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Two new species in the *Resartor*-group (Phthiraptera: Ischnocera) complicate and simplify genus limits

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Abstract. The *Resartor*-group is a group of ten genera and subgenera within the *Brueelia*-complex, parasitizing a broad range of hosts in the Old World tropics. Genera within this group are morphologically similar, and the generic limits are somewhat ambiguous, particularly among the genera, *Resartor* Gustafsson & Bush, 2017, *Timalinirmus* Mey, 2017, and *Turdinirmoides* Gustafsson & Bush, 2017. Following the collection of two morphologically aberrant species in this group in central China, we examined genetic data from six of the 14 species of *Resartor* and one of the two species of *Timalinirmus*, as well as representatives of four other genera in the group. These data suggest that *Timalinirmus* is nested within *Resartor*, which resolves there being no significant morphological differences between these two genera, apart from head shape. One of the morphologically aberrant species is also nested within *Resartor*. It appears that morphological variation of this genus is wider than previously understood. In contrast, the other morphologically aberrant species is clustered with the genus *Aratricerca* Gustafsson & Bush, 2017, despite not sharing any morphological characters with this genus. We suggest that *Timalinirmus* would have been considered a synonym of *Resartor*, but find that the name was never made available under the International Code of Zoological Nomenclature, and thus does not formally exist. The species previously placed in this genus are here reassigned to *Resartor*. An assessment of the relationships between *Resartor, Aratricerca* and *Turdinirmus* Eichler, 1951 must await more data. The two species from Hubei are here described as *Resartor acutotemporalis* sp. nov. ex *Sinosuthora webbiana suffusa* Swinhoe, 1871, and *Resartor breviceps* sp. nov. ex *Erythrogenys gravivox gravivox* (David, 1873). An updated checklist to the genus *Resartor* is given.

Keywords. *Brueelia*-complex, genus limits, new species, China.

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Introduction

The *Brueelia*-complex (sensu Gustafsson & Bush 2017) is one of the largest radiations of ischnoceran lice, comprising over 600 species divided into 41 genera. These genera fall into one of four groups, one of the smaller of which is the *Resartor*-group, comprising 51 known species in nine genera. The group is known only from the Old World tropics and Australasia, with many genera seemingly limited to one host family (Gustafsson *et al*. 2022). Most of the species in the *Resartor*-group have been described within the last decade (Gustafsson & Bush 2017, 2022; Mey 2017; Gustafsson *et al*. 2018, 2021, 2022), but relationships among some of the genera in this group are unclear. Above all, relationships among the four slender-bodied genera, *Aratricerca* Gustafsson & Bush, 2017, *Resartor* Gustafsson & Bush, 2017, *Timalinirmus* Mey, 2017, and *Turdinirmoides* Gustafsson & Bush, 2017, are unclear, as the known species show a patchwork of characters (Gustafsson *et al*. 2019a).

The largest of these four genera is *Resartor*, with 14 known species all collected from "babblers" (mainly Leiothrichidae Swainson, 1832) from South and Southeast Asia. Members of this genus can easily be identified even with the naked eye by the elongated, somewhat trapezoidal heads (Fig. 1A–B). This contrasts with members of *Turdinirmoides,* which have short, triangular heads (Fig. 1C). In *Aratricerca*, head shape is more variable (Fig. 1D–E), whereas the head shape of the two known species of *Timalinirmus* are intermediate between those of *Resartor* and *Turdinirmoides* spp. (Fig. 1F–G). Other morphological characters are generally either variable within genera (e.g., abdominal chaetotaxy) or more or less similar between genera (e.g., male genitalia), although a number of structural characters of the thorax and abdomen show consistent differences among three of the four genera (Table 1). No morphological differences between *Resartor* and *Timalinirmus* are known, and both genera parasitize related host species.

Following the collection of two new species of lice in the *Resartor*-group from babblers caught at a previously unsampled area in Hubei Province, China, we found that the head shape of these species (Fig. 1H–I) deviated from all previously known members of the *Resartor*-group known from babblers (Fig. 1A–B), and more resembled members of other genera. Specifically, one species (Fig. 1H) has a head most similar to that of species in *Turdinirmoides* (Fig. 1C) or *Aratricerca* (Fig. 1D), whereas the other (Fig. 1I) has a head similar to those found in species of *Turdinirmus* (Fig. 1J). Neither of these head shapes are previously recorded for any species of *Resartor.* Abdominal chaetotaxy is reduced in both species, as is common in most *Resartor*-group genera, but abdominal plates follow the structure found in *Resartor* and *Timalinirmus* (Table 1). The generic placement of these two species is thus ambiguous and cannot be resolved by morphology alone.

Here, we examine the placement of these two species within the *Resartor*-group, one from *Erythrogenys gravivox* (David, 1873), and one from *Sinosuthora webbiana* Gould, 1852, based on two molecular markers (the mitochondrial cytochrome oxidase subunit I, *COI*, and the nuclear elongation factor 1 α, *EF-1α*). In addition, we sequenced one of the two known species of *Timalinirmus* from a yuhina (Zosteropidae, Bonaparte, 1853), as well as unidentified *Resartor*-group female specimens from two other species of yuhinas from South China. We also include a specimen of *Psammonirmus* Gustafsson & Bush, 2017, a genus with some similarities to the *Resartor*-group, but whose relationship to other *Brueelia*-complex genera is unclear.

Table 1. Selected structural characters variable among the four genera in the *Resartor*-group. Data derived from Najer *et al.* (2012), Gustafsson & Bush (2017), Mey (2017), Gustafsson *et al.* (2018, 2019a, 2022, 2024), and specimens examined here.

Character	***Aratricerca*** **Gustafsson & Bush, 2017**	***Resartor*** **Gustafsson & Bush, 2017**	***Timalinirmus*** **Mey, 2017**	***Turdinirmoides*** **Gustafsson & Bush, 2017**
Pterothorax near-hexagonal	Yes	No	No	No
Sternite II thickened	Yes	No	No	No
Male sternite VII fused to subgenital plate	No	Yes	Yes	No
Sternal setae on male abdominal segment VII	Yes	No	No	Yes
Female subgenital plate fused to cross-piece	Cross-piece absent	Yes	Variable?	No
Distal male abdomen extended into triangular tail	Yes	No	No	No
Female tergopleurites IX-XI fused	No	Yes	Yes	Yes

Material and methods

Specimens were collected from various birds across South China between 2012–2024 (Table 2), following the fumigation protocol outlined by Gustafsson *et al*. (2019b). Host taxonomy follows Clements *et al*. (2024). Collected lice were stored in 95% ethanol at -80˚C. Specimens of the *Brueelia*-complex were identified to genus level under a dissection microscope (Zeiss SteREO Discovery V8, Carl Zeiss, Germany), using the key of Gustafsson & Bush (2017). DNA was extracted from specimens using DNeasy tissue kit (Qiagen, Shanghai, China), after which polymerase chain reactions (PCRs) were carried out using Cytiva PureTaq ready-to-go beads (GE Healthcare, Vienna, Austria), following Grossi *et al*. (2024). For *COI*, primers L6625 and H7005 (Hafner *et al*. 1994) were used, and for *EF-1α*, primers EF1- For3 and EF1- CH10 (Danforth & Ji 1998) were used. Exoskeletons of lice retrieved from the extraction were mounted in Canada balsam (Palma 1978) and identified morphologically to species level using the keys of Gustafsson *et al*. (2018, 2022).

DNA sequences were assembled using the de novo assemble tool and aligned in Geneious Prime ver. 2025.1.2 (GraphPad Software LLC 2025). For the phylogenetic analysis, in addition to our sequences, we also included all sequences representing *Resartor*-group lice published by Bush *et al*. (2016), as well as other lice from the *Brueelia*-group from the same source to serve as outgroups. See Table 2 for an overview of the specimens included. Substitution models were estimated in MEGA12 (Kumar *et al.* 2024), which determined that GTR+G+I was the best model for the *COI* dataset, whereas HKY+G+I was best for the *EF-1α* dataset. A phylogenetic analysis of the linked alignments was run in BEAST ver. 10.5.0 (Suchard *et al.* 2018) for $1x10^8$ generations. After removing the first 10% of the resulting trees as burnin in TreeAnnotator ver. 10.5.0, a maximum clade credibility tree was created, and later edited for clarity in FigTree ver. 1.4.4 (Rambaut 2018) and InkScape ver. 1.4 (Inkscape Developers 2024).

Slide-mounted exoskeleton vouchers of all specimens extracted here examined using a Nikon Eclipse N*i* microscope (Nikon Corporation, Tokyo, Japan), with a drawing tube attached for making illustrations.

Drawings were scanned, then compiled and edited in GIMP (www.gimp.org). Measurements (all in mm; see Table 3) were made from live images in NIS-Elements (Nikon Corporation, Tokyo, Japan).

Abbreviations

The following abbreviations are used throughout.

Measurements

AW = abdominal width (at segment V)
HL = head length (at midline)
HW = head width (at widest point of temples)
PRW = prothoracic width
PTW = pterothoracic width
TL = total length (at midline)

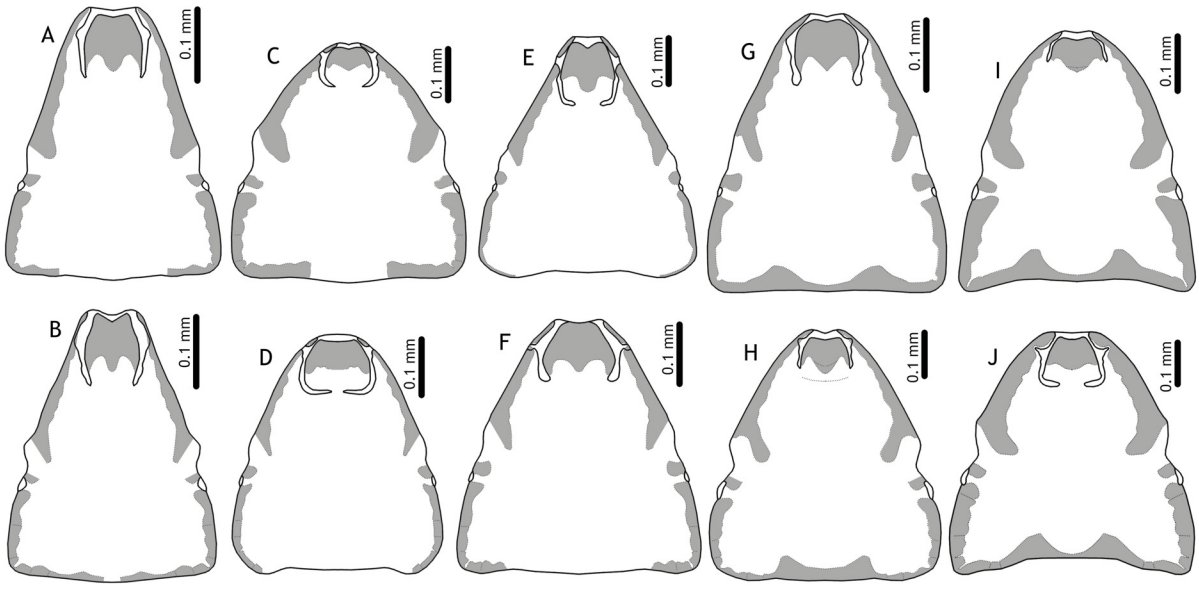

Fig. 1. Outlines of heads in dorsal view, with setae, antennae, and other characters removed for clarity, of male representatives of the *Resartor*-group. Marginal carinae and the area of the dorsal anterior plate enclosed by the displaced median section of the marginal carina indicated in grey; note that the entire dorsal anterior plate is not thickened. **A**. *Resartor longisuturalis* Gustafsson *et al*., 2018. Redrawn from Gustafsson *et al.* (2018: fig. 22). **B**. *Resartor extraneus* Gustafsson *et al*., 2018. Redrawn from Gustafsson *et al.* (2018: fig. 36). **C**. *Turdinirmoides rozsai* Gustafsson *et al*., 2022. Redrawn from Gustafsson *et al.* (2022: fig. 29). **D**. *Aratricerca cerata* Gustafsson *et al*., 2022. Redrawn from Gustafsson *et al.* (2022: fig. 3). **E**. *Aratricerca macki* Gustafsson *et al*., 2022. Redrawn from Gustafsson *et al.* (2022: fig. 10). **F**. "*Timalinirmus" curvus* Gustafsson *et al.,* 2022. Redrawn from Gustafsson *et al.* (2022: fig. 36). **G**. "*Timalinirmus" hrabali* (Najer & Sychra, 2012). Redrawn from Najer *et al*. (2012: fig. 3B). **H**. *Resartor acutitemporalis* sp. nov. **I**. *Resartor breviceps* sp. nov. **J**. *Turdinirmus australissimus* Gustafsson & Bush, 2017. Redrawn from Gustafsson & Bush (2017: fig. 191).

Table 2 (continued on next three pages). Overview of specimens used for phylogenetic reconstruction. Host ID numbers are given only for specimens collected by us in China. Note that many of the specimens published by Bush *et al.* (2016) are listed on GenBank as '*Brueelia* sp.', but in cases where the identity is known, or where the species has changed genus following the revision by Gustafsson & Bush (2017), the updated name is given here. Under 'additional sequences' data are listed for the six *Resartor breviceps* sp. nov., collected from Hubei Province, for which *EF-1α* could not be sequenced; these sequences were not used in our phylogeny, and they are included here for completeness and to verify that at least the *COI* sequences for this species are similar among provinces.

Louse taxon	**Host taxon**	**Host ID**	**Locality**	***COI* GenBank Accession number**	***EF-1α* GenBank Accession number**
Acronirmus gracilis	*Delichon urbicum*		Malawi	KT892075	KT892367
Aratricerca macki	*Randia pseudozosterops*		Madagascar	KT892334	KT892624
Brueelia cela	*Cacicus cela*		Panama	KT892114	KT892406
Brueelia phasmasoma	*Coereba flaveola*		Panama	KT892134	KT892426
Brueelia sp.	*Vidua macroura*		Malawi	KT892274	KT892564
Indoceoplanetes (*Capnodella*) sp.	*Coracina coerulescens*		Philippines	KT892133	KT892425
Indoceoplanetes (*Capnodella*) sp.	*Coracina striata*		Philippines	AY149390	AY149420
Indoceoplanetes (*Capnodella*) sp.	*Cyanograculus azureus*		Ghana	KT892131	KT892423
Indoceoplanetes (*Indoceoplanetes*) *indonesiana*	*Coracina striata*		Philippines	KT892079	KT892371
Indoceoplanetes (*Indoceoplanetes*) sp.	*Coracina novaehollandiae*		Australia	KT892140	KT892432
Indoceoplanetes (*Indoceoplanetes*) sp.	*Coracina pectoralis*		Malawi	KT892142	KT892434
Maculinirmus sp.	*Cinclosoma punctatum*		Papua New Guinea	KT892125	KT892417
Maculinirmus sp.	*Cinclosoma punctatum*		Australia	KT892126	KT892418
Maculinirmus sp.	*Oriolus auratus*		Malawi	KT892215	KT892505

Table 2 (continued). Overview of specimens used for phylogenetic reconstruction. Host ID numbers are given only for specimens collected by us in China. Note that many of the specimens published by Bush *et al.* (2016) are listed on GenBank as '*Brueelia* sp.', but in cases where the identity is known, or where the species has changed genus following the revision by Gustafsson & Bush (2017), the updated name is given here. Under 'additional sequences' data are listed for the six *Resartor breviceps* sp. nov., collected from Hubei Province, for which *EF-1α* could not be sequenced; these sequences were not used in our phylogeny, and they are included here for completeness and to verify that at least the *COI* sequences for this species are similar among provinces.

Louse taxon	Host taxon	Host ID	Locality	*COI* GenBank Accession number	*EF-1α* GenBank Accession number
Maculinirmus sp.	*Oriolus auratus*		Malawi	KT892216	KT892506
Maculinirmus sp.	*Oriolus flavocinctus*		Australia	KT892217	KT892507
Maculinirmus sp.	*Oriolus flavocinctus*		Australia	KT892218	KT892508
Maculinirmus sp.	*Oriolus larvatus*		Mozambique	KT892219	KT892509
Maculinirmus sp.	*Oriolus larvatus*		Mozambique	KT892220	KT892510
Maculinirmus sp.	*Sphecotheres viridis*		Australia	KT892263	KT892553
Mirandofures kamena	*Erythrura trichroa*		Papua New Guinea	KT892162	KT892454
Paragoniocotes sp.	*Aratinga astec*		Mexico	AY149404	AY149434
Psammonirmus lunatipectus	*Serilophus lunatus*	J0629-1	Yunnan, China	PZ580896	PZ595534
Resartor acutitemporalis	*Suthora webbiana*	J5641-1	Hubei, China	PZ580904	PZ595546
Resartor acutitemporalis	*Suthora webbiana*	J5641-2	Hubei, China	PZ580905	PZ595547
Resartor acutitemporalis	*Suthora webbiana*	J5647-2	Hubei, China	PZ580906	PZ595548
Resartor aterrimus	*Minla ignotincta*	J0176-1	Yunnan, China	PZ580889	PZ595527
Resartor aterrimus	*Minla ignotincta*	J0176-2	Yunnan, China	PZ580890	PZ595528
Resartor elugeus	*Alcippe fratercula*	J3764-1	Yunnan, China	PZ580900	PZ595538
Resartor elugeus	*Stachyris nigriceps*	J4866-2	Yunnan, China	PZ580903	PZ595542
Resartor breviceps	*Erythrogenys gravivox*	J0098-1	Hunan, China	PZ580888	PZ595526
Resartor extraneus	*Lioparus chrysotis*	J2272-1	Sichuan, China	PZ580898	PZ595536
Resartor extraneus	*Lioparus chrysotis*	J2272-2	Sichuan, China	PZ580897	PZ595535

Table 2 (continued). Overview of specimens used for phylogenetic reconstruction. Host ID numbers are given only for specimens collected by us in China. Note that many of the specimens published by Bush *et al.* (2016) are listed on GenBank as '*Brueelia* sp.', but in cases where the identity is known, or where the species has changed genus following the revision by Gustafsson & Bush (2017), the updated name is given here. Under 'additional sequences' data are listed for the six *Resartor breviceps* sp. nov. , collected from Hubei Province, for which *EF-1α* could not be sequenced; these sequences were not used in our phylogeny, and they are included here for completeness and to verify that at least the *COI* sequences for this species are similar among provinces.

Louse taxon	**Host taxon**	**Host ID**	**Locality**	***COI* GenBank Accession number**	***EF-1α* GenBank Accession number**
Resartor extraneus	*Lioparus chrysotis*	J3784-1	Yunnan, China	PZ580901	PZ595539
Resartor guangxiensis	*Trochalopteron milnei*		China	KT892298	KT892588
Resartor guangxiensis	*Trochalopteron milnei*	J5116-2	Yunnan, China	PZ091290	PZ595544
Resartor guangxiensis	*Trochalopteron milnei*	J5119-2	Yunnan, China	PZ091291	PZ595545
Resartor longisuturalis	*Actinodura cyanouroptera*	J0178-1	Yunnan, China	PZ580891	PZ595529
Resartor sp.	*Heterophasia desgodinsi*	J0250-3	Yunnan, China	PZ580893	PZ595531
Resartor sp.	*Heterophasia desgodinsi*	J4220-1	Yunnan, China	PZ580902	PZ595540
Resartor sp.	*Yuhina flavicollis*	J4806-1	Yunnan, China	PZ091264	PZ595541
Resartor sp.	*Yuhina gularis*	J0215-1	Yunnan, China	PZ580892	PZ595530
Timalinirmus curvus	*Yuhina castaniceps*	J0376-1	Guangdong, China	PZ580894	PZ595532
Timalinirmus curvus	*Yuhina castaniceps*	J0377-1	Guangdong, China	PZ580895	PZ595533
Turdinirmus daumae	*Zoothera dauma*	J3404-1	Yunnan, China	PZ580899	PZ595537
Turdinirmus sp.	*Zoothera dixoni*	J5030-1	Yunnan, China	PZ091282	PZ595543
Additional sequences					
Resartor breviceps	*Erythrogenys gravivox*	J5674-1	Hubei, China	PZ580907	–
Resartor breviceps	*Erythrogenys gravivox*	J5674-2	Hubei, China	PZ580908	–
Resartor breviceps	*Erythrogenys gravivox*	J5674-3	Hubei, China	PZ580909	–
Resartor breviceps	*Erythrogenys gravivox*	J5674-4	Hubei, China	PZ580910	–
Resartor breviceps	*Erythrogenys gravivox*	J5674-5	Hubei, China	PZ580911	–
Resartor breviceps	*Erythrogenys gravivox*	J5674-6	Hubei, China	PZ580912	–

Setal characters

Terminology for chaetotaxy and structural characters, and the abbreviations thereof, follow Gustafsson *et al*. (2024), and include:

ads = anterior dorsal seta
aps = accessory post-spiracular seta
dsms = dorsal submarginal seta
gpmes = gonoporal posterior mesosomal seta
lpmes = lateral posterior mesosomal seta
ps = paratergal seta
psps = principal postspiracular seta
pst1–2 = parameral setae 1–2
ss = sutural seta
tps = tergal posterior seta
vms = vulval marginal seta
vos = vulval oblique seta
vss = vulval submarginal seta

These setae are indicated in the figures for *Resartor acutitemporalis* sp. nov.

Repository

IZGAS = Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, Guangdong Province, China

Results

Sequencing of *EF-1α* did not work for six separate samples from *Erythrogenys gravivox* collected in Hubei Province despite several attempts, and a specimen of this species collected from Hunan Province had to be used instead in our phylogeny. *COI* sequences of the samples from Hunan and Hubei are identical (data not shown), and the specimens represent the same morpho-species. We therefore consider these specimens to be conspecific.

Monophyly of the *Resartor*-group was not supported in our analysis, but *Indoceoplanetes* Gustafsson & Bush, 2017*, Maculinirmus* Złotorzycka, 1964*,* and *Turdinirmus*, were all found to be monophyletic separately (Fig. 2). A clade containing all specimens identified as *Resartor* was supported (PP = 1.00), but this clade also includes one specimen of *Aratricerca*, all specimens of *Timalinirmus*, and the two new species from Hubei Province. This clade was divided basally into one containing *Aratricerca* and one of the Hubei species (PP = 1.00), and one containing all other species of *Resartor* and *Timalinirmus* (PP = 1.00).

The genus *Psammonirmus*, was not nested within the *Resartor*-group. Its placement within the *Brueelia*-complex remains unclear.

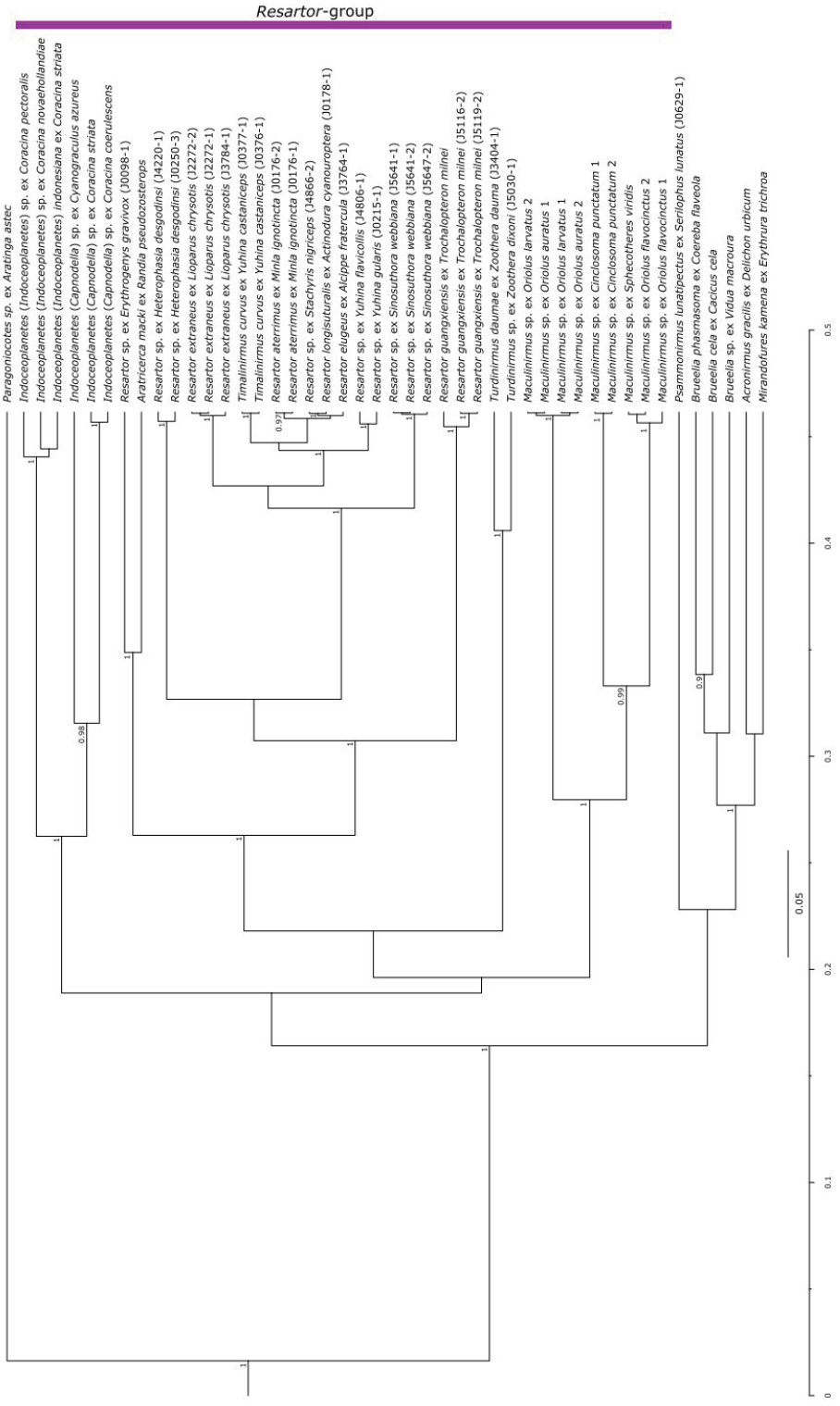

Fig. 2. Phylogeny of representatives of most *Resartor*-group genera, produced in BEAST based on the mitochondrial *COI* and nuclear *EF-1α* genetic markers. The vertical line at the top shows the limits of the *Resartor*-group. Numbers in parentheses after taxon names denote voucher ID numbers. For GenBank Accession numbers of all specimens, see Table 2.

Taxonomy

Class Insecta Linnaeus, 1758
Order Phthiraptera Haeckel, 1896
Parvorder Ischnocera Kellogg, 1896
Family Philopteridae Burmeister, 1838
Brueelia-complex sensu Gustafsson & Bush, 2017

Genus ***Resartor*** Gustafsson & Bush, 2017

Brueelia Kéler, 1936: 257 (in partim).
Resartor Gustafsson & Bush, 2017: 104.
Leiothrichinirmus Mey, 2017: 166.
Timalinirmus Mey, 2017: 170 [unavailable name; see below].

Timalinirmus – Gustafsson *et al.* 2019a: 276.

Type species

Brueelia impressifrons Ansari, 1956: 152, by original designation.

Remarks

During the preparation of this manuscript, it was called to our attention (Doug Yanega, in litt.) that *Timalinirmus* was not formally made available by Mey (2017) under the rules of the International Code of Zoological Nomenclature (ICZN, 1999; hereafter: the Code). Mey (2017: 182) included a list of synonymizations of many of his proposed genera with those of Gustafsson & Bush (2017), published a mere month earlier. As these synonymizations were included in the same publication as the original descriptions, the latter are not considered available under Article 11.5 of the Code, which states that to be available, "a name must be used as valid for a taxon when proposed". Moreover, Article 11.6.3 of the Code states that names "first published after 1960 and treated as a junior synonym on that occasion cannot be made available from that act". The existence of a question mark before the synonymy of *Timalinirmus* in Mey's addendum does not matter, as this still indicates that Mey (2017) was not confident in the validity of this taxon (Yanega, in litt.).

Thus, the question before us is not whether either of these two new species should be placed in *Resartor* or "*Timalinirmus*", but whether there are any data supporting separation of "*Timalinirmus*" from *Resartor*, in which case a new genus name would be needed for this genus. Based on genetic data presented here, and our re-examination of the original description of the type species of *"Timalinirmus*" and the only other species in this genus, we find no basis for separation between these and the rest of *Resartor*, beyond differences in head shape. In all previously known species of *Resartor*, the head is conspicuously longer and more trapezoidal than in the known species of "*Timalinirmus*".

However, the species described here, and the genetic data in Fig. 2, suggest that the head shape of *Resartor* is more variable than previously thought (e.g., Gustafsson *et al*. 2018). We therefore conclude that the species previously placed in "*Timalinirmus*", as well as both new species described here, belong to *Resartor*. Notably, this action does not require any modifications to the morphological circumscription of *Resartor*; more specimens of *Resartor curvus* (Gustafsson *et al*., 2022) comb. nov. are needed to establish whether the detached cross-piece of the female subgenital plate of this species is truly detached, or whether that was an artifact of slide-mounting for specimens examined by Gustafsson *et al.* (2022). The characters listed in Table 1 are sufficient to separate all known members of *Aratricerca*, *Resartor*, and *Turdinirmoides*. Furthermore, this suggests that the two undescribed species of "*Timalinirmus*"

shown in the photographs published by Mey (2017) belong to *Turdinirmoides*, as suggested by Mey (2017: 182), who synonymized *Timalinirmus* with this genus.

Included species

Resartor acutitemporalis sp. nov.
Resartor albofulvus Gustafsson *et al.*, 2018
Resartor apimimus Gustafsson *et al.*, 2018
Resartor aterrimus Gustafsson *et al.*, 2018
Resartor breviceps sp. nov.
Resartor curvus (Gustafsson *et al*., 2022) comb. nov.
Resartor effronte (Ansari, 1956)
Resartor elugeus Gustafsson *et al.*, 2021
Resartor extraneus Gustafsson *et al.*, 2018
Resartor grammatoptiliphagus (Mey, 2017)
Resartor guangxiensis Gustafsson *et al.*, 2018
Resartor hrabali (Najer & Sychra in Najer *et al*. 2012) comb. nov.
Resartor impressifrons (Ansari, 1956)
Resartor himalayana (Mey, 2017)
Resartor longisuturalis Gustafsson *et al.*, 2018
Resartor novofacies (Ansari, 1956)
Resartor seminudus Gustafsson *et al.*, 2018
Resartor weigoldi (Mey, 2017)

Host distribution

Most species are known from hosts in the Leiothrichidae (Passeriformes Linnaeus, 1758), but some species also infest Paradoxornithidae Horsfield & Moore, 1854 and Timaliidae Vigors & Horsfield, 1827.

Geographical range

All known species are limited to South and Southeast Asia, with the species described here from Central China being at the northeastern extreme of the range.

Resartor acutitemporalis sp. nov.
urn:lsid:zoobank.org:act:1C464305-10F3-42F8-AE3F-D048231B4726
Figs 3–4

Diagnosis

Resartor acutitemporalis sp. nov. can be separated from all known species of *Resartor* by its unique head shape (Fig. 4A): preantennal area not markedly longer than postantennal area, rounded distally, with clearly convex lateral margins; postantennal head with temples forming acute angles and occiput concave.

Etymology

Specific name constructed from '*acutus'*, Latin for 'sharp, acute', and '*tempus'*, Latin for 'temple', referring to the unique postantennal head shape of this species.

Type material

Holotype (ex *Suthora webbiana suffusa***)**
CHINA • ♂; Hubei Province, Enshi, Erxianyan Provincial Wetland Nature Reserve; 24 Apr. 2024; Zhengzhen Wang leg.; bird ID J5647; louse ID GD-PHTH-01333; IZGAS.

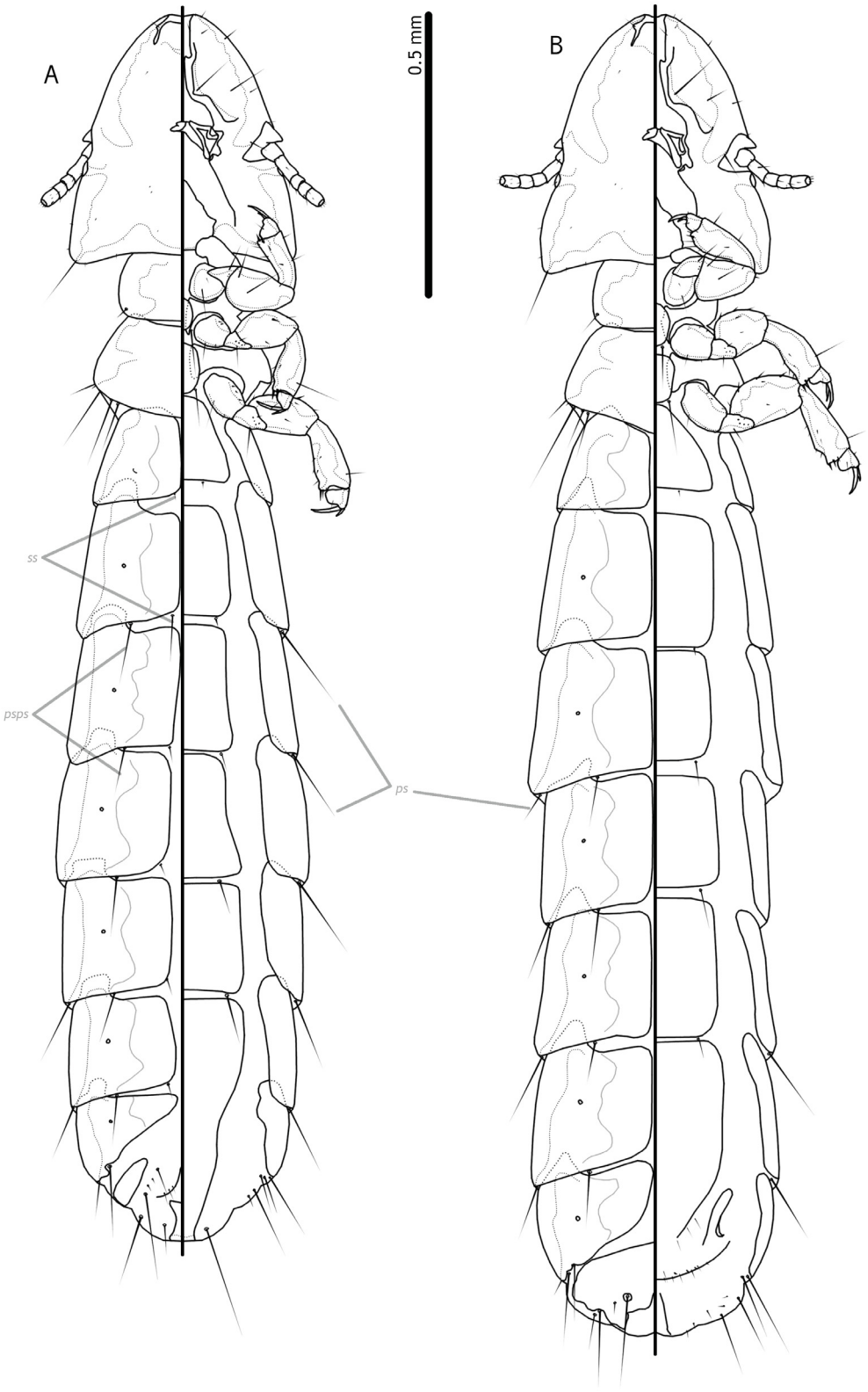

Fig. 3. *Resartor acutitemporalis* sp. nov. **A**. Holotype, ♂ (ID GD-PHTH-01333), habitus, dorsal and ventral views. **B**. Paratype, ♀ (ID GD-PHTH-013334), habitus, dorsal and ventral views.

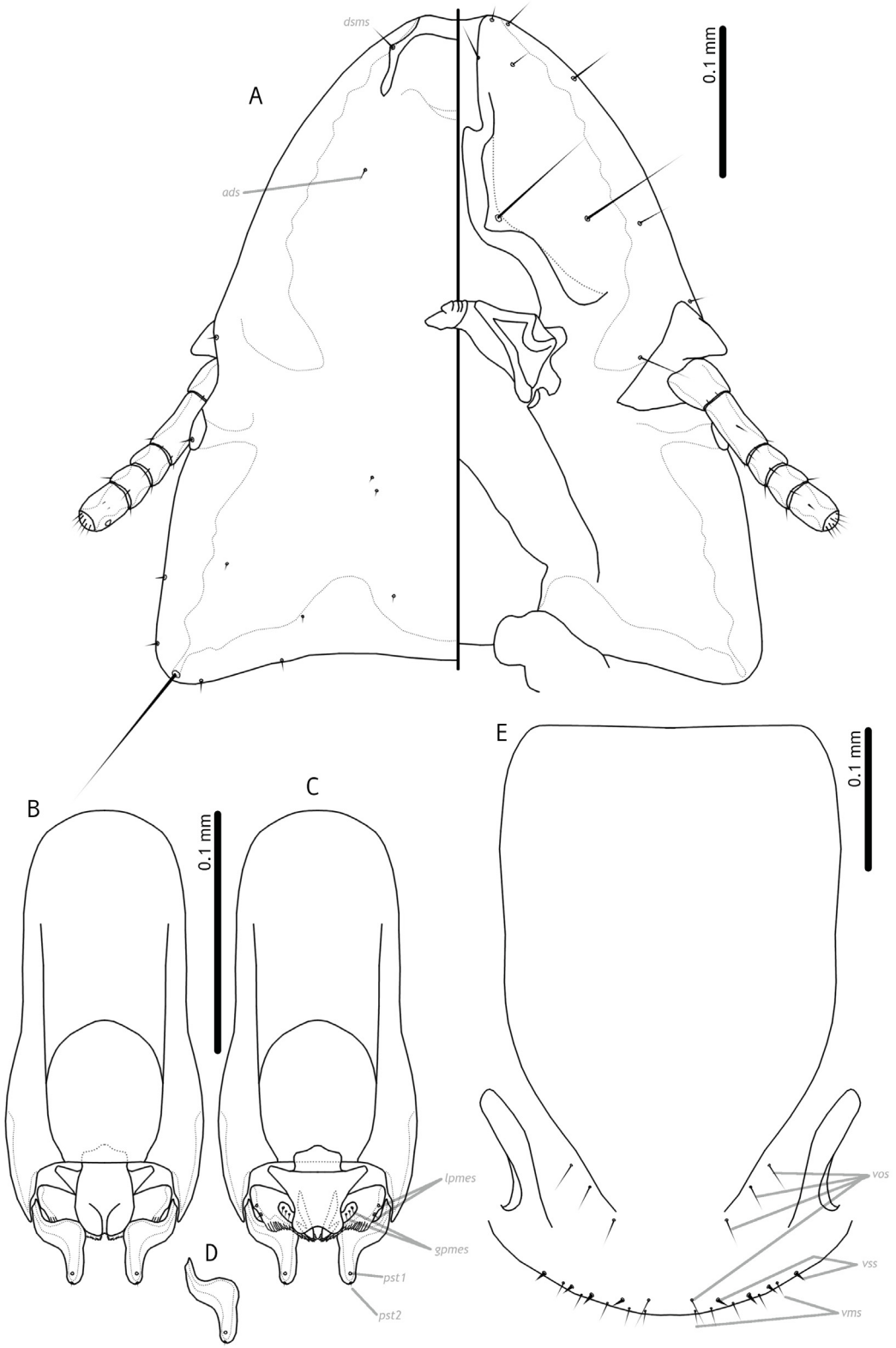

Fig. 4. *Resartor acutitemporalis* sp. nov. **A–D**. Holotype, ♂ (ID GD-PHTH-01333). **A**. Head, dorsal and ventral views. **B**. Genitalia, dorsal view. **C**. Genitalia, ventral view. **D**. Paramere, dorsal view. **E**. Paratype, ♀ (ID GD-PHTH-013334), subgenital plate and vulval margin, ventral view. Abbreviations: see Material and methods.

Table 3. Measurements (in mm) of the two species of *Resartor* Gustafsson & Bush, 2017, described herein. Abbreviations used: AW = abdominal width (at segment V); HL = head length (at midline); HW = head width (at widest point of temples); PRW = prothoracic width; PTW = pterothoracic width; TL = total length (at midline). Note that several specimens are poorly preserved and could not be measured.

Species	Sex	#	TL	HL	HW	PRW	PTW	AW
Resartor acutotemporalis sp. nov.	M	2	1.91–1.02	0.39–0.40	0.37	0.21	0.30	0.28–0.36
	F	1	2.36	0.44	0.41	0.24	0.34	0.42
Resartor breviceps sp. nov.	M	5	2.88–2.92	0.49–0.51	0.42–0.49	0.30–0.32	0.40–0.43	0.46–0.52
	F	7	3.08–3.22	0.49–0.55	0.45–0.50	0.31–0.35	0.42–0.47	0.47–0.57

Paratypes (ex *Suthora webbiana suffusa***)**
CHINA • 1 ♂; same data as for holotype; bird ID J5641; louse ID GD-PHTH-013334; IZGAS • 1 ♀; same data as for holotype; bird ID J5642; louse ID GD-PHTH-013335; IZGAS.

Type host

Suthora webbiana suffusa Swinhoe, 1871 – vinous-throated parrotbill.

Type locality

Erxianyan Provincial Wetland Nature Reserve, Enshi, Hubei Province, China.

Description

Both sexes

Preantennal head not much longer than postantennal head (Fig. 4A), frons concave, lateral margins of preantennal head clearly convex. Dorsal preantennal suture reaching *dsms* but not *ads*, and not medianly continuous. Head chaetotaxy as in Fig. 4A. Temples forming acute angles, occiput clearly concave. Thoracic and abdominal segments and pigmentation as in Fig. 3A–B. Pterothorax with lateral margins clearly flaring posteriorly. Measurements as in Table 3.

Male

Abdominal chaetotaxy: *ss* present on tergopleurites II–VII; *psps* present on tergopleurites III–VIII; *tps* and *aps* absent; *ps* present on abdominal segments III–VIII. Basal apodeme proportionately broad (Fig. 4B–C), rounded proximally. Proximal mesosome broad, with proximal margin convergent to median rounded point; distally somewhat bilobed dorsally. Mesosomal lobes broad, with distal margin fringed; 2 *lpmes* microsetae visible sublaterally on each side; 2–3 *gpmes* microsetae visible on each side lateral to gonopore. Gonopore large, elongated, flaring proximally, with proximal margin slightly concave, and distal margin bilobed. Parameres with small, bifid heads (Fig. 4D), strongly sinuous, distally blunt, with *pst1–2* as in Fig. 4D.

Female

Abdominal chaetotaxy: *psps* present on tergopleurites IV–VII; *ss, tps, aps* absent; *ps* present on abdominal segments IV–VIII. Subgenital plate roughly rectangular (Fig. 4E), cross-piece and connection not clearly visible in examined female because of gut contents and lack of pigmentation. Vulval margin gently rounded, with 5–8 short, slender *vms* and 4 short, thorn-like *vss* on each side; subgenital plate with 3–4 short, slender *vos* on each side, the distalmost of which is median to *vss*.

Resartor breviceps sp. nov.
urn:lsid:zoobank.org:act:2273B14E-CBA7-47BE-8CA0-1886C8506850
Figs 5–6

Diagnosis

Resartor breviceps sp. nov. can be separated from all other known species of *Resartor* by the head shape (Fig. 6A). Whereas in all previously described species (except *R. acutitemporalis*), the preantennal area is elongated, with almost parallel, barely convex or in some species, concave lateral margins (Fig. 1A–B), in *R. breviceps* the preantennal area is not elongated, with more markedly convergent and convex lateral margins. Moreover, whereas in other species of *Resartor*, the temples are angular, in *R. breviceps*, the temples are gently rounded. In these characters, and overall habitus, *R. breviceps* is more reminiscent of species in the genera *Turdinirmoides* (Fig. 1C) or *Aratricerca* (Fig. 1D). However, *R. breviceps* can be separated from species in these genera based on having characters typical for *Resartor* in Table 1, and lacking the characters typical for *Turdinirmoides* and *Aratricerca* in that table (see Figs 5–6).

Etymology

Specific name is constructed from '*brevis'*, Latin for 'short', and '*caput'*, Latin for 'head', referring to the unusually small head of this species, compared to other members of the genus.

Type material

Holotype (ex *Erythrogenys gravivox cowensae***)**
CHINA • ♂; Hubei Province, Enshi, Erxianyan Provincial Wetland Nature Reserve; 26 Apr. 2024; Zhengzhen Wang leg.; bird ID J5674; louse ID GD-PHTH-01337; IZGAS.

Paratypes (ex *Erythrogenys gravivox cowensae***)**
CHINA • 2 ♂♂; same data as for holotype; louse ID GD-PHTH-01338–9; IZGAS • 2 ♂♂, 6 ♀♀; Hunan Province, Badagongshan, "Tea Station"; 23 Jul. 2012; Dongdong Su leg.; bird ID J0098; louse ID GD-PHTH-00404–7; IZGAS • 3 ♀♀; same data as for preceding; bird ID J0103; louse ID GD-PHTH-00408–9; IZGAS.

Type host

Erythrogenys gravivox cowensae (Deignan, 1952) – black-streaked scimitar-babbler.

Type locality

Erxianyan Provincial Wetland Nature Reserve, Enshi, Hubei Province, China.

Description

Both sexes

Preantennal head not much longer than postantennal head (Fig. 6A), frons concave, lateral margins of preantennal head clearly convex. Dorsal preantennal suture reaching *dsms* but not *ads*, and not medianly continuous. Head chaetotaxy as in Fig. 6A. Temples rounded. Thoracic and abdominal segments and pigmentation as in Fig. 5A–B. Pterothorax with lateral margins clearly flaring posteriorly. Measurements as in Table 3.

Male

Abdominal chaetotaxy: *ss* present on tergopleurites II–VII; *psps* present on tergopleurites III–VIII; *tps* and *aps* absent; *ps* present on abdominal segments III–VIII. Basal apodeme proportionately slender (Fig. 6B–C), with proximal end rounded. Proximal mesosome elongated, rounded rectangular; distal mesosome much broader, rounded dorsally, with median incision on distal margin; ventrally, distal

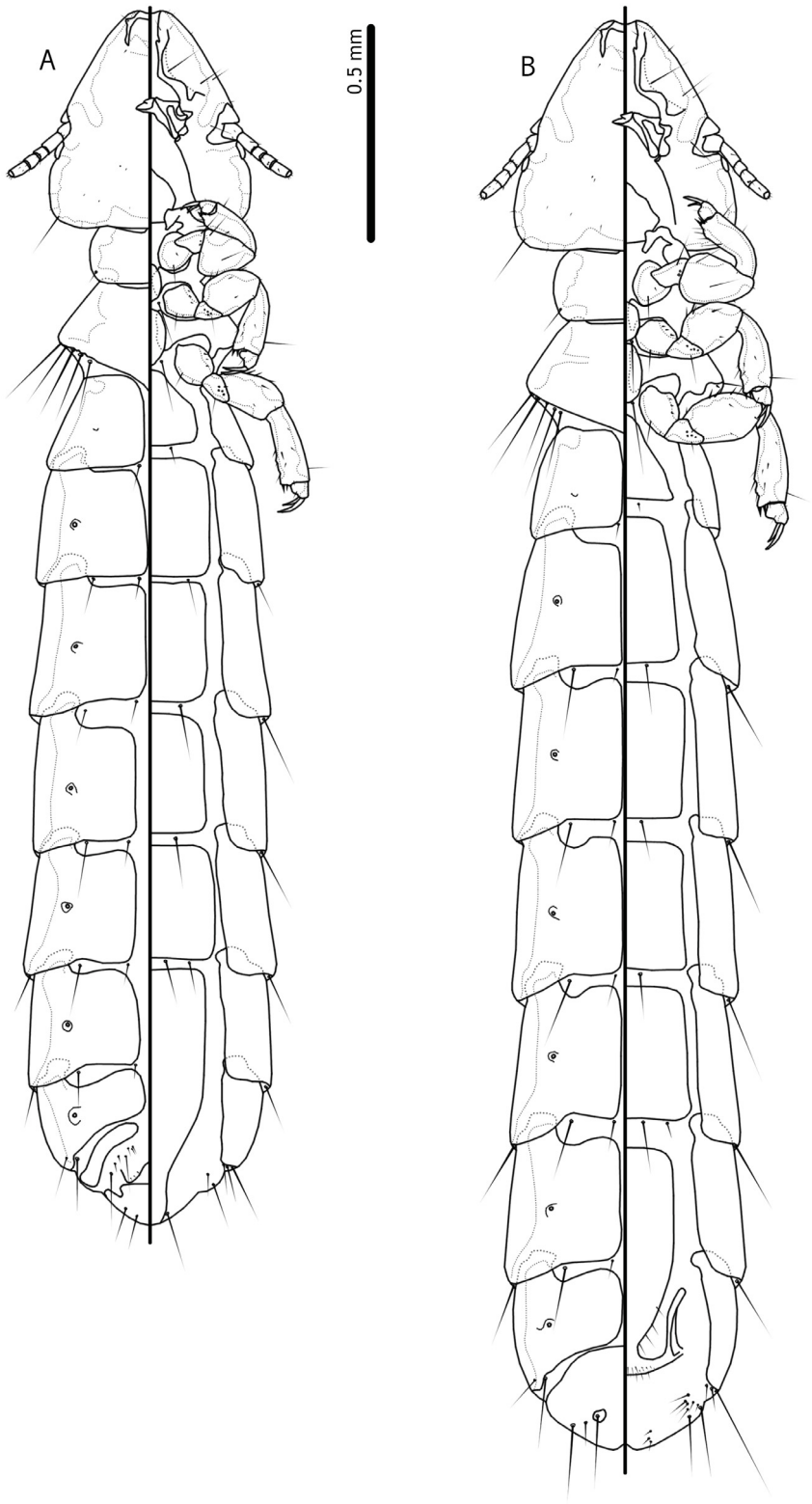

Fig. 5. *Resartor breviceps* sp. nov. **A**. Holotype, ♂ (ID GD-PHTH-01337), habitus, dorsal and ventral views. **B**. Paratype, ♀ (ID GD-PHTH-00408), habitus, dorsal and ventral views.

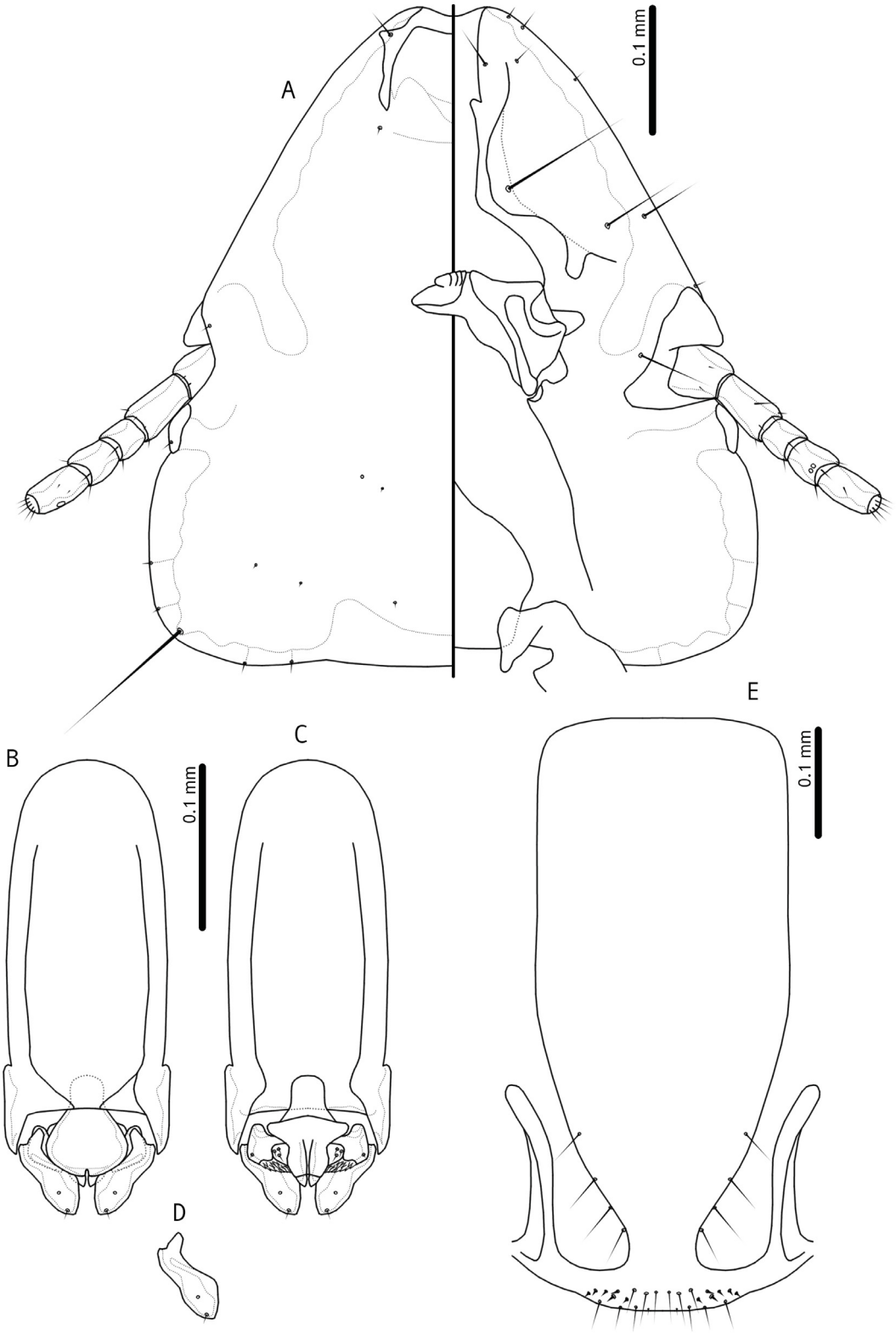

Fig. 6. *Resartor breviceps* sp. nov. **A–D**. Holotype, ♂ (ID GD-PHTH-01337) **A**. Head, dorsal and ventral views. **B**. Genitalia, dorsal view. **C**. Genitalia, ventral view. **D**. Paramere, dorsal view. **E**. Paratype, ♀ (ID GD-PHTH-00408), subgenital plate and vulval margin, ventral view.

mesosome broad, with antero-lateral corners extended proximally, and distal margin fringed; 1 *lpmes* microseta visible sublaterally on each side near distal corner of mesosomal lobes; 2–3 *gpmes* microsetae visible on each side lateral to gonopore. Gonopore roughly T-shaped, with proximal margin bluntly convergent to median point and distal ends deeply incised. Parameres with large, bluntly bifid heads (Fig. 6D), parameral blades somewhat rounded, with *pst1–2* as in Fig. 6D.

Female

Abdominal chaetotaxy: *ss* present in tergopleurites II–VII; *psps* present on tergopleurites III–VIII; *tps* and *aps* absent; *ps* present on abdominal segments III–VIII. Subgenital plate elongated rectangular (Fig. 6E), with lateral margins slightly concave to straight; connection to slender cross-piece relatively broad. Vulval margin flattened medianly, with 4–5 short, slender *vms* and 5–6 short, slender *vss* on each side; subgenital plate with 5–7 short, slender *vos* on each side, the distal 2–3 of which are situated median to the *vss*.

Discussion

Based on the analysis of genetic data presented here, and the morphological data from two new species in the *Resartor*-group, the genus "*Timalinirmus*" appears to be nested within *Resartor* (Fig. 2). This solves the problem of having to provide a new name for the "*Timalinirmus*" group, as all species in this genus can be placed in *Resartor*. However, *Aratricerca macki* Gustafsson *et al*., 2022 is the only member of its genus for which DNA sequences are available. Its placement as sister to *Resartor breviceps* sp. nov. complicates complicate matters, because *Resartor* and *Aratricerca* are well separated morphologically (Gustafsson & Bush 2017; Gustafsson *et al*. 2018, 2022; Table 1). Although *R. breviceps* is unusual within *Resartor*, it exhibits none of the characters typical for *Aratricerca*. Presumably, lack of specimens from *Aratricerca* and *Turdinirmoides* may be responsible for their close relationship in our analysis.

Similarly, the small number of species of most other *Resartor*-group genera with available DNA data, and the small number of genetic markers available, may be the basis for the lack of support for monophyly of the *Resartor*-group (Fig. 1). Notably, the genera *Indoceoplanetes, Turdinirmus* and *Maculinirmus* were all found to be monophyletic with good support, but the relationships among them are not supported. More data are needed for all genera in the *Resartor*-group, particularly for the three genera for which no genetic data are presently available (Gustafsson *et al*. 2022). Data from these genera may also solve the placement of *Psammonirmus*, which was placed as sister to *Brueelia* and some close relatives in our analysis, but without support.

The placement of *Resartor acutitemporalis* and *R. curvus* within *Resartor* among species with a more conventional head shape for the genus highlights how this character may vary within louse genera. Similar variation in head shape is seen in e.g., *Guimaraesiella* Eichler, 1949 and *Brueelia* (see Gustafsson *et al*. 2019a), and may perhaps be expected in other genera within the *Brueelia*-complex, once more species are known. It is notable that *R. acutitemporalis*, *R. curvus*, and *R. breviceps* sp. nov. parasitize hosts outside the Leiothrichidae, whereas almost all previously known species of *Resartor* parasitize hosts within this family. The typical elongated, trapezoidal head shape of *Resartor* may be related to some feature of their hosts, or possibly microhabitat preferences on their hosts. However, *R. extraneus* Gustafsson *et al.,* 2018 and *R. hrabali* (Najer & Sychra in Najer *et al.* 2012) comb. nov., the only previously known *Resartor* species from non-leiothrichid hosts, have more typical head shapes for the genus.

Resartor as circumscribed here is known from at least one host in four bird families, considerably expanding the known host range of this genus (Table 4). Gustafsson *et al*. (2025) estimated that the true diversity of *Resartor* may be 164 species and *Timalinirmus* 206 species, based on Indices of Specificity

Table 4. (continued on next page). Updated louse-host checklist of the genus *Resartor* Gustafsson & Bush, 2017. Sources are given only for host records published outside the original description of the taxon. Host family is indicated after the host name, and type hosts are indicated with an asterisk (*). Only country and province (when known) are given for type localities.

Louse name	Host name and family	Type locality	Source
Resartor acutitemporalis sp. nov.	*Suthora webbiana suffusa* Swinhoe, 1871 (Paradoxornithidae)*	China: Hubei	
Resartor albofulvus Gustafsson *et al.*, 2018	*Heterophasia desgodinsi desgodinsi* (Oustalet, 1877) (Leiothrichidae)*	China: Dali	
Resartor apimimus Gustafsson *et al.*, 2018	*Heterophasia picaoides wrayi* (Ogilvie-Grant, 1910) (Leiothrichidae)*	Malaysia: Perak	
Resartor aterrimus Gustafsson *et al.*, 2018	*Minla ignotincta mariae* La Touche, 1921 (Leiothrichidae)*	China: Yunnan	
Resartor breviceps sp. nov.	*Erythrogenys gravivox cowensae* (Deignan, 1952) (Timaliidae)*	China: Hubei	
Resartor curvus (Gustafsson *et al*., 2022)	*Staphida castaniceps plumbeiceps* Godwin-Austes, 1877 (Zosteropidae)*	China: Guangxi	
Resartor effronte (Ansari, 1956)	*Trochalopteron squamatum* (Gould, 1835) (Leiothrichidae)*	India: Manipur	
Resartor elugeus Gustafsson *et al.*, 2021	*Alcippe fratercula yunnanensis* Harington, 1913 (Leiothrichidae)*	China: Yunnan	
	Leiothrix argentauris vernayi (Mayr & Greenway, 1938) (Leiothrichidae)		Grossi *et al.* 2026
	Leiothrix lutea calipyga (Hodgson, 1837) (Leiothrichidae)		Grossi *et al.* 2026
	Liocichla ripponi ripponi (Oates, 1900) (Leiothrichidae)		Grossi *et al.* 2026
	Stachyris nigriceps coltarti Harington, 1913 (Timaliidae)		Grossi *et al.* 2026
Resartor extraneus Gustafsson *et al.*, 2018	*Lioparus chrysotis swinhoii* (Verreaux, 1871) (Paradoxornithidae) *	China: Sichuan	

Table 4. (continued). Updated louse-host checklist of the genus *Resartor* Gustafsson & Bush, 2017. Sources are given only for host records published outside the original description of the taxon. Host family is indicated after the host name, and type hosts are indicated with an asterisk (*). Only country and province (when known) are given for type localities.

Louse name	Host name and family	Type locality	Source
Resartor grammatoptiliphagus (Mey, 2017)	*Grammatoptila striata sikkimensis* Ticehurst, 1924 (Leiothrichidae)*	India: Sikkim	
Resartor guangxiensis Gustafsson *et al.*, 2018	*Trochalopteron milnei sinianum* Stresemann, 1930 (Leiothrichidae)*	China: Guangxi	
Resartor hrabali (Najer & Sychra in Najer *et al*. 2012)	*Macronus gularis* (Horsfield, 1822) (Timaliidae)*	Vietnam: Ninh Binh	
Resartor impressifrons (Ansari, 1956)	*Trochalopteron affine affine* (Blyth, 1843) (Leiothrichidae)*	Nepal	
	Trochalopteron affine bethalae (Rand & Fleming, 1956) (Leiothrichidae)		Gustafsson & Bush 2017
Resartor himalayana (Mey, 2017)	*Trochalopteron affine blythi* Verreaux, 1871 (Leiothrichidae)*	China: Sichuan	
Resartor longisuturalis Gustafsson *et al.*, 2018	*Actinodura cyanouroptera wingatei* (Ogilvie-Grant, 1900) (Leiothrichidae)*	China: Yunnan	
Resartor novofacies (Ansari, 1956)	*Trochalopteron milnei sharpei* Rippon, 1901 (Leiothrichidae)		Grossi *et al*. 2026
	Trochalopteron subunicolor subunicolor Blyth, 1843 (Leiothrichidae)*	India: Sikkim	
Resartor seminudus Gustafsson *et al.*, 2018	*Leiothrix argentauris tahanensis* (Yen, 1934) (Leiothrichidae)*	Malaysia: Perak	
Resartor weigoldi (Mey, 2017)	*Trochalopteron formosum formosum* (Verreaux, 1869) (Leiothrichidae)*	China: Sichuan	

calculated for the species known at the time. With an extended host range to include species from Zosteropidae and Timaliidae, the true diversity of *Resartor* may be much higher than currently suspected.

However, the description of *R. acutitemporalis* and *R. breviceps* sp. nov. reinforces a distributional pattern related to elevation for lice in this group. Gustafsson *et al*. (2022) noted that lice in the genera *Turdinirmoides*, *Aratricerca*, and *Timalinirmus* are generally found at high elevations. The two new species described here were collected above 1500 m, which seems to be the general elevational cut-off point for most species in these genera and *Resartor*. At least in China, virtually no members of these genera have been collected below 1500 m (Gustafsson & Grossi, *in prep.*). The causes of this distribution are unknown, and other genera in the *Resartor*-group are apparently not restricted by elevation. More data are needed from high elevations to explore these patterns further. If true, the true diversity of *Resartor* may be limited by the elevational ranges of potential host species.

Acknowledgments

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