the other species mentioned above, see Table 4. From the *Philopterus* species from which we managed to get molecular data (Najer, unpublished results), following three species are the nearest relatives of *Ph. gustafssoni* sp. nov.: *Ph. acrocephalus* – net interspecific *p*-distances 23.1% for *COI*, 1.6% for *hyp*, 0.8% for *TMEDE6* and 9.7% for the concatenated sequences, *Ph. fringillae* – 18.0% for *COI*, 1.6% for *hyp*, 0.4% for *TMEDE6* and 7.6% for the concatenated sequences, and *Ph. citrinellae* – 14.8% for *COI*, 1.6% for *hyp*, 0.4% *TMEDE6* and 6.4% for the concatenated sequences); more details are given in Table 5.

Discussion

As we already mentioned, the most recent descriptions of *Philopterus* from Acrocephalidae and Regulidae (Złotorzycka 1964; Złotorzycka & Lucińska 1976) are not sufficient for clear morphological diagnosis of these species. Their insufficiency consists mainly in too general morphological characteristics

Table 5. Net interspecific *p*-distances of *Philopterus acrocephalus* Carriker, 1949, *Philopterus gustafssoni* sp. nov., *Philopterus citrinellae* (Schrank, 1776) and *Philopterus fringillae* (Scopoli, 1772) computed from *COI*, *hyp*, *TMEDE* and concatenated gene sequences.

<i>COI</i>	<i>Ph. acrocephalus</i>	<i>Ph. gustafssoni</i> sp. nov.	<i>Ph. citrinellae</i>	<i>Ph. fringillae</i>
<i>Philopterus acrocephalus</i> (n = 2)		0.231	0.198	0.245
<i>Philopterus gustafssoni</i> sp. nov. (n = 4)	0.231		0.148	0.180
<i>Philopterus citrinellae</i> (n = 6)	0.198	0.148		0.189
<i>Philopterus fringillae</i> (n = 2)	0.245	0.180	0.189	
<i>hyp</i>	<i>Ph. acrocephalus</i>	<i>Ph. gustafssoni</i> sp. nov.	<i>Ph. citrinellae</i>	<i>Ph. fringillae</i>
<i>Philopterus acrocephalus</i> (n = 2)		0.016	0.018	0.018
<i>Philopterus gustafssoni</i> sp. nov. (n = 4)	0.016		0.016	0.016
<i>Philopterus citrinellae</i> (n = 6)	0.018	0.016		0.016
<i>Philopterus fringillae</i> (n = 2)	0.018	0.016	0.016	
<i>TMEDE6</i>	<i>Ph. acrocephalus</i>	<i>Ph. gustafssoni</i> sp. nov.	<i>Ph. citrinellae</i>	<i>Ph. fringillae</i>
<i>Philopterus acrocephalus</i> (n = 2)		0.008	0.012	0.014
<i>Philopterus gustafssoni</i> sp. nov. (n = 4)	0.008		0.004	0.004
<i>Philopterus citrinellae</i> (n = 6)	0.012	0.004		0.009
<i>Philopterus fringillae</i> (n = 2)	0.014	0.004	0.009	
concatenated	<i>Ph. acrocephalus</i>	<i>Ph. gustafssoni</i> sp. nov.	<i>Ph. citrinellae</i>	<i>Ph. fringillae</i>
<i>Philopterus acrocephalus</i> (n = 2)		0.097	0.086	0.105
<i>Philopterus gustafssoni</i> sp. nov. (n = 4)	0.097		0.064	0.076
<i>Philopterus citrinellae</i> (n = 6)	0.086	0.064		0.081
<i>Philopterus fringillae</i> (n = 2)	0.105	0.076	0.081	

and illustrations. As a result, when one gets any *Philoaterus* specimens from family Acrocephalidae or Regulidae, they often key to several, if not all, species described in the aforementioned papers. Furthermore, often it is rather difficult to clearly define differences between particular species, and this might cause the impression that the new species descriptions were based solely on the presumption of strict host specificity. Another case of insufficient descriptions is represented by two names which were used without any obvious attempts of delimitation – *Philoaterus subflavescens* (Geoffroy, 1762) and *Docophorus communis* (Nitzsch in Burmeister 1838).

As explained by Clay & Hopkins (1950: 269), the names used by Geoffroy (1762, including *Ph. subflavescens*) are not binominal, being rather descriptive phrases, and therefore they are invalid. Nevertheless, the name *Ph. subflavescens* has been incorrectly used as a valid species commonly occurring on passerines (e.g., Balat 1953; Bechet 1956; Blagoveshtchensky 1940, 1951). Peters (1936) reported *Ph. subflavescens* from 42 birds and noted that this is due to the fact that insufficient attention had been given to differentiating variations in the parasite that might be sufficient to establish new species or varieties. It seems that any philoaterid louse found on passerines was named by this name in the past (Clay & Hopkins 1950; Sychra *et al.* 2014b).

Concerning Acrocephalidae and Regulidae, *Ph. subflavescens* was reported from oriental reed-warbler, *Acrocephalus orientalis* (Temminck & Schlegel, 1847) (Uchida 1948), *A. a. arundinaceus* and *A. scirpaceus* (Balat 1953) and *Regulus regulus* (Blagoveshtchensky 1940, 1951). Uchida (1948) synonymized *Ph. subflavescens* with *Docophorus communis* (Nitzsch in Burmeister 1838).

The original description of *D. communis* consists of only a few words; however, this name was also previously known from a vast number of host species (Burmeister 1838; Denny 1842; Giebel 1874; Piaget 1880; Kellog 1896; Uchida 1917, 1948) including *Acrocephalus* (Paz Martin-Mateo & Jimenez Millan 1967 reported *Philoaterus communis* from *A. schoenobaenus*). Uchida (1948) also placed this species into his newly erected genus *Bitrabeculus* Uchida, 1948, which should be morphologically distinguished according to “two pairs of trabeculae”. Within the same genus he also described *Bitrabeculus mitsusui* Uchida, 1948, which was later moved to genus *Philoateroides* (Mey 2004), so he apparently considered the large conical as second trabeculae. Price *et al.* (2003) presented *D. communis* (named as *Philoaterus*, referring to Hopkins & Clay 1952) as a synonymy of *Ph. citrinellae*.

Since we confirmed *Ph. acrocephalus* as a native parasite of several species of Acrocephalidae we suggest that all lice previously reported from these hosts as *Ph. subflavescens* or *D. communis* in fact represent *Ph. acrocephalus*. A similar scenario is true for *Ph. subflavescens* reported by Blagoveshtchensky (1940, 1951) from *R. regulus*, because we were able to examine his slides and can thus confirm that they represent *Ph. gustafssoni* sp. nov.

***Philoaterus acrocephalus* Carriker, 1949**

Philoaterus acrocephalus was described based on a single female collected from *Acrocephalus luscinus*, an endemic species from Guam that is extinct nowadays. Therefore in future we cannot expect to find any additional specimens from the type host. However, the holotype shows almost complete morphological unity with *Philoaterus* collected by us from *Acrocephalus melanopogon*. A record of *Philoaterus* in this host species was already published by Balat (in Hudec 1983), Vas *et al.* (2012a), and Diakou *et al.* (2017) but it was not determined at the species level. With the determination of individuals collected by us we are here able to amend the original description with a more detailed morphological description (description of male being published for the first time), figures (Figs. 1–5, 8) and also a genetic delimitation of this species (Table 5). The latter is based on comparison of the DNA sequences of one mitochondrial (*COI*) and two nuclear (*hyp* and *TMEDE6*) genes and their concatenated sequences; it is also the first attempt to apply the techniques of molecular biology to the taxonomy of the *Philoaterus*-

complex. As a result of this comparison, we present net interspecific *p*-distances of *Ph. acrocephalus* from three *Philoaterus* species, *Ph. gustafssoni* sp. nov., *Ph. citrinellae* and *Ph. fringillae* (Table 5). These three *Philoaterus* species are noticeably genetically distant from *Ph. acrocephalus*, however, of all the *Philoaterus*-complex specimens from which we managed to gather DNA sequences they are still its nearest relatives (Najer, unpublished results). Morphologically none of them is similar to *Ph. gustafssoni* sp. nov., so we do not include their comparison into morphological descriptions. Hence, we are aware that the hereby presented net interspecific distances have only limited predicative value. We believe that in future we will manage to get DNA sequences of the species which should be reportedly (Mey 1988) more closely related to *Ph. gustafssoni* sp. nov.

When we compare the net interspecific to net intraspecific (Table 4) *p*-distances of particular species, it is worth noting that the intraspecific variability of *Ph. acrocephalus* is mainly zero and minimal in *Ph. fringillae*. In both cases, just two lice from the single host species and the same location were analyzed. In contrast, in *Ph. gustafssoni* sp. nov. and *Ph. citrinellae* specimens from more than one host species and from several locations were analyzed, so the intraspecific variability is accordingly higher.

Beside the material collected by us, we also morphologically examined museum slides found either during the search for type material of already described species or randomly, while investigating other *Philoaterus*-complex groups. In this way we discovered several undetermined slides containing *Philoaterus* from *Acrocephalus schoenobaenus*, *Iduna aedon rufescens*, *Iduna rama*, and undetermined species from *Locustella* warblers and *Locustella ochotensis*. Despite being in variable conditions (with some data unreadable or even absent), all these specimens were determined as *Ph. acrocephalus* after comparison to both the holotype and material collected by us. Except for *A. schoenobaenus*, this finding is the first record of *Philoaterus* in the remaining host species, and in the case of *Locustella* sp. and *Locustella ochotensis* also the first record of a *Philoaterus*-complex louse in Locustellidae. A record of head lice outside the *Philoaterus*-complex is already known in Locustellidae (*Sturnidoecus tulackovae* Balat, 1981 in *Locustella fluviatilis* (Wolf, 1810)), so this raises the question to what extent these two convergent groups are able to share one host family. The occurrence of *Ph. acrocephalus* in Locustellidae also shows the surprisingly low specificity of *Ph. acrocephalus* with regard to both host family and host body size (*Locustella ochotensis* vs *Iduna aedon*; Dyrce 2018a, 2018b).

***Philoaterus* spp. from other reed warblers**

In terms of museum material, we further examined one *Philoaterus* female from *A. schoenobaenus* collected in Egypt and labeled as *Philoaterus necopinatus* and one male and two nymphs from *Iduna aedon* labeled only with host species and collection date. Both adult lice (the female from *A. schoenobaenus* and the male from *I. aedon*) are morphologically different from both *Ph. acrocephalus* and supposed *Ph. fedorenkoae*. They also differ from each other in general head morphology (shape of preantennal part, ADP etc.) but since they belong to different genders we are not able to estimate whether they should be individuals of the same species. The description of *Ph. necopinatus* (Złotorzycka 1964) is based on a single male from Poland that is currently lost (Jaloszynski *et al.* 2014). Złotorzycka & Lucińska (1976) present the female as unknown, so the female could not be determined at the species level and there is no clear reason for its designation as *Ph. necopinatus*. The male from *I. aedon* is in relatively good condition but not dissected. This enables assessment of its head features (on which the comparison with *Ph. acrocephalus* and supposed *Ph. fedorenkoae* is based) but part of the abdominal chaetotaxy and genitalia is not visible due to dark gut content. In general, it can be said that both individuals combine the particular features of both *Ph. acrocephalus* and *Ph. fedorenkoae* in different ways (e.g., shape of ADP or female subgenital plate), so morphologically they seem to be ‘something in between’ these two species. There is only one other report about *Ph. necopinatus* by Paz Martin-Mateo (2009), who mentioned that this species was found by Paz Martin-Mateo & Jimenez Millan (1967) in

A. scirpaceus. In the original paper (Paz Martin-Mateo & Jimenez Millan 1967), it is reported under the name *Philoaterus communis* (at least Paz Martin-Mateo 2009 states that this is the record) and the host is *A. schoenobaenus* instead of *A. scirpaceus*. We tried to get more information about this specimen by contacting M. Paz Martin-Mateo, but so far without success.

It seems that *A. schoenobaenus* could be the host of two species of *Philoaterus* – *Ph. acrocephalus* and *Ph. necopinatus*. While we can confirm *Ph. acrocephalus* on this host, the status of *Ph. necopinatus* is still questionable until either type material or new material from the type location will be found and examined.

Also the next species, described by Złotorzycka (1964) – *Philoaterus mirificus* – was described on the basis of one single specimen from Poland, which is currently lost (Jaloszynski *et al.* 2014). There is another report of *Philoaterus* from *A. palustris* – the type host of *Ph. mirificus* – from Bulgaria by Ilieva (2009). We have found the Bulgarian specimens but up to this day we were not able to examine them, so their identity remains questionable.

The last described species, *Philoaterus fedorenkoae*, was already reported from Turkmenistan (Mey 1983), Romania (Adam & Sandor 2004) and some specimens from the type host – *A. arundinaceus* – from Czechia and Slovakia were found also in Balat's collection in MMBC. Based on examined material from Balat's collection, we can confirm that *Ph. fedorenkoae* is different from *Ph. acrocephalus*, so it may represent a valid species. However, all our attempts to find the type material of *Ph. fedorenkoae* failed, so we cannot consider this conclusion as absolutely sure.

Apart from the four described species of *Philoaterus* from *Acrocephalus* hosts, there are some other reports without proper species description from the following hosts: Uchida (1948) reported *Ph. subflavescens* from *Acrocephalus orientalis* from Japan. Since this name is invalid, we assume that these lice may represent genus *Philoaterus*. We looked for these specimens in NHML, where most of the Uchida's collection is stored, but we found neither them nor any other *Philoaterus* from Acrocephalidae, so we could not confirm this determination. Furthermore, some *Philoaterus* were reported from *A. arundinaceus* from eastern Asia (McClure *et al.* 1973) and *Acrocephalus agricola* (Jerdon, 1845) from Romania (Adam *et al.* 2009). Finally, there is a note about *Philoaterus "eichleri"* (syn.: *Docophorus "eichleri"*) (Mey 1977) from *Acrocephalus scirpaceus* reported from Germany. This 'species' was not described; Mey (1977) mentioned that he would describe it in future, however, this description was never realized. In all these cases, we tried to find these specimens in the institutions where they should be stored. However, all our effort was unsuccessful, often with people not replying to our inquiries, so we are not able to evaluate its quality and identification.

Apart from the taxonomic issues, we consider as interesting the 100% ($n = 28$) prevalence of *Ph. acrocephalus* in *A. melanopogon* at Gbelce. This is in striking contrast to the fact that T. Najer and O. Sychra through the years examined hundreds of birds of five other *Acrocephalus* species (*A. scirpaceus*, *A. schoenobaenus*, *A. arundinaceus*, *A. palustris* and a few individuals of *A. paludicola* (Vieillot, 1817)) in both Czechia and Slovakia and never recorded any *Philoaterus*. This might relate to the fact that *A. melanopogon* is the only *Acrocephalus* species wintering in the Mediterranean region; all others are sub-Saharan migrants (Stastny & Hudec 2011). Sychra *et al.* (2011) published consistent conclusions proving that the prevalence of lice was higher in non-migratory birds. Nonetheless, in their study the difference was not so striking as here.

The research at Gbelce took place in three years (2008, 2009, 2016) and always in the second half of April. At Nea Agathoupoli, where the prevalence was much lower (20%, $n = 10$), it took place in July (2013). This may imply that in the pre-breeding period the prevalence of lice is higher than post-breeding, which is in contrast to previous Czech studies dedicated to this topic (Sychra *et al.* 2008,

2011). However, it confirms the assumption of Price *et al.* (2003), which is also discussed by Sychra *et al.* (2011). According to this statement, birds in spring should have a higher prevalence and abundance of lice because of both easier horizontal transfer and more time spent feeding (at the cost of preening, compensation for the loss of energy during migration). After breeding, the lice are already vertically transferred to young birds, so the prevalence of lice is lower. Furthermore, the adults are in relatively good condition, preparing themselves for autumn migration. The higher infestation by lice in spring may be also affected by higher air humidity in this time (Clayton *et al.* 2016).

Sychra *et al.* (2011) showed a noticeable difference between pre- and post-breeding prevalence also in two *Philopterus* species, *Ph. modularis* (Denny, 1842) and *Ph. turdi* (Denny, 1842) collected from the Eurasian blackbird, *Turdus merula* Linnaeus, 1758. In *Ph. turdi* collected from another host, *Turdus philomelos* Brehm, 1831, and two other *Philopterus* species, *Ph. rubeculae* (Denny, 1842) and *Ph. citrinellae*, the difference is very slight. *Turdus merula* and *Pyrrhula pyrrhula* (Linnaeus, 1758) (from which they collected *Ph. citrinellae*) do not migrate. On the other hand, *Turdus philomelos* and *Prunella modularis* (Linnaeus, 1758) (host of *Ph. modularis*) winter in the Mediterranean region. This shows that the differences between pre- and post-breeding period are mixed with several migration strategies, so there is no apparent coherence with them.

Such large differences between pre- and post-breeding infestation rates do not occur in other lice genera (e.g., *Menacanthus*), which represent the vast majority of lice studied by Sychra *et al.* (2011). This leads to their recorded prevalence being practically the same in both periods. Apart from this study, it is not known whether any other head lice show such differences between pre- and post-breeding prevalence. From this point of view it would be interesting to compare, e.g., populations of *Sturnidoecus sturni* (Schrank, 1776) in both migrating and non-migrating populations of starling, *Sturnus vulgaris* Linnaeus, 1758.

***Philopterus* from Regulidae**

Compared to *Philopterus* from Acrocephalidae, *Ph. reguli* was up to date the only species known so far in the family Regulidae. It was originally described based on a single female from *Regulus regulus* (Denny 1842). The records of males were published more than a century later, however, just as inaccurately described as *Ph. acrocephalus* (Złotorzycka 1964; Złotorzycka & Lucińska 1976). When we examined all the abovementioned material, it turned out that the female described as *Ph. reguli* and the material described in the two later studies are two different species. Whereas the material described by Złotorzycka (1964) and Złotorzycka & Lucińska (1976) represents the same species as other *Philopterus* material known from Regulidae (see above), the holotype of *Ph. reguli* differs from it in, e.g., noticeably wider preantennal head. Therefore, we combine results of examination of all to us known *Philopterus* specimens from Regulidae and describe it as a new species, *Ph. gustafssoni* sp. nov., including its genetic delimitation (Table 5).

Beside material from the type host, *Regulus regulus*, we also provide a record of *Ph. gustafssoni* sp. nov. in a second host species, *Regulus ignicapillus*. Since we genetically examined lice from two host species and two geographically distant areas (Czechia and the Azores), the ascertained intraspecific genetic variability of *Ph. gustafssoni* sp. nov. is notably higher than that of *Ph. acrocephalus* and *Ph. fringillae* (Table 4). Three different subspecies of *Regulus regulus* occur on the Azores (*R. r. azoricus*, *R. r. sanctaemariae* and *R. r. inermis* Murphy & Chapin, 1929) (Clements *et al.* 2018) with several more living throughout Eurasia, so this host–parasite association could serve as a good model for phylogeographic studies (similar to, e.g., Stefka *et al.* 2011), if a more robust set of samples would be collected.

In *Ph. gustafssoni* sp. nov., it is also worth noting that, according to observations of I. Literak (unpublished observation), the lice did not occur only on the head of the hosts but reportedly also on

their nape, mantle and throat. A further thorough study of the ecology of the *Philopterus*-complex would by all means be more than welcome to confirm or reject whether such a distribution is accidental or regular.

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