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New genus and species of lice in the *Oxylipeurus*-complex (Phthiraptera, Ischnocera, Philopteridae), with an overview of the distribution of ischnoceran chewing lice on galliform hosts

Daniel R. Gustafsson[1], Chunpo Tian[1,2], Mengjiao Ren[1], Zhu Li[3], Xiuling Sun[4], Fasheng Zou[1]

1 *Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Library of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences, 105 Xingang West Road, Haizhu District, Guangzhou, 510260, Guangdong Province, China*

2 *College of Life Sciences, Shaanxi Normal University, 620 West Chang'an Street, Chang'an District, Xi'an City, 710119, Shaanxi Province, China*

3 *Department of Life Sciences, National Natural History Museum of China, 126, Tianqiao South St. Dongcheng District, Beijing, 100050, China*

4 *Collections Department, National Natural History Museum of China, 126, Tianqiao South St. Dongcheng District, Beijing, 100050, China*

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Corresponding author: Daniel R. Gustafsson (kotatsu@fripost.org)

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Abstract

Here, we describe a new genus of lice (Phthiraptera, Ischnocera) in the *Oxylipeurus*-complex, parasitising galliform hosts in the genera *Tragopan* Cuvier, 1829. This genus, *Pelecolipeurus* **gen. nov.**, is separated from other members of the complex by the unique shape of the male subgenital plate and stylus, the male genitalia and other characters. The only previously-known species in the genus is *Lipeurus longus* Piaget, 1880, which is here tentatively re-described as *Pelecolipeurus longus* (Piaget, 1880), based on specimens from a non-type host, *Tragopan temminckii* (Gray, 1831). In addition, we describe a new species, *Pelecolipeurus fujianensis* **sp. nov.**, based on specimens from *Tragopan caboti* (Gould, 1857). An overview of the distribution patterns of ischnoceran lice on galliforms is presented, which suggests that host phylogeny, host biogeography and host biotope, as well as elevation of host range, may all be important factors that have structured louse communities on landfowl. We transfer the genus *Afrilipeurus* from the *Oxylipeurus*-complex to the *Lipeurus*-complex and include an emended key to the *Oxylipeurus*-complex.

Key Words

chewing lice, Galliformes, new genus, *Oxylipeurus*-complex, Phthiraptera

Introduction

Chewing lice (Phthiraptera) in the *Oxylipeurus*-complex mainly parasitise gamefowl (Galliformes; Price et al. (2003)) and most species are known from Asian galliforms. Traditionally, most of the species have been placed in the one genus, *Oxylipeurus* (e.g. Clay (1938a); Hopkins and Clay (1952); Price et al. (2003)). However, this classification was challenged by, for example, von Kéler (1958) and Carriker (1967), who considered several groups of *Oxylipeurus* to be sufficiently distinct to form separate genera. Mey (2009) considered several of these genera valid and, since then, a large number of new genus-level taxa within this complex have been established (Gustafsson and Zou 2020a, b, 2023; Gustafsson et al. 2020a, b).

Assessing taxon limits in this complex is difficult, as the overall chaetotaxy and morphology, including that of the male genitalia, are conserved in many genera and species are often delimited by more nebulous characters, such as head shape, mesosome shape and degree of reticulation of the cuticle (e.g. Gustafsson et al. (2020a)). Moreover, many species are poorly known and have not been fully described or illustrated; the last detailed revisions of the complex were published by Clay (1938a) and von Kéler (1958).

Gustafsson et al. (2020a) tentatively considered *Lipeurus longus* Piaget, 1880, to belong to the genus *Reticulipeurus* Kéler, 1958, based on its placement by Clay (1938a), von Kéler (1958) and Złotorzycka (1966); however, they stated that they had not examined any specimens and that some aspects of the morphology of this species were aberrant for *Reticulipeurus*. Here, we describe this group as a separate genus, *Pelecolipeurus* gen. nov., based on specimens examined from two hosts in China and examination of photos and illustrations of *Lipeurus longus* Piaget, 1880. We tentatively re-describe the only previously-known species (*L. longus*) and add a second species, *Pelecolipeurus fujianensis* sp. nov.

Given that this new genus is the third *Oxylipeurus*-complex genus to be described in recent years from the same host group, we also take this opportunity to summarise what is known about host-associations amongst ischnoceran lice parasitising galliform hosts. Finally, we update the key to the genera of the *Oxylipeurus*-complex previously published by Gustafsson et al. (2020b).

Materials and methods

Previously, slide-mounted specimens deposited at the National Natural Museum of Natural History, China (NNHM) were examined with a Nikon Eclipse N*i* (Nikon Corporation, Tokyo, Japan), with a drawing tube attached for making illustrations. Drawings were scanned, then compiled and edited in GIMP 2.10 (www.gimp.org). Measurements (all in mm) were made from slide-mounted specimens in the digital measuring software ImageJ 1.48v (Wayne Rasband; imagej.net): AW = abdominal width (at segment V); HL = head length (at mid-line); HW = head width (at widest point of temples); PRW = prothoracic width; PTW = pterothoracic width; TL = total length (at mid-line).

Host taxonomy follows Clements et al. (2022). Terminology for chaetotaxy and other structures of the lice follows Clay (1951), Mey (1994) Gustafsson and Bush (2017) and Gustafsson et al. (2020a). Abbreviations used in the text follow Gustafsson and Bush (2017) and Gustafsson et al. (2020a) and include: *mds* = mandibular seta; *mms* = marginal mesometathoracic setae; mths = metathoracic thorn-like seta; *mtrs* = metathoracic trichoid seta; *mts1–3* = marginal temporal setae 1–3; *os* = ocular seta; *pos* = preocular seta; *ps* = paratergal seta; *pst1–2* = parameral setae 1–2; *s1–8* = sensilla 1–8 of dorsal head; *sts* = sternal seta; *vms* = vulval marginal setae; *vss* = vulval submarginal setae.

Systematics

PHTHIRAPTERA Haeckel, 1896

Phthiraptera Haeckel, 1896: 703.

Ischnocera Kellogg, 1896

Ischnocera Kellogg, 1896: 63.

Philopteridae Burmeister, 1838

Philopteridae Burmeister, 1838: 422.

Oxylipeurus-complex

Included genera:
- *Calidolipeurus* Gustafsson et al., 2020b: 2.
- *Cataphractomimus* Gustafsson et al., 2020a: 206.
- *Chelopistes* Kéler, 1940: 180.
  - *Virgula* Clay, 1941: 119.
- *Eiconolipeurus* Carriker, 1945: 91.
- *Epicolinus* Carriker, 1945: 104.
- *Gallancyra* Gustafsson & Zou, 2020a: 11.
- *Megalipeurus* Kéler, 1958: 327.
- *Oxylipeurus* Mjöberg, 1910: 91.
- *Pelecolipeurus* gen. nov.
- *Reticulipeurus* Kéler, 1958: 332.
  - Subgenus: *Reticulipeurus* (*Forcipurellus*) Gustafsson & Zou, 2023:497.
  - Subgenus: *Reticulipeurus* (*Reticulipeurus*) Kéler, 1958: 332.
- *Sinolipeurus* Gustafsson et al., 2020a: 229.
- *Splendoroffula* Clay & Meinertzhagen, 1941: 343.
  - *Splendopeurus* Kéler, 1958: 309.
- *Talegallipeurus* Mey, 1982: 242.
- *Trichodomedea* Carriker, 1946: 365.
- *Valimia* Gustafsson & Zou, 2020b: 490.

Pelecolipeurus gen. nov.

https://zoobank.org/FBCCEB4D-7E49-4BFE-88D7-A71559102743

Type species. *Pelecolipeurus fujianensis* sp. nov.

Diagnosis. *Pelecolipeurus* gen. nov. keys to *Reticulipeurus* Kéler, 1958, in the key of Gustafsson et al. (2020b). Species of *Pelecolipeurus* can be separated from *Reticulipeurus* and all other members of the *Oxylipeurus*-complex by the following combination of characters: frons rounded to slightly flattened (Figs 3, 17); dorsal pre-antennal suture present, transversal, but not reaching lateral margins of head (Figs 3, 17); *mms* gathered into a single sublateral bunch (Figs 1, 2, 15, 16); male tergopleurites II–VII medianly interrupted and intertergal sclerites absent (Figs 1, 15); male tergopleurites IX–XI fused to form single plate (Figs 1, 15); female tergopleurites IX–XI fused laterally, but not medianly, forming two distinct plates (Figs 2, 16); male subgenital plate of unique shape, with lateral extensions at base of stylus (Figs 7, 21); stylus subterminal, elongated to reach beyond distal margin of abdomen (Figs 7, 21); female vulval margin narrowly concave, without lateral accessory vulval plates (Figs 8, 22); male genitalia very long, reaching anteriorly to abdominal segment III (Figs 5, 19); denticulate genital sac present in male genitalia (Figs 5, 19); male genitalia symmetrical, with parameres present, mesosome dominated by large gonopore (Figs 6, 20).

Description. ***Both sexes.*** Male longer than female (Table 1). Head longer than wide, frons rounded to slightly flattened (Figs 3, 17). Dorsal pre-antennal suture present, but often not well-defined and visible as pale band across head; suture not reaching lateral margins of head. Interior thickenings of pre-antennal head present as double, undulating carinae anterior to suture. Head chaetotaxy as in Figs 3, 17; *mds* may be absent in female; *s2* (?) located median to *s1*; *s5* absent; *s6–8* present; *mts3* only temporal mesoseta, but *os* may be longer than *pos* and *mts1–2* in males. Antennae sexually dimorphic, with male scape and pedicel elongated and swollen compared to female (cf. Figs 3, 4, 17, 18); male flagellomere I with distal, finger-like extension and intensely scaly inner surface (Figs 3, 17). Temples rounded, somewhat bulging. Thoracic and abdominal segments as in Figs 1, 2, 15, 16. Legs II and III much longer than legs I; coxae I–II close together. Meso- and metasterna fused. Metepisternum long, reaching almost to mesometasternum. Pronotum with lateral and posterior setae; pteronotum with microsetae in antero-lateral corners and short seta submedianly in distal half; *mms* in single sublateral bunch; *mths* and *mtrs* roughly dorsal. Tergopleurites II–VII in both sexes medianly interrupted; male tergopleurites IX–XI fused into a medianly continuous plate; female tergopleurites IX–XI fused laterally, but not medianly (Figs 2, 16). Male subgenital plate with lateral extensions in distal section (Figs 7, 15); stylus slender, elongated, tapering, attached subterminally and extending beyond distal margin of abdomen. Female subgenital plates reduced to near vulval margin; exact extent of these often not clearly visible. Leg chaetotaxy as in Figs 9–14.

Male. Male scape, pedicel and flagellomere I modified compared to female. Male genitalia very long (Figs 5, 19), with basal apodeme reaching to at least abdominal segment III, but diffuse anteriorly. Genital sac present, irregularly, but densely denticulate (Figs 6, 20). Distal third of basal apodeme with irregularly thickened lateral margins articulating with parameral heads. Mesosome simple, with central sclerite on ventral surface associated with 2–3 sensilla; three additional sensilla in oblique, distally divergent rows lateral to this sclerite. Gonopore large, dominating mesosome. Parameres short, slender, *pst1* sensilla in distal third, *pst2* microsetae, situated more or less apically.

Female. Vulval margin deeply and narrowly concave (Figs 8, 22). Three sets of genital setae: long, slender *vms*, the more median setae shorter than the more lateral setae; short, slender or lightly stout *vss* in median part of vulval margin; single seta on each side situated further submarginally and apart from *vss*. Subvulval sclerites present, slender and elongated, reaching to vulval margin.

Host distribution. Presently known only from tragopans (genus *Tragopan* Cuvier, 1829), Phasianidae, Galliformes. Some specimens from other hosts (see below) may represent stragglers or contaminations.

Geographical range. All known species are from China or the Himalayas, corresponding roughly to the combined range of the known hosts.

Etymology. The name *Pelecolipeurus* is derived from "*pélekus*", Greek for "two-headed axe" and the traditional name for long slender lice, *Lipeurus* Nitzsch, 1818. This refers to the shape of the male subgenital plate.

Remarks. Gustafsson et al. (2020a) tentatively included *Lipeurus longus* Piaget, 1880, in *Reticulipeurus* Kéler, 1958, following von Kéler (1958) and Złotorzycka (1966). They noted that they had not examined any specimens and that this placement was doubtful, based on the illustrations published by Clay (1938a) and von Kéler (1958). The examined collection at NNHM includes two different species belonging to the same morphological group as *L. longus* and these are sufficiently different morphologically from all other members of the *Oxylipeurus*-complex that the erection of a separate genus is warranted.

Unfortunately, no specimens from the type host of *Lipeurus longus* were found at NNHM and no specimens of this species have been examined from other collections. A lectotype and five paratypes are available at the Natural History Museum, London (NHML), but we had no opportunity to examine or borrow these. A photo of the lectotype female at the NHML homepage (https://data.nhm.ac.uk/dataset) confirms that this species belongs to *Pelecolipeurus*, but is insufficiently detailed to compare adequately with the specimens we have examined at the NNHM. Only two modern illustrations of *L. longus* have been published (Clay 1938a; von Kéler 1958), both of which depict the ventral view of the distal end of the male abdomen. Allowing for individual variation and differences in illustration techniques, we cannot separate the specimens illustrated in these publications from specimens we have seen from *Tragopan temminckii* (Gray, 1831) (see below) and these specimens are here tentatively considered conspecific with *L. longus*; however, this will need to be confirmed by comparison with type specimens of *L. longus* and a re-description of this species.

As the type specimens of *L. longus* could not be examined, we select the species that could be examined as the type species of *Pelecolipeurus*.

Included species.

Pelecolipeurus fujianensis sp. nov. Type host: *Tragopan caboti* (Gould, 1857).

Pelecolipeurus longus (Piaget, 1880: 370) [in *Lipeurus*]. Type host: *Tragopan satyra* (Linnaeus, 1758).

Table 1. Measurements of the species of *Pelecolipeurus*. Measurements (all in mm) were made in the digital measuring software ImageJ 1.48v (Wayne Rasband; imagej.net): AW = abdominal width (at segment V); HL = head length (at mid-line); HW = head width (at widest point of temples); PRW = prothoracic width; PTW = pterothoracic width; TL = total length (at mid-line).

Species	Host	Sex	N	TL	HL	HW	PRW	PTW	AW
Pelecolipeurus fujianensis	*Tragopan caboti*	M	20[1]	4.00–4.41 (4.20)	0.78–0.93 (0.85)	0.50–0.63 (0.57)	0.39–0.58 (0.48)	0.59–0.84 (0.71)	0.63–0.90 (0.77)
		F	30[2]	3.45–4.05 (3.74)	0.81–0.91 (0.86)	0.55–0.67 (0.61)	0.40–0.58 (0.49)	0.62–0.85 (0.73)	0.69–1.09 (0.89)
Pelecolipeurus longus s. lat.	*Tragopan temminckii*	M	6	3.56–4.40	0.70–0.90	0.48–0.71	0.41–0.61	0.58–0.80	0.58–0.91
		F	15	3.24–3.94 (3.59)	0.76–0.91 (0.83)	0.55–0.71 (0.63)	0.38–0.57 (0.47)	0.64–0.84 (0.74)	0.80–1.12 (0.96)

[1] N = 15 for TL; N = 18 for AW.
[2] N = 24 for TL; N = 29 for PTW; N = 38 for AW.

Pelecolipeurus fujianensis **sp. nov.**

https://zoobank.org/1CEB3DAA-D063-4616-A4A7-703CE2B2544F

Figs 1–14

Type host. *Tragopan caboti* (Gould, 1857) – Cabot's tragopan.

Type locality. Fujian Province, China.

Specimens examined. Type material. Ex *Tragopan caboti*: China • ***Holotype*** ♂; Fujian Province; 29 Sep 1990; collector unknown; box E0026199, slide 65 (NNHM) [Male in lower right corner, near where cover glass is broken, marked with black dot on slide]. ***Paratypes*** 7♂, 9♀, 8 nymphs; Fujian Province; 29 Sep 1990; collector unknown; box E0026199, slides 64–66, 95 (NNHM). 1♂, 3♀; Fujian Province; 16 Dec 1988; collector unknown; box E0026199, slide 68 (NNHM). 1♀, 3 nymphs; Fujian Province, Jianou; 7 Jan 1997; collector unknown; box E0026195, slide 3 (NNHM). 1♂, 2♀, 6 nymphs; Fujian Province, Wuyi Mountain; Dec. 1989; collector unknown; box E0026011, slide 15, box E0026198, slide 74 (NNHM). 11♂, 15♀, 11 nymphs; Zhejiang Province; 8 Dec 1980; collector unknown; box E0026010, slide 76, box E0026199, slides 88–92 (NNHM).

Diagnosis. Due to the limited illustrations published for *Pelecolipeurus longus* from the type host (see above), we here compare *P. fujianensis* sp. nov. with the specimens tentatively identified as *P. longus* from *T. temminckii*, which we consider conspecific with the species illustrated by Clay (1938a) and von Kéler (1958). A re-description of *P. longus* from the type host is necessary to determine additional characters separating this species from *P. fujianensis*.

Pelecolipeurus fujianensis can be separated from *P. longus* as illustrated by Clay (1938a) and von Kéler (1958) by the following characters: male fused abdominal segment IX–XI with more or less straight lateral margins in *P. longus*, but with concave lateral margins in *P. fujianensis* (Fig. 7); proximal mesosome of *P. longus* with flattened anterior margin, but with medianly pointed anterior end in *P. fujianensis* (Fig. 6); parameres more curved in *P. longus* than in *P. fujianensis* (Fig. 6).

In addition, *P. fujianensis* can be separated from the population from *T. temminckii* described above by the following characters: frons more flattened in *P. longus* s. lat. (Fig. 17) than in *P. fujianensis* (Fig. 3); male sternal plate VI with 2 *sts* of more or less equal length in *P. longus* s. lat. (Fig. 15), but with lateral seta on each side much shorter than median seta on each side in *P. fujianensis* (Fig. 1); female sternal plate VI with 1 *sts* on each side and sternal plate VII with 3 medium-length setae and up to 2 microsetae on each side in *P. fujianensis* (Fig. 2), but sternal plate VI with 2 *sts* on each side and sternal plate VII without microsetae in *P. longus* s. lat. (Fig. 16); male subgenital plates of different shape (cf. Figs 7, 21) and stylus evenly tapering distally in *P. longus* s. lat. (Fig. 21), but with convex lateral margins in distal half in *P. fujianensis* (Fig. 7); female subgenital plate medianly continuous in *P. longus* s. lat. (Fig. 22), but medianly interrupted in *P. fujianensis* (Fig. 8); proximal mesosome with flattened to slightly concave anterior margin in *P. longus* s. lat. (Fig. 20), but with pointed anterior margin in *P. fujianensis* (Fig. 6); ventral sclerite of mesosome and shape of gonopore and distal mesosome also differ between species (cf. Figs 6, 20). Male antennal characters may be more similar in these two species than illustrated here (Figs 3, 17), as their shape is affected by mounting. However, scape appears to be broader and the distal process of flagellomere I appears to be longer in *P. fujianensis* (Fig. 3) than in *P. longus* s. lat. (Fig. 17).

Description. *Both sexes*. Head shape and structure as in Fig. 3; frons gently rounded. No prominent reticulation on head. Marginal carina of moderate width, not widening posteriorly. Dorsal pre-antennal suture prominent, not reaching marginal carina laterally. Head chaetotaxy as in Fig. 3; most dorsal sensilla visible as microsetae in most examined specimens. Antennae sexually dimorphic. Thoracic and abdominal segments and chaetotaxy as in Figs 1, 2.

Male. Antennae as in Fig. 3; scape, pedicel and flagellomere I swollen and modified in shape compared to female; scape with slight process in proximal third; flagellomere I with prominent distal projection and restricted rugose area, which does not extend to proximal bulbous process of segment. Abdominal chaetotaxy as in Fig. 9; inner ventral *ps* present on segments V–VIII; median *sts* on sternite VI much longer than lateral *sts*. Subgenital plate, stylus and terminalia as in Fig. 7; stylus broadening in distal half, not tapering evenly. Genitalia as in Figs 5, 6. Proximal mesosome with narrow median point, widening distally. Ventral sclerite small, roughly rounded-rectangular, with minute postero-lateral extensions; 1 sensillum on each side associated with sclerite; 3 sensilla on each side lateral to ventral sclerite, forming distally divergent rows. Distal mesosome oval, dominated by large oval gonopore. Parameres curved slightly medianly, with median and lateral fingers of parameral head roughly equal in size. Measurements as in Table 1.

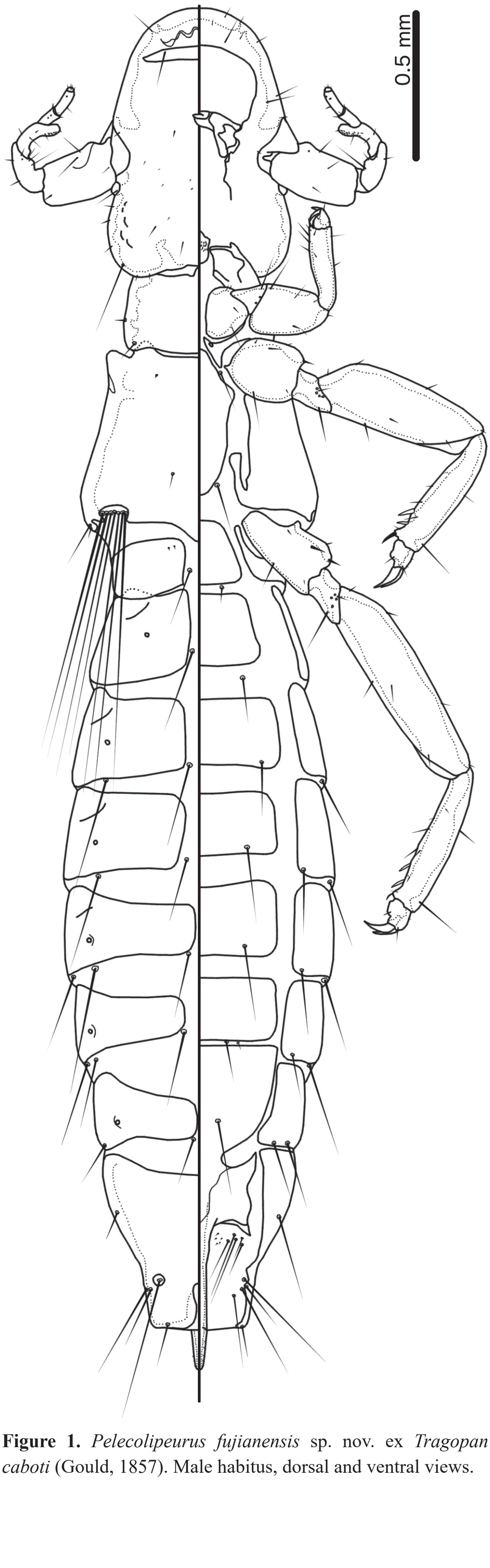


Figure 1. *Pelecolipeurus fujianensis* sp. nov. ex *Tragopan caboti* (Gould, 1857). Male habitus, dorsal and ventral views.

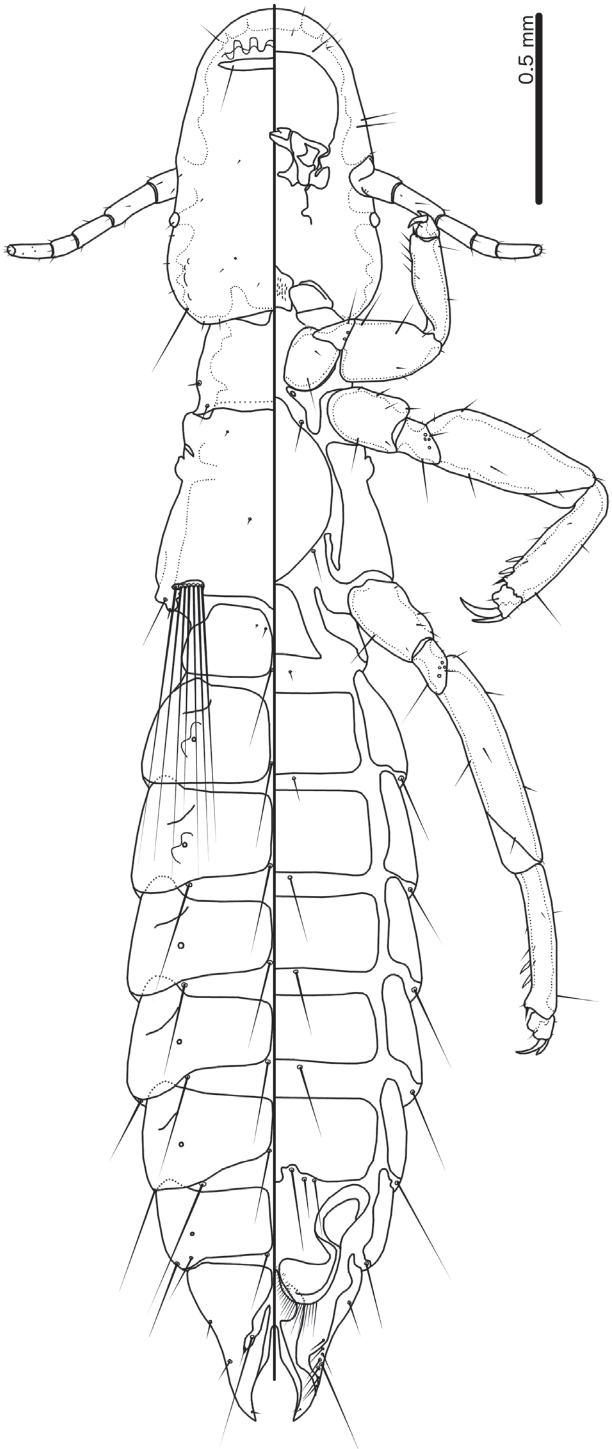
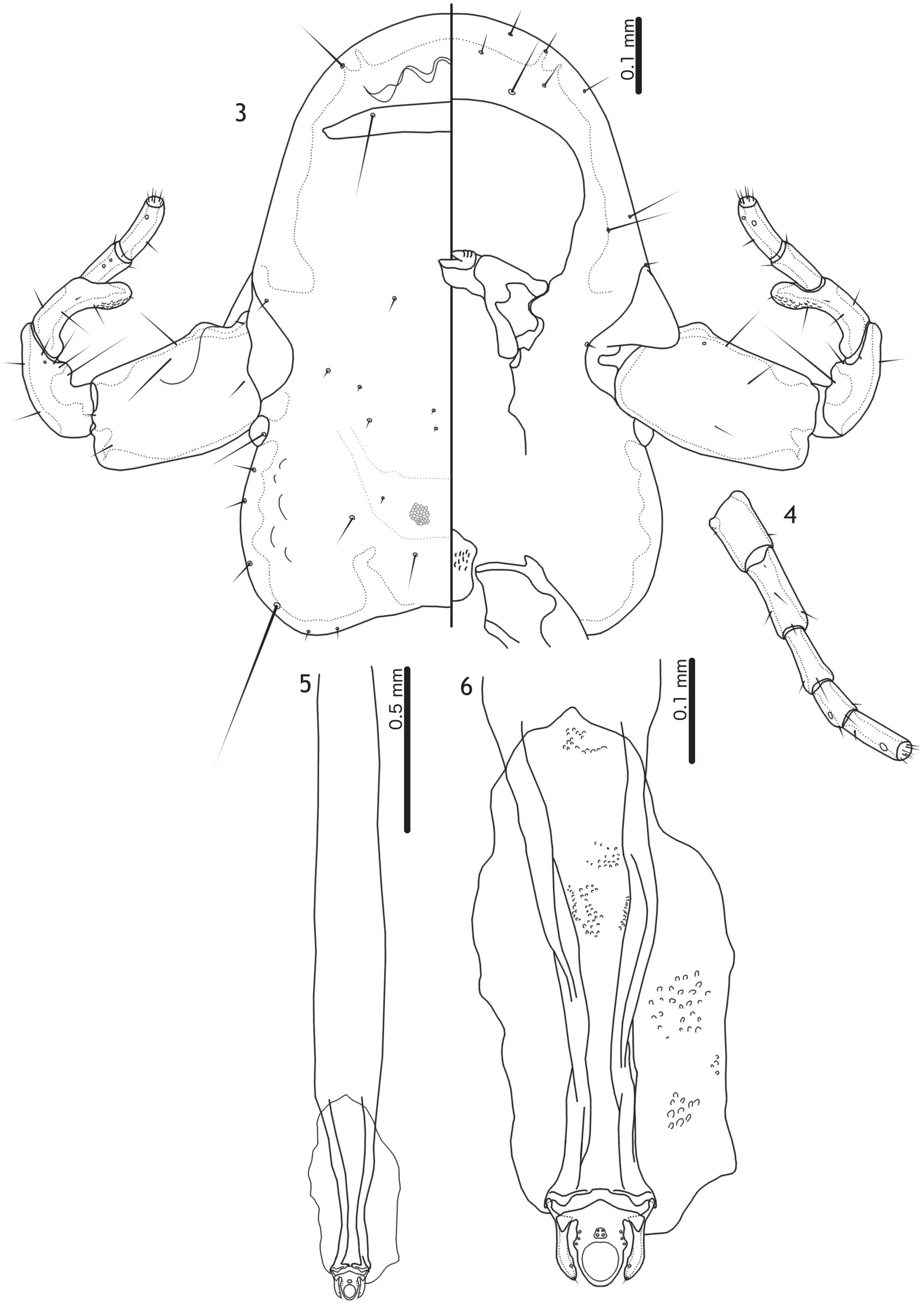


Figure 2. *Pelecolipeurus fujianensis* sp. nov. ex *Tragopan caboti* (Gould, 1857). Female habitus, dorsal and ventral views.

Female. Antennae as in Fig. 4. Abdominal chaetotaxy as in Fig. 2; sternal plate VI with 1 *sts* on each side. Subgenital plate, vulval margin and terminalia as in Fig. 8; subgenital plate divided medianly. Vulval margin with 17–23 medium-length, slender *vms* and 6–10 short, slender *vss* on each side; median *vms* shorter than lateral *vms*. Measurements as in Table 1.

Etymology. The specific name is derived from the type locality.



Figures 3–6. *Pelecolipeurus fujianensis* sp. nov. ex *Tragopan caboti* (Gould, 1857). **3.** Male head, dorsal and ventral views; **4.** Female antenna, ventral view; **5.** Male genitalia, ventral view; **6.** Distal male genitalia, ventral view.

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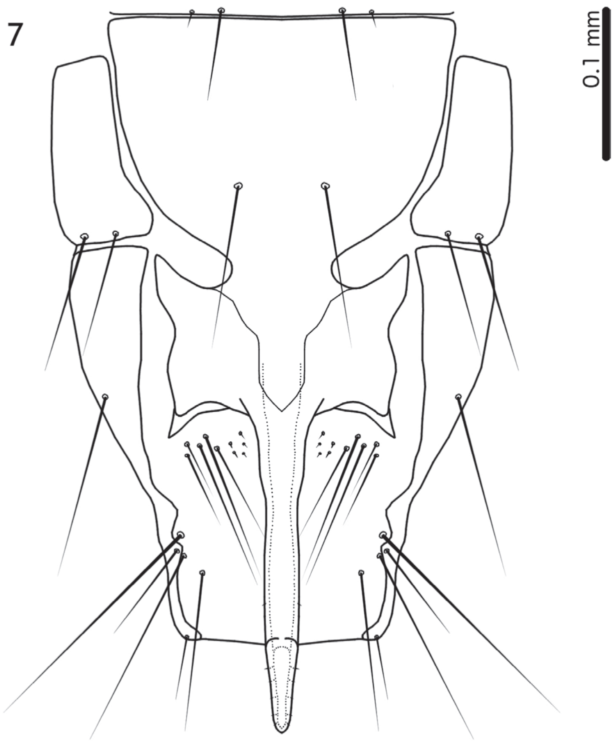

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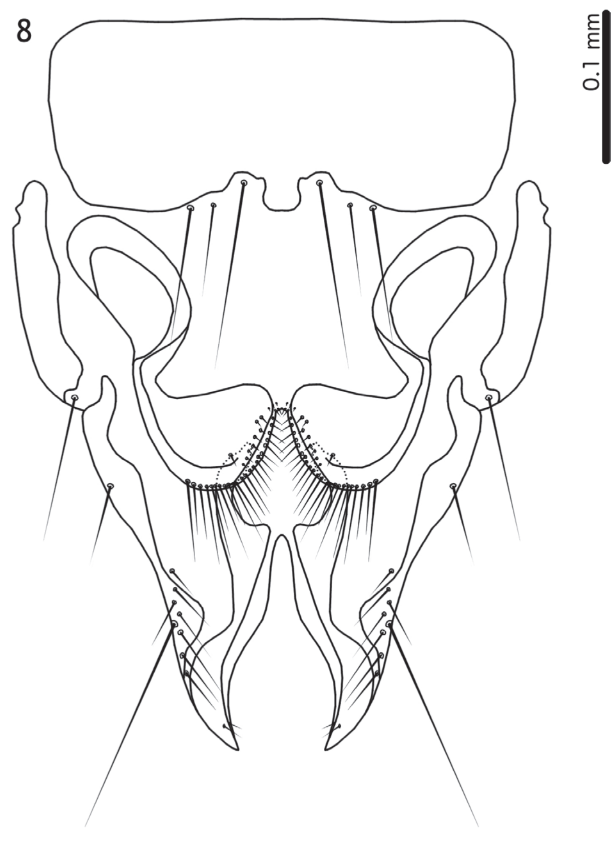


Figures 7, 8. *Pelecolipeurus fujianensis* sp. nov. ex *Tragopan caboti* (Gould, 1857). **7.** Male subgenital plate and abdominal segments VIII–XI, ventral view; **8.** Female subgenital plate and abdominal segments VIII–XI, ventral view.

Pelecolipeurus longus (Piaget, 1880), comb. nov.

Figs 15–22

Lipeurus longus Piaget, 1880: 370.
Oxylipeurus longus (Piaget), 1880; Clay, 1938a: 171.
Reticulipeurus longus (Piaget, 1880); Kéler, 1958: 332.

Type host. *Tragopan satyra* (Linnaeus, 1758) – satyr tragopan.

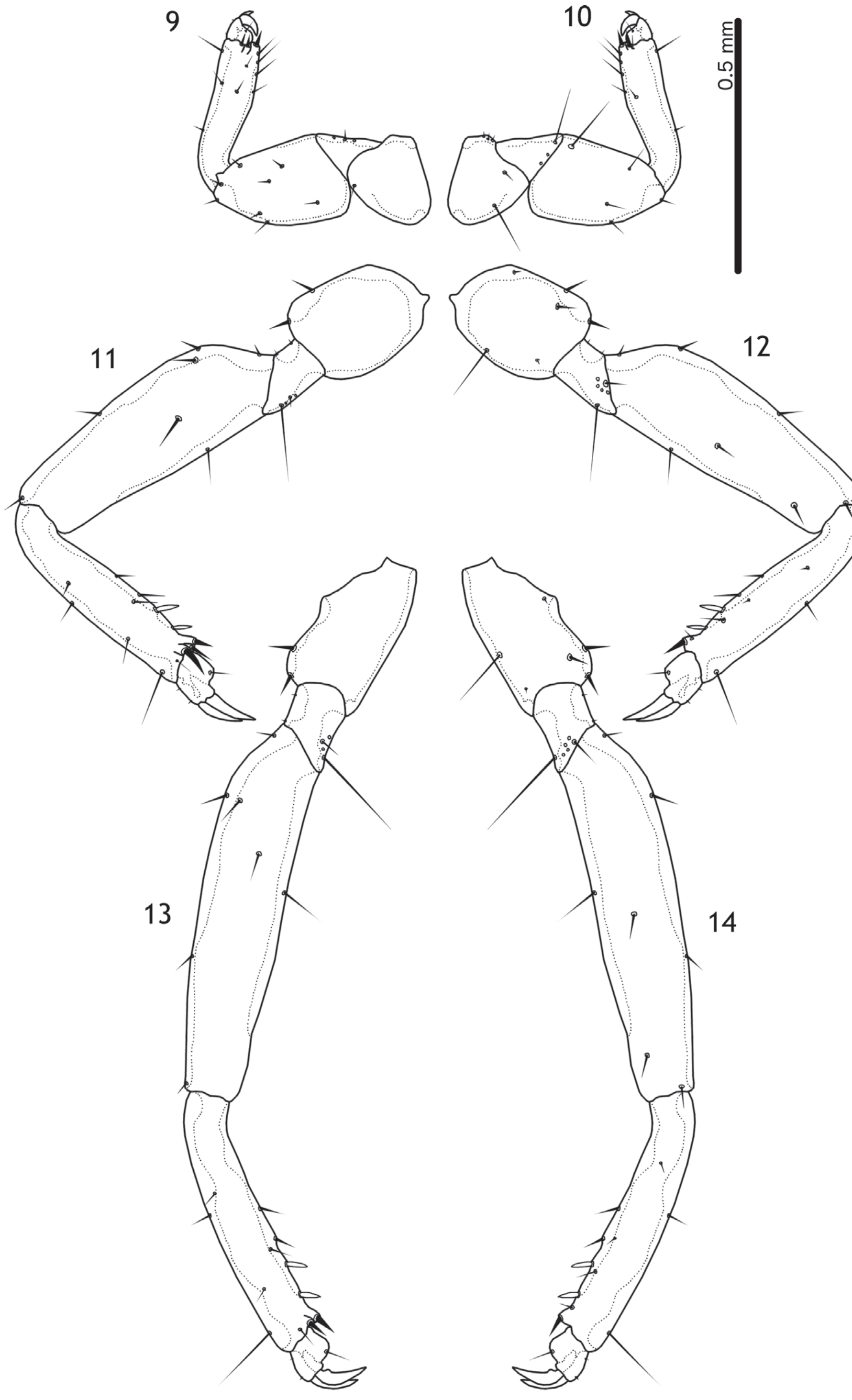
Type locality. The Hague, Netherlands (captive bird; host is limited to the Himalayas).

Other hosts. *Tragopan temminckii* (Gray, 1831) – Temminck's tragopan [tentative]. *Tragopan melanocephalus* (Gray, 1829) – western tragopan [uncertain; Clay 1938a: 172].

Specimens examined. Ex *Tragopan temminckii*: China • 2♂, 2♀; Shanghai, Shanghai Zoo; 12 Sep. 1988; Shi Xinquan leg.; box E0026199, slides 73–76 (NNHM). 5♀; Beijing, Beijing Zoo; 10 Oct 1973; collector unknown; box E0026199, slides 78–82 (NNHM). 4♂, 6♀; Sichuan Province, Beichuan; 4 May 1984; collector unknown; box E0026199, slides 84–87 (NNHM). Ex *Crossoptilon auritum* [straggler?]: China • 1♀; no locality; 30 Oct 1990; collector unknown; box E0026199, slide 67 (NNHM). Ex *Lophura nycthemera fokiensis* [straggler?]: China • 1♂; Fujian Province; Dec 1990; collector unknown; box E0026199, slide 71 (NNHM). Ex *Tragopan* sp.: China • 1♀; no collection data; box E0026199, slide 83 (NNHM).

Diagnosis. Both specimens from *T. temminckii* and those illustrated from the type host by Clay (1938a) and von Kéler (1958) can be separated from *P. fujianensis* sp. nov. by the following characters: male fused abdominal segment IX–XI with more or less straight lateral margins in *P. longus*, but with concave lateral margins in *P. fujianensis* (Fig. 7); proximal mesosome of *P. longus* with flattened anterior margin, but with medianly pointed anterior end in *P. fujianensis* (Fig. 6); parameres more curved in *P. longus* than in *P. fujianensis* (Fig. 6). Specimens from *T. temminckii* can be further separated from *P. fujianensis* by the characters listed under this species above, but examination of specimens from the type host of *P. longus* is necessary to establish whether the population on this host can also be separated from *P. fujianensis* by the same characters and whether the populations on *T. satyra* and *T. temminckii* are conspecific.

Description (of specimens from *Tragopan temminckii*). *Both sexes.* Head shape, structure and reticulation pattern as in Fig. 17; frons somewhat flattened. Marginal carina of moderate width, widening posteriorly. Dorsal pre-antennal suture prominent, reaching to or nearly to marginal carina laterally. Head chaetotaxy as in Fig. 17; many dorsal sensilla very small and difficult to see. Antennae sexually dimorphic. Thoracic and abdominal segments and chaetotaxy as in Figs 15, 16.



Figures 9–14. *Pelecolipeurus fujianensis* sp. nov. ex *Tragopan caboti* (Gould, 1857). **9.** Male leg I, dorsal side; **10.** Male leg I, ventral side; **11.** Male leg II, dorsal side; **12.** Male leg II, ventral side; **13.** Male leg III, dorsal side; **14.** Male leg III, ventral side.

Male. Antennae as in Fig. 17; scape, pedicel and flagellomere I swollen and modified in shape compared to female; scape with seemingly hyaline, broad process in proximal third; flagellomere I with intensely rugose surface and intensely rugose bulbous process near proximal base. Abdominal chaetotaxy as in Fig. 15; inner ventral *ps* absent on all tergopleurites; *sts* on sternite VI of about equal length. Subgenital plate, stylus and terminalia as in Fig. 21; stylus tapering more or less evenly towards distal end. Genitalia as in Figs 19, 20. Proximal mesosome flattened to slightly concave, with short, stout antero-lateral extensions bent slightly anteriorly. Ventral sclerite inverse V-shaped, with up to 3 sensilla on each side associated with its distal margin; 3 sensilla on each side lateral to ventral sclerite, forming distally divergent rows. Distal mesosome rounded rectangular, dominated by large, roughly rounded-trapezoidal gonopore. Parameres roughly parallel; *pst1–2* as in Fig. 20. Measurements as in Table 1.

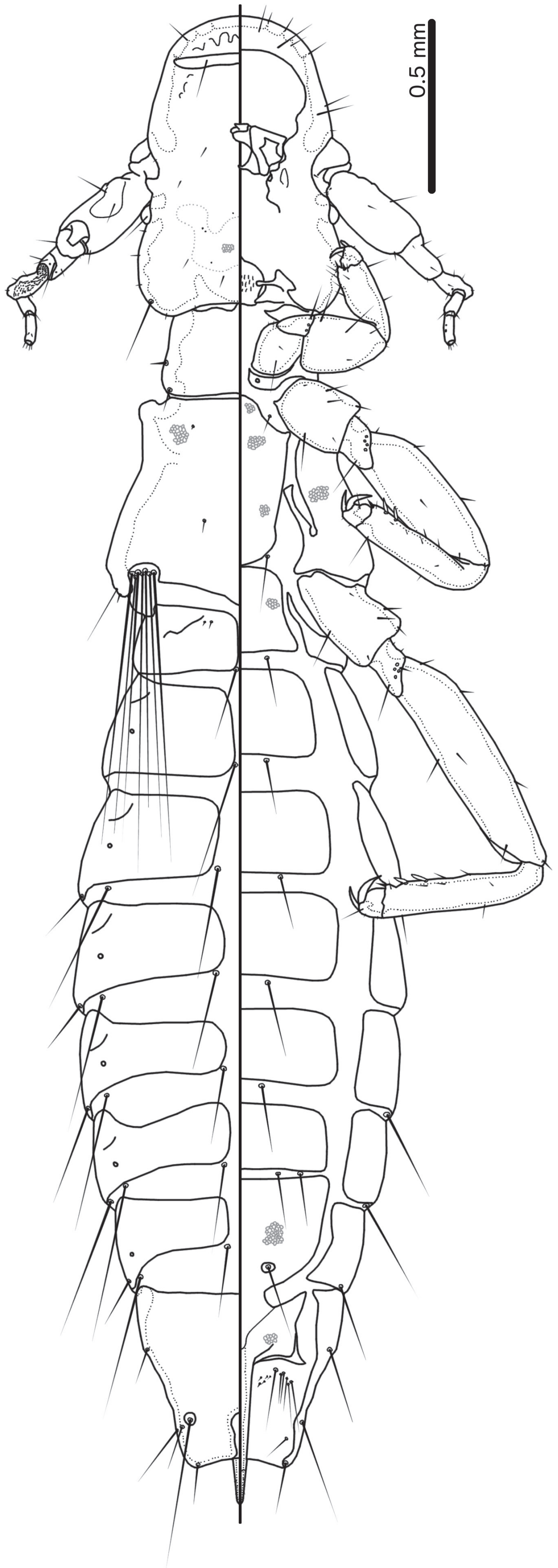


Figure 15. *Pelecolipeurus* cf. *longus* (Piaget, 1880) ex *Tragopan temminckii* (Gray, 1831). Male habitus, dorsal and ventral views.

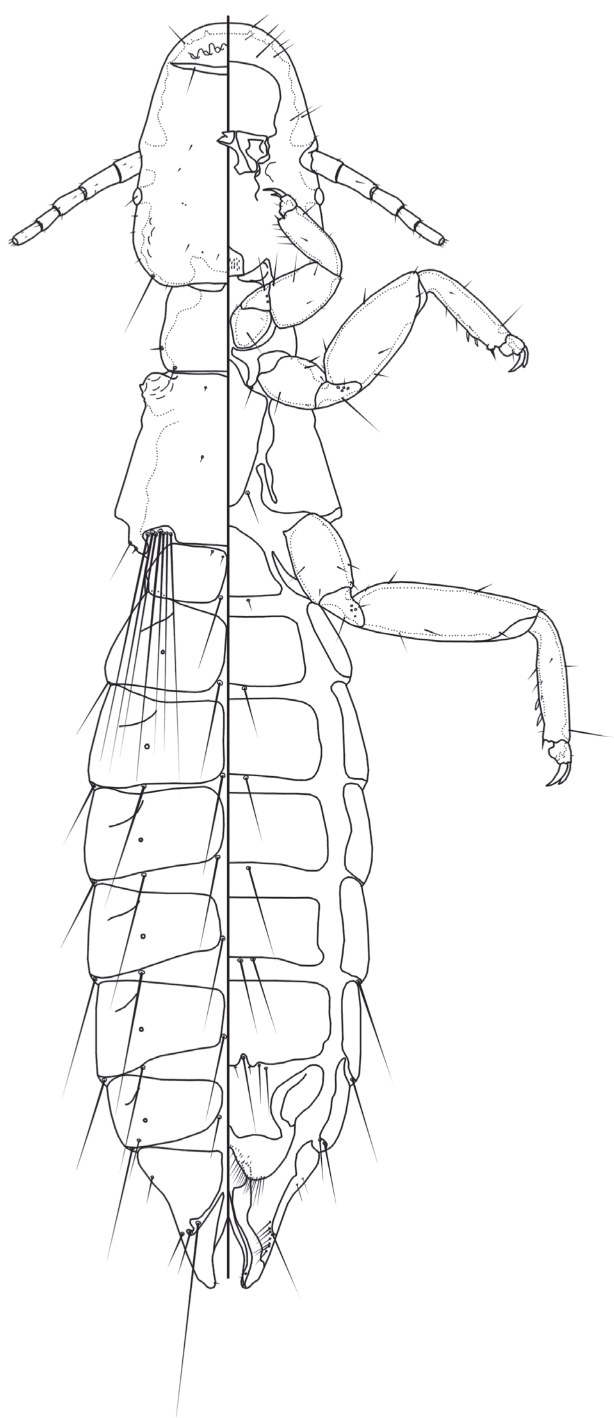
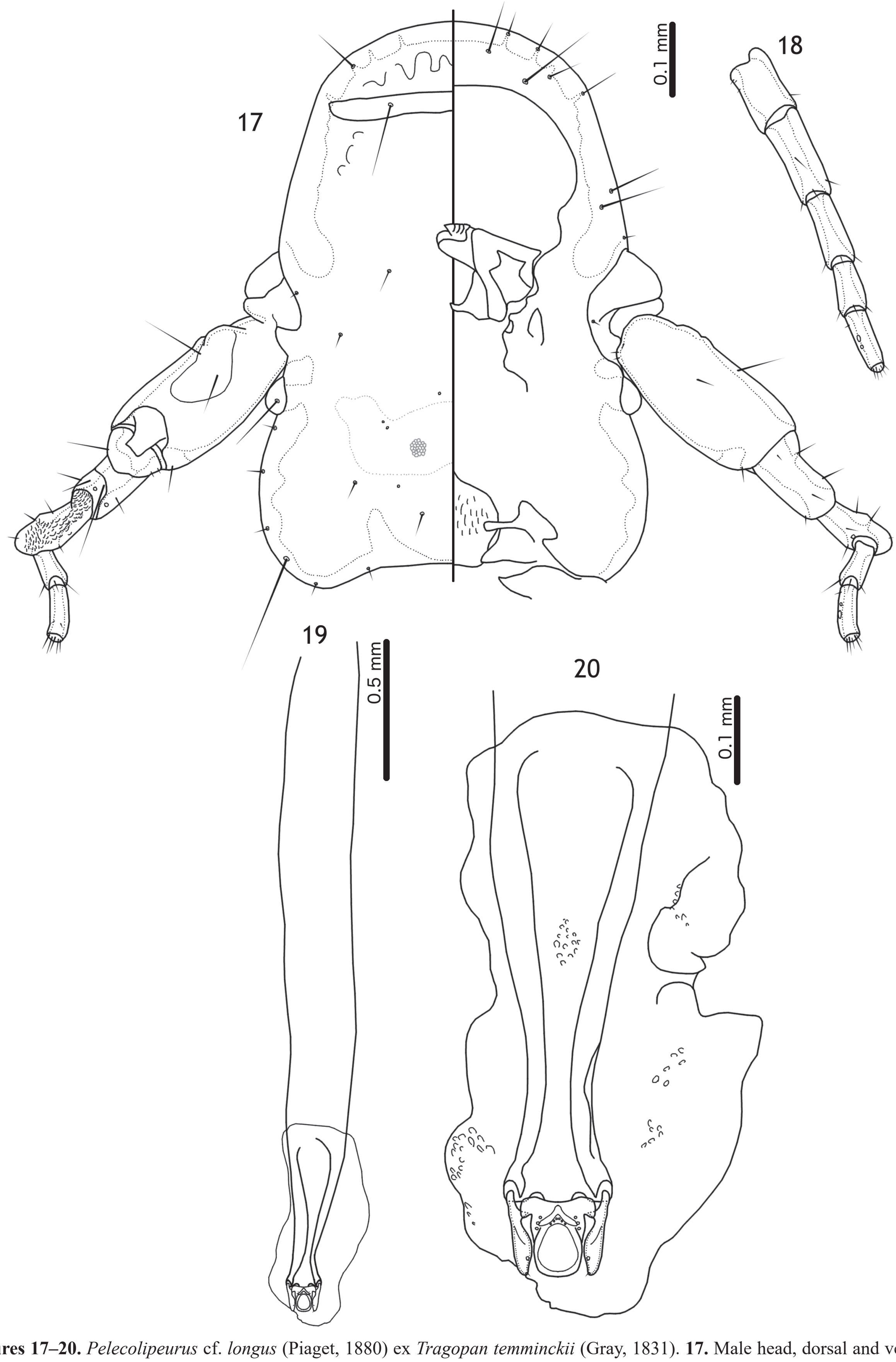


Figure 16. *Pelecolipeurus* cf. *longus* (Piaget, 1880) ex *Tragopan temminckii* (Gray, 1831). female habitus, dorsal and ventral views.

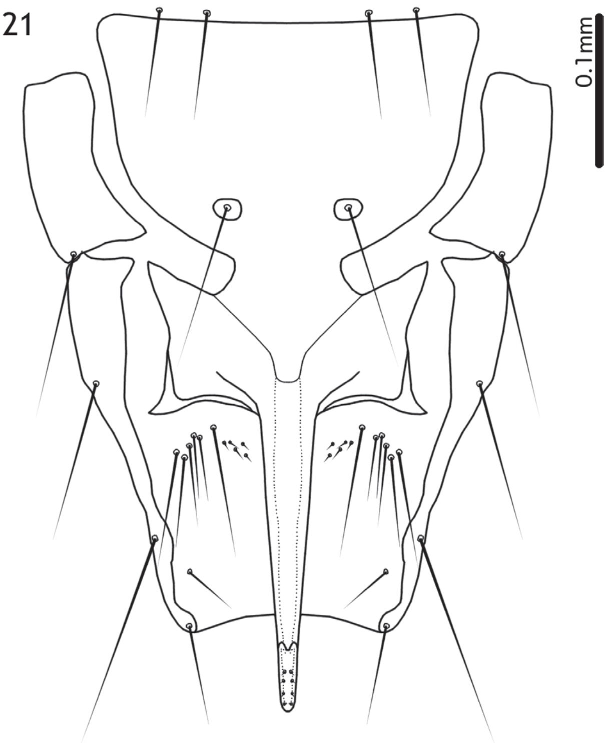
Female. Antennae as in Fig. 18. Abdominal chaetotaxy as in Fig. 16; sternal plate VI with 2 *sts* on each side. Subgenital plate, vulval margin and terminalia as in Fig. 22; subgenital plate continuous medianly. Vulval margin with 17–22 medium-length, slender *vms* and 8–12 short, slender *vss* on each side; median *vms* shorter than lateral *vms*. Measurements as in Table 1.

Remarks. We have not seen any specimens of *L. longus* from the type host. The original illustrations (Piaget



Figures 17–20. *Pelecolipeurus* cf. *longus* (Piaget, 1880) ex *Tragopan temminckii* (Gray, 1831). **17.** Male head, dorsal and ventral views; **18.** Female antenna, ventral view; **19.** Male genitalia, ventral view; **20.** Distal male genitalia, ventral view.

21



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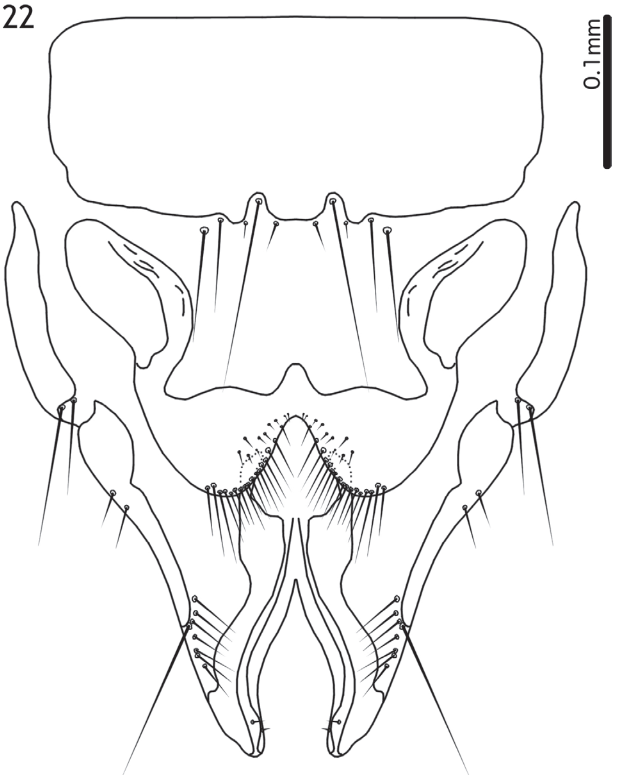


Figures 21, 22. *Pelecolipeurus* cf. *longus* (Piaget, 1880) ex *Tragopan temminckii* (Gray, 1831). **21.** Male subgenital plate and abdominal segments VIII–XI, ventral view; **22.** Female subgenital plate and abdominal segments VIII–XI, ventral view.

1880; figs 8, 8a, 8b) are insufficiently detailed to establish its identity beyond placing it in *Pelecolipeurus*. Clay (1938a: 171, figs 33b, 35a) and Kéler (1958: fig. 34) illustrated the male terminalia and male genitalia of this species, confirming our placement of *L. longus* in the new genus *Pelecolipeurus*. Kéler (1958: 327–333) provided some additional morphological details, but did not consider it possible to separate this species from *Reticulipeurus*, even subgenerically. Złotorzycka (1966) placed *P. longus* in *Reticulipeurus*; this was followed tentatively by Gustafsson et al. (2020a), but they did not examine any specimens and noted that the species may need to be moved to a separate genus.

Piaget (1880) treated specimens from both hosts as conspecific. Specimens of *Pelecolipeurus* from *Tragopan temminckii* are similar to *P. longus* (Piaget, 1880) as illustrated by Clay (1938a) and Kéler (1958), but published illustrations and descriptions (Piaget 1880; Clay 1938a; von Kéler 1958) are insufficient to establish the status of these populations adequately. As in illustrations of *L. longus*, the male specimens from *T. temminckii* have largely flat lateral margins of abdominal segment IX–XI, suggesting they are conspecific. However, Clay's illustration of the male mesosome of *L. longus* (Clay 1938a: fig. 35a) indicates that there may be differences in the shape of the mesosome between *L. longus* and specimens we have examined. In our previous experience with Clay's illustrations in this publication (e.g. Gustafsson et al. (2020a)), details such as these are not always reliable when compared to specimens examined by Clay, presumably due to limitations of the microscopy and illustration techniques of the time. Clay (1938a: 172) stated that she had also examined specimens from *T. temminckii* and *Tragopan melanocephalus* and that it was "impossible to say whether [*P. longus*] normally occurs on these two hosts or whether Piaget's specimens are stragglers".

A photo of the lectotype female of *P. longus* is available online at the NHML's homepage (https://data.nhm.ac.uk/dataset). In this photo, the distal claspers of the abdomen are more attenuated than illustrated here and the sclerotisations following the vulval margin may be narrower, but this is not clear in the photo. Moreover, these characters may be affected by mounting or be subject to individual variation within the *Oxylipeurus*-complex and cannot be used alone as reliable indicators of species identity. Other characters, such as vulval chaetotaxy, cannot be seen in the photo. A re-examination of the lectotype and the six paralectotypes of *P. longus* will be necessary to establish the identity of specimens from *T. temminckii* (and other hosts) listed here, but, unfortunately, we were not able to either examine the specimen at the NHML, nor borrow this specimen.

We presently consider populations from both *T. satyra* and *T. temminckii* to be conspecific, but note that *P. longus* from the type host is in need of re-description and that such a re-description may warrant the recognition of the specimens described here as a separate species.

Discussion

Galliforms have some of the most diverse chewing louse faunas of any bird orders. Price et al. (2003) recognised 21 genera of lice from galliform hosts, whereas Mey (2009) recognised a total of 64 genera from the same hosts. Including the new genus described here, an additional eight genera of lice have been described from galliform hosts since 2009, all except two in the *Oxylipeurus*-complex (Mey 2010, 2013; Gustafsson and Zou 2020a, b, 2023; Gustafsson et al. 2020a, b, 2023). In the checklist of Price et al. (2003), lice on galliform hosts represent almost 10% (21 of 212) of all avian louse genera accepted as valid; if genera accepted by Mey (2009) and those described from other host groups since 2003 are added (in total 49 genera; for example, Mey (2004); Gustafsson and Bush (2017); Gustafsson et al. (2020a, b)), this would imply that over 23% (72 of 302) of the known louse genera occur on galliform hosts, despite Galliformes itself comprising ~ 2.66% of bird diversity (290 of 10906 spp.; Clements et al. (2022)).

Clearly, the diversity of lice on galliform hosts is disproportionate to the diversity of host species in this group. The reasons for this over-diversity are unclear. Galliformes constitutes an ancient lineage of birds, with fossil records going back to perhaps the late Cretaceous (Clarke 2004; Agnolin et al. 2006). However, age itself does not necessarily indicate that a host group should have a diverse louse fauna. For instance, the closely-related anseriforms comprise 180 species (~ 1.65% of bird diversity; Clements et al. (2022)), but are only parasitised by 11 (Price et al. 2003) or 14 (Mey 2009) louse genera, constituting 3.61% or 4.61% of louse genera, respectively; note that taxonomic richness of lice is lower in diving than in non-diving birds (Felsõ and Rózsa 2006), which may affect this comparison.

Probably, as more becomes known of the lice of galliform hosts, clear patterns may emerge in the distribution of these louse genera that could explain the unexpectedly high diversity of lice on landfowl. However, some patterns are already dimly visible in the known distribution of lice on these hosts. In Table 2, we list the distribution of ischnoceran lice parasitising galliforms, roughly following the classification of Mey (2009), but with some modifications, based on our own examinations of specimens (DRG, unpublished data). It should be noted that no characters are known that can consistently separate the *Goniodes*- and *Goniocotes*-complexes as currently circumscribed (Gustafsson et al. 2021) and Johnson et al. (2011) found both complexes to be paraphyletic. The structure of the male genitalia may ultimately be useful for defining the *Goniocotes*-complex, but this complex is likely nested inside the *Goniodes*-complex as defined by Price et al. (2003; as *Goniodes*), Mey (2009) and here.

Each of the groups of lice included in Table 2 show different patterns of distribution and the Ischnocera of galliform hosts include both generalist genera occurring over several of the major radiations and genera that are more restricted. Of particular interest are the lice of tragopans and allies (genera *Lophophorus* Temminck, 1813, *Tetraophasis* Elliot, 1871 and *Tragopan*). These three genera together form a monophyletic clade, with no close relatives (Meng et al. 2008; Bao et al. 2010; Liu et al. 2014; Wang et al. 2014, 2017; Kimball et al. 2021). We here refer to this group as the "tragopan group" for simplicity.

Oxylipeurus-complex

The *Oxylipeurus*-complex is widely distributed across galliforms, being absent only from numidid hosts (Table 2); the genus *Afrilipeurus* Mey, 2010, was originally described from species known from numidid hosts, but this genus appears to be a member of the *Lipeurus*-complex (see below) and only superficially similar to lice in the *Oxylipeurus*-complex. Amongst the genera within the *Oxylipeurus*-complex, most are restricted to certain host groups.

There is a clear division in the *Oxylipeurus*-complex between genera occurring mainly on New World host groups and those occurring mainly on Old World host groups. With the exception of *Chelopistes lervicola* (Clay, 1941), all members of the genera *Chelopistes* Kéler, 1940, *Eiconolipeurus* Carriker, 1945, *Epicolinus* Carriker, 1945, *Labicotes* Kéler, 1940, *Trichodomedea* Carriker, 1946 and *Valimia* Gustafsson & Zou, 2020b, are found only on New World hosts. In contrast, the genera *Megalipeurus* Kéler, 1958, *Pelecolipeurus* gen. nov., *Calidolipeurus* Gustafsson et al., 2020b, *Cataphractomimus* Gustafsson et al., 2020a, *Gallancyra* Gustafsson & Zou, 2020a,. and *Sinolipeurus* Gustafsson et al., 2020a, are only found on Old World hosts. The genera *Oxylipeurus* Mjöberg, 1910 and *Talegallipeurus* Mey, 1982, are exclusively known in Australia and Wallacea. That leaves only one cosmopolitan genus, *Reticulipeurus* Kéler, 1958, which is known both in the Old and New Worlds.

Reticulipeurus also has wider host associations than most other genera in this complex, being known from both Cracidae and Phasianidae II–III. However, the species known from Phasianidae III belong to a different subgenus (Gustafsson and Zou 2023). The species from cracid hosts have not been revised in recent years and may represent a separate radiation. *Reticulipeurus*, as currently understood, may represent a plesiomorphic morphotype, from which other, morphologically more distinct, groups of *Oxylipeurus*-complex lice, have evolved. If not, the distribution of *Reticulipeurus* on two distinct host groups – mainly Asian phasianids and almost entirely Neotropical cracids – requires further study to understand.

Similarly, Gustafsson et al. (2020a) noted that the widely distributed genus *Megalipeurus* slightly differs morphologically amongst different host groups and may also represent several distinct lineages. Most other genera are more restricted: *Eiconolipeurus* and *Epicolinus* on odontophorid hosts, *Labicotes* on cracid hosts, *Trichodomedea* on cracid and odontophorid hosts and *Calidolipeurus*, *Gallancyra* and *Valimia* being known from one

Table 2. Distribution of ischnoceran lice across different galliform hosts. The host groupings are based on Kimball et al. (2021); host taxonomy follows Clements et al. (2022). Associations are based on Mey (2006, 2009, 2010, 2013), Gustafsson and Zou (2020a, b, 2023), Gustafsson et al. (2020a,b, 2023) and here; note that the *Goniodes*-, *Goniocotes*- and *Lipeurus*-complexes have not been comprehensively revised since Clay (1938a, 1940) and von Kéler (1940) and some of these taxa may not form meaningful groups. In *Goniocotes* Burmeister, 1838 (sensu Price et al. (2003)), four morphologically distinct groups are denoted by Roman numerals; due to the lack of detail in original descriptions of many species in this genus, it is not possible to assess whether these groups represent distinct genera or just well-marked species groups. In *Goniodes* Nitzsch, 1818 (sensu Price et al. (2003)), nine morphologically distinct groups are denoted by Arabic numerals; if *Goniodes* is divided as suggested by Mey (2009), these groups would represent separate genera for which no genus name has ever been published. Note that Price et al. (2003) used a more conservative classification, in which all genera were placed as synonyms of *Goniocotes*, *Goniodes*, *Lipeurus* Nitzsch, 1818 and *Oxylipeurus* Mjöberg, 1910, except for *Pachyskelotes* Kéler, 1940 and *Passonomedea* Carriker, 1944. Some genera treated as synonyms of *Goniodes* by Price et al. (2003) are probably closer to *Goniocotes* (see Mey (1997)), based on the morphology of the male genitalia. Conversely, it seems likely that *Pavoniocotes* Gustafsson et al., 2023 and the groups denoted *Goniocotes III–IV* here are more closely related to the *Goniodes*-complex than to the *Goniocotes*-complex. For ease of reference, the position of these species follows Price et al. (2003); these genera are marked with an asterisk (*) in the list. A few species of *Goniodes* cannot be identified from their available illustrations and descriptions and are here entered as “unknown”.

Host group and genus	*Oxylipeurus*-complex	*Goniocotes*-complex	*Goniodes*-complex	*Lipeurus*-complex	Other genera
Megapodiidae					
Aepypodius	*Oxylipeurus*		*Homocerus**, *Weelahia**	*Megathellipeurus*	*Megapodiella*
Alectura	*Oxylipeurus*		*Homocerus**, *Weelahia**	*Megathellipeurus*	
Eulipoa					
Leipoa			*Leipoiella**, *Megatheliella**	*Megathellipeurus*	*Megapodiella*
Macrocephalon		*Goniocotes I*		*Megathellipeurus*	
Megapodius	*Oxylipeurus*, *Talegallipeurus*		*Euligoniodes**, *Lobicrotaphus**, *Maleoicus**	*Malaulipeurus*	
Talegalla	*Talegallipeurus*		*Homocerus**, *Maleophilus**	*Lipeuroides*, *Megathellipeurus*	*Megapodiella*
Cracidae					
Aburria	*Labicotes*				
Chamaepetes	*Labicotes*, *Trichodomedea*				
Crax	*Labicotes*, *Reticulipeurus*, *Trichodomedea*				
Mitu	*Reticulipeurus*, *Trichodomedea*				
Nothocrax					
Oreophasis	*Trichodomedea*				
Ortalis	*Reticulipeurus*, *Trichodomedea*				
Pauxi	*Reticulipeurus*, *Trichodomedea*				
Penelope	*Reticulipeurus*, *Trichodomedea*				
Penelopina	*Labicotes*, *Trichodomedea*				
Pipile					
Numididae					
Acryllium		*Goniocotes II*		*Lipeurus*	
Agelastes			*Stenocrotaphus*	*Lipeurus*	
Guttera		*Goniocotes II*	*Clayarchigoniodes*, *Stenocrotaphus*	*Afrilipeurus*, *Lipeurus*	
Numida		*Goniocotes I*, *Goniocotes II*	*Clayarchigoniodes*, *Stenocrotaphus*	*Lipeurus*, *Numidilipeurus*	
Odontophoridae					
Callipepla	*Epicolinus*		Genus 8, Unknown		*Colinicola*
Colinus	*Epicolinus*		*Solenodes*?*, Genus 8	*Lipeurus*	*Colinicola*, *Cuclotogaster*
Cyrtonyx					*Colinicola*
Dactylortyx	*Eiconolipeurus*, *Trichodomedea*				
Dendrortyx	*Eiconolipeurus*, *Epicolinus*, *Trichodomedea*				
Odontophorus	*Eiconolipeurus*, *Trichodomedea*		*Passonomedea*		
Oreortyx			Genus 8		*Colinicola*
Philortyx					*Colinicola*
Ptilopachus			*Solenodes**		*Cuclotogaster*
Rhynchortyx			Genus 8		
Phasianidae I					
Afropavo		*Goniocotes III*, *Goniocotes IV*	*Archigoniodes*	*Lipeurus*	
Alectoris		*Goniocotes I*	*Solenodes**, Genus 6		*Cuclotogaster*
Ammoperdix			*Oulocrepis*		*Cuclotogaster*
Argusianus			*Pachyskelotes*, Unknown		
Bambusicola			*Oulocrepis*		

Host group and genus	*Oxylipeurus*-complex	*Goniocotes*-complex	*Goniodes*-complex	*Lipeurus*-complex	Other genera
Campocolinus					
Coturnix			*Astrocotes*		*Cuclotogaster*
Francolinus		*Goniocotes I*		*Lipeurus*	*Cuclotogaster*
Galloperdix	*Megalipeurus*	*Goniocotes I*			
Gallus	*Gallancyra*	*Goniocotes I*	*Oulocrepis*, *Stenocrotaphus*	*Lipeurus*, *Numidilipeurus*	*Cuclotogaster*, *Lagopoecus*
Haematortyx					
Margaroperdix			*Oulocrepis*		*Cuclotogaster*
Ophrysia					
Ortygornis			*Stenocrotaphus*		*Cuclotogaster*
Pavo		*Goniocotes I*, *Pavoniocotes*	*Goniodes*, Genus 1	*Lipeurus*	
Peliperdix					*Cuclotogaster*
Perdicula					*Cuclotogaster*
Polyplectron	*Megalipeurus*			*Lipeurus*	
Pternistis		*Goniocotes I*	*Oulocrepis*, *Stenocrotaphus*	*Lipeurus*	*Cuclotogaster*
Rheinardia				*Lipeurus*	
Scleroptila		*Goniocotes I*	*Oulocrepis*, Genus 6		*Cuclotogaster*, *Lagopoecus*
Synoicus			*Astrocotes*		
Tetraogallus			*Oulocrepis*		*Cuclotogaster*
Tropicoperdix	*Megalipeurus*			*Lipeurus*	
Phasianidae II					
Bonasa			*Oulocrepis*		*Lagopoecus*
Canachites					
Catreus			*Oulocrepis*		
Centrocercus			*Oulocrepis*		*Lagopoecus*
Chrysolophus	*Reticulipeurus*		*Oulocrepis*	*Lipeurus*	
Crossoptilon	*Reticulipeurus*	*Dictyocotes*	Genus 5	*Lipeurus*	*Lagopoecus*
Dendragapus			*Oulocrepis*		*Lagopoecus*
Falcipennis					
Ithaginis	*Reticulipeurus*		*Oulocrepis*		*Lagopoecus*
Lagopus			*Oulocrepis*		*Lagopoecus*
Lerwa	*Chelopistes*				*Lerwoecus*
Lophophorus	*Cataphractomimus*	*Dictyocotes*	*Margaritenes*, Genus 2	*Lipeurus*	*Lagopoecus*
Lophura	*Reticulipeurus*	*Goniocotes I*	*Oulocrepis*	*Lipeurus*	*Cuclotogaster*
Lyrurus					*Lagopoecus*
Meleagris	*Chelopistes*, *Valimia*	*Goniocotes I*		*Lipeurus*	
Perdix		*Goniocotes I*	*Solenodes**	*Lipeurus*	*Cuclotogaster*
Phasianus	*Reticulipeurus*	*Goniocotes I*	*Oulocrepis*, *Solenodes**	*Lipeurus*	*Cuclotogaster*, *Lagopoecus*
Pucrasia	*Reticulipeurus*		*Oulocrepis*		
Rhizothera	*Reticulipeurus*			*Lipeurus*	
Syrmaticus	*Reticulipeurus*	*Goniocotes I*	*Oulocrepis*	*Lipeurus*	*Lagopoecus*
Tetrao	*Reticulipeurus*		*Oulocrepis*		*Lagopoecus*
Tetraophasis	*Sinolipeurus*	*Dictyocotes*	Genus 4		
Tetrastes					*Lagopoecus*
Tragopan	*Cataphractomimus*, *Pelecolipeurus*, *Sinolipeurus*	*Dictyocotes*	Genus 3		*Lagopoecus*
Tympanuchus			*Oulocrepis*		*Lagopoecus*
Phasianidae III					
Arborophila	*Megalipeurus*, *Reticulipeurus*	*Goniocotes I*	*Astrodes*, *Kelerigoniodes*		*Cuclotogaster*, *Galliphilopterus*
Caloperdix	*Megalipeurus*	*Goniocotes I*		*Lipeurus*	
Melanoperdix				*Lipeurus*	
Rollulus	*Calidolipeurus*		*Astrodes*	*Lipeurus*	
Xenoperdix					

host genus each. The perplexing distribution of the genus *Chelopistes* was discussed in detail by Mey (2006).

Notably, the genera in the tragopan group are hosts to three genera of *Oxylipeurus*-complex that are, so far, not known from hosts outside that clade (*Cataphractomimus*, *Pelecolipeurus*, *Sinolipeurus*). The distribution of lice in these genera on the hosts of this radiation is summarised in Table 3. In at least one case, lice from all three genera are known from the same host species, echoing the radiation into three congeneric species of the genus *Valimia* on the same host species (Gustafsson and Zou 2020b). To date, there is no example of all three genera occurring on the same host individual. However, data from any galliform host are rather limited, not least because many birds in this radiation are protected. Examinations of birds in, for example, rescue centres may be necessary to establish

Table 3. Known distribution of *Oxylipeurus*-complex lice on *Tragopan* spp., *Tetraophasis* spp. and *Lophophorus* spp. These three host genera form a monophyletic clade with no close relatives (Meng et al. 2008; Bao et al. 2010; Liu et al. 2014; Wang et al. 2014, 2017; Kimball et al. 2021). Dashes ("---") indicate that no species of lice in this genus has, so far, been described from this host. Records suspected to be stragglers or contaminations (see *Pelecolipeurus longus*) are not listed here.

Host species	*Cataphractomimus* Gustafsson et al., 2020a	*Pelecolipeurus* gen. nov.	*Sinolipeurus* Gustafsson et al., 2020a
Lophophorus impejanus (Latham, 1790)	*Cataphractomimus burmeisteri* (Taschenberg, 1882)	---	---
Lophophorus lhuysii Geoffroy Saint-Hilaire, 1866	*Cataphractomimus mirapelta* Gustafsson et al., 2020a	---	---
Lophophorus sclateri Jerdon, 1870	*Cataphractomimus impervius* Gustafsson et al., 2020a	---	---
Tetraophasis obscurus (Verreaux, 1869)	---	---	*Sinolipeurus tetraophasis* (Clay, 1938)
Tetraophasis szechenyii Madarasz, 1885	---	---	---
Tragopan blythii (Jerdon, 1870)	---	---	---
Tragopan caboti (Gould, 1857)	---	*Pelecolipeurus fujianensis* sp. nov.	---
Tragopan melanocephalus (Gray, 1829)	*Cataphractomimus himalayensis* (Rudow, 1869)	*Pelecolipeurus longus* (Piaget, 1880)?	---
Tragopan satyrus (Linnaeus, 1758)	*Cataphractomimus ceratornis* (Eichler, 1958)	*Pelecolipeurus longus* (Piaget, 1880)	---
Tragopan temminckii (Gray, 1830)	*Cataphractomimus junae* Gustafsson et al., 2020a	*Pelecolipeurus longus* (Piaget, 1880)?	*Sinolipeurus sichuanensis* Gustafsson et al., 2020a

whether the three *Oxylipeurus*-complex genera on hosts in the tragopan group ever co-occur on the same host individual and, if so, if they then partition the plumage amongst them.

Goniocotes-complex

Lice in the *Goniocotes*-complex are conspicuously absent from both the mainly New World host radiations, Odontophoridae and Cracidae, as well as from all New World genera in the other host radiations. The sole exception is the turkey, which is sometimes parasitised by *Goniocotes gallinae* (Linnaeus, 1758), normally found on domestic chicken. *Goniocotes gallinae* never seems to be reported from wild turkey in their native range (e.g. Hightower et al. (1953); Kellogg et al. (1969); Nelder and Reeves (2005); Cruz et al. (2013); Camacho-Escobar et al. (2014)) and this host association is likely based only on domestic birds which have been in contact with domestic chicken. Based on current knowledge, the *Goniocotes*-complex would, thus, seem to be an exclusively Old World radiation.

Based on the structure of the male genitalia, lice of the *Goniodes*-complex, listed from megapodiid hosts in Table 2, are likely more closely related to *Goniocotes* than to *Goniodes*. Mey (1997) circumscribed the genera on megapodiid hosts as a distinct group, but excluded the one known *Goniocotes* species from this group. If this group is considered part of the *Goniodes*-complex (as by, for example, Price et al. (2003)), it must be considered an aberrant group within this genus. The only known *Goniocotes* species from a megapodiid host may, as Mey (1997) pointed out, be evidence either of a secondary infestation or of a relict association.

Goniocotes sensu lato is widely distributed across Old World landfowl (Table 2) and do not show any obvious patterns of distribution. At least six morphologically different groups can be found within *Goniocotes*, but the relationship between these groups is unclear. Only one of these groups, *Goniocotes I*, is widely distributed across Numididae and Phasianidae I–III. The poorly-known *Goniocotes II* group is only known from numidid hosts, where it may overlap in distribution with species in *Goniocotes I*. *Goniocotes III–IV* are only known from the Congo peafowl and both groups are poorly known and may not be closely related to the rest of *Goniocotes* (see Clay (1938b)). A fifth group, only known from peafowl, was recently described as the genus *Pavoniocotes* Gustafsson et al., 2023.

The distribution patterns of the sixth group, previously called *Dictyocotes* Kéler, 1940, mirrors that of the three *Oxylipeurus*-complex genera summarised in Table 3, being found mainly on hosts in the tragopan group. However, some species of *Dictyocotes* are also known from hosts in the genus *Crossoptilon* Hodgson, 1838, another high-altitude group of birds, mainly distributed in and around China. The presence of a mesosome in the male genitalia in this group, as well as other morphological characters, suggests that *Dictyocotes* should be separated from *Goniocotes*; this will be discussed in more detail elsewhere (DRG, in prep.).

Goniodes-complex

The *Goniodes*-complex is by far the most diverse of the ischnoceran louse groups known from galliform hosts and almost half (28 of 60; 46.7%) of the groups identified in Table 2 belong to this complex. Of these, at least eight currently have no genus-level name and, with the exceptions of *Pachyskelotes* Kéler, 1940 and *Passonomedea* Carriker, 1944, all were treated as members of a highly polytypic *Goniodes* by Price et al. (2003). To discuss the distribution of morphologically distinct groups within this complex, we here follow Mey (2009) in resurrecting numerous older names within this complex and use the numbers 1–8 to denote some groups that have no available genus names. We deviate from Mey (2009) only in considering *Zlotorzyckella* Eichler [in Eichler and Vasjukova 1981], 1981, as a synonym of *Oulocrepis* Kéler, 1940. Note that, as some species in this complex have never been adequately described or illustrated, the exact limits of these proposed genera and groups is in some cases tentative. A small number of species are so poorly described that they are noted as "Unknown" genera in Table 2 and not discussed further here.

Goniodes-complex lice are unknown from cracid hosts and if the *Goniodes*-complex genera parasitising megapodiid hosts discussed above are moved to the *Goniocotes*-complex, no *Goniodes*-complex lice would be known from members of this host family either. Otherwise, lice in the *Goniodes*-complex occur across all major radiations of galliforms. However, only three groups within this complex could reasonably be said to be widely distributed: *Oulocrepis* Kéler, 1940, *Solenodes* Kéler, 1940 and *Stenocrotaphus* Kéler, 1940. The remaining genera and groups in this complex are known only from single host families or even single host genera (Table 2). *Stenocrotaphus* is mainly known from numidid hosts and African and South Asian francolins and spurfowl, but has, secondarily, also become established on chicken.

Oulocrepis is more widely distributed, occurring on many different host genera in Phasianidae I–II. Morphological variation, above all, in the male genitalia in this group is large (see, for example, Clay (1940)) and, above all, the type species (*Goniodes dissimilis* Denny, 1842) is somewhat different from all other species in the group with regards to head shape and male genitalia; however, other characters, such as female genitalia, indicate a close relationship. The genus as circumscribed here seems to be established on hosts in different geographical regions, from the Arctic to Sub-Saharan Africa and, in many cases, seems to occur on the same host species as other *Goniodes*-complex lice.

Solenodes is a widely distributed group, which as circumscribed here, occurs on hosts from Odontophoridae and Phasianidae I–II. Notably, most of the hosts of species in *Solenodes* are associated with drier grasslands. The male genitalia of this group are more reminiscent of those of the *Goniocotes*-complex than those of any other group of *Goniodes*-complex lice; however, as these genitalia are much reduced in complexity, it is possible that the group is artificial and, in reality, comprises several different lineages. Several species here placed in this genus are poorly described and illustrated and a revision of the group is needed to establish its limits.

The tragopan group of birds is collectively parasitised by four *Goniodes*-complex genera, of which only one presently has a proposed name: *Margaritenes* Kéler, 1940; the others are here referred to as Genera 2–4. Amongst these, only Genus 2 and Genus 3 appear to be closely related, sharing similarities in the structure of the male antennae and a unique fusing of the pteronotum and tergopleurite II. Potentially, as these species are studied in more detail, further similarities may be found, but, at present, there seems to be nothing to indicate that all four genera are part of the same radiation within the *Goniodes*-complex.

Lipeurus-complex

Lice in the *Lipeurus*-complex are the most morphologically homogeneous amongst the groups of ischnoceran lice occurring on galliforms. Lice in this complex are unknown from all New World hosts, except the turkey, which is parasitised by *Lipeurus caponis* (Linnaeus, 1758) naturally found on domestic chicken. Two genera in this complex are known from numidid hosts only (but secondarily established on domestic chicken) and three genera are unique to the Megapodiidae (Table 2). Based on the structure of the tergopleurites, female genitalia, male subgenital plate, abdominal chaetotaxy and other characters, it seems likely that *Afrilipeurus* belongs in this complex (see below); thus, three different genera occur on numidid hosts, although only two genera are known to occur on the same host genus. As with the *Goniodes*- and *Oxylipeurus*-complexes, the *Lipeurus*-complex genera known from megapodiid hosts are unique to that radiation, highlighting the distinction of the louse fauna on megapodes.

No *Lipeurus*-complex species have been described from any species of *Tetraophasis* or *Tragopan* and the only species of the genus *Lipeurus* known from *Lophophorus* spp. needs verification and may represent a contamination. As both *Lipeurus*- and *Oxylipeurus*-complex lice are of the wing louse ecomorph, it is conceivable that the multitude of *Oxylipeurus*-complex lice on hosts in the tragopan group have prevented *Lipeurus*-complex lice from establishing themselves there. However, the louse fauna of many members of the tragopan group remain poorly known and the absence of *Lipeurus*-complex species on these hosts needs verification. Moreover, the mechanisms of interspecific competition in lice are poorly known and cases are known where the same host species is parasitised by multiple louse species of the same ecomorph (e.g. head lice on common blackbird; Oslejskova et al. (2020)).

Other ischnoceran genera

Several smaller groups of ischnoceran louse genera are also known from galliform hosts. Of these, *Megapodiella* Emerson & Price, 1972, is only known from megapodiid hosts, *Colinicola* Carriker, 1946, only from odontophorid hosts, *Lerwoecus* Mey, 2006, only from *Lerwa lerwa* (Hodgson, 1833) and *Galliphilopterus* Emerson & Elbel, 1957, only from *Arborophila brunneopectus* Blyth,

1855. It should be noted that *Colinicola* may be polytypic, based on the structure of the male genitalia and other characters, but this has no major implications for the distribution of this genus. The remaining two genera, *Cuclotogaster* Carriker, 1936 and *Lagopoecus* Waterston, 1922, are more widely distributed.

Cuclotogaster is known from hosts in Odontophoridae and Phasianidae I–III; however, the species from New World odontophorid hosts needs verification and may be an introduction following the European colonisation of the Americas. Otherwise, *Cuclotogaster* is absent from all New World hosts, despite being widely distributed in the Old World. Species of *Cuclotogaster* from *Arborophila* spp. are morphologically different from other species, with much narrowed male genitalia and possibly some differences in the tergopleurites and the female genitalia; these characters are poorly studied. The genus has not been thoroughly revised since Clay (1938a) and the overall variation in *Cuclotogaster* is poorly known. Notably, most known hosts are in Phasianidae I and are associated with drier, open country (e.g. savannah, grassland). Species occurring on hosts outside this radiation also often share the same kind of habitat, suggesting that host-switching between sympatric host species may have occurred.

In contrast, the genus *Lagopoecus* is mainly known from hosts in the Phasianidae II radiation, with a few species known from hosts in Phasianidae I; at least the association with domestic fowl may be due to straggling in domestic settings. Species of *Lagopoecus* occur in both the Old and New World and are often associated with more boreal or mountain- or forest-dwelling hosts, but exceptions are known (Table 2). In general, *Lagopoecus* occurs on lowland hosts in the boreal area, but seems more restricted to mountain-dwelling hosts further south and is largely absent south of the Equator.

Galliforms in the tragopan group are parasitised by lice in the genus *Lagopoecus*, but no species of *Cuclotogaster* are known from these hosts. The *Lagopoecus* species parasitising *Lophophorus* spp. are morphologically distinct, lacking the dorsal pre-antennal suture, but species known from *Tragopan* spp. are not similar to these and do not appear to be closely related. The genus *Lagopoecus* has not been comprehensively reviewed since Clay (1938a) and the patterns of variation are poorly known. Nevertheless, based on our current knowledge, there is nothing to suggest that the *Lagopoecus* species on tragopan group hosts form a unique radiation within this genus.

Contrasting and overlapping patterns

It is clear from this brief overview that no single factor can be used to explain distribution patterns amongst the Ischnocera that parasitise galliform hosts. Overall, both host phylogeny, host biogeography and host ecology appear to influence the known host associations in the groups included in Table 2. Moreover, in some cases, it is not clear which factors are most important, as several factors overlap.

Undoubtedly, host phylogeny is an important factor structuring host associations in louse communities on galliforms. For instance, there appears to be little overlap between the lice of megapodiid hosts and other landfowl (Table 2), likely reflecting that megapodiids are the sister group of all other galliforms (Kimball et al. 2021). Similarly, many of the groups of lice occurring on numidid hosts do not occur on other host groups naturally (but some have spread to, for example, domestic chicken in domestic settings). Numerous smaller groups are also limited to one or a few closely-related genera, especially in the *Goniodes*-complex.

There is also a distinct difference between most of the New World and Old World galliforms, with *Trichodomedea* being shared by two New World host families, but absent on all Old World hosts and most *Cuclotogaster* and *Goniocotes* being absent from New World hosts despite being widely distributed across the Old World. Notably, African odontophorids are not parasitised by the same lice as New World members of this family, but by *Cuclotogaster*, which is widely distributed on other African hosts.

Contrasting with the large-scale biogeographical pattern, some patterns may have more to do with host biotope than with faunal regions. For instance, even if *Cuclotogaster* is largely limited to hosts in Phasianidae I, the genus also occurs on some members of Phasianidae II that occur in less forested areas, such as *Phasianus* Linnaeus, 1758 and *Perdix* Brisson, 1760 (Table 2). Similarly, *Oulocrepis* is found across both these radiations, often on birds that inhabit more open, grassy areas; *Solenodes* and *Stenocrotaphus* also appear to be distributed mainly on hosts in the same type of biotope and include at least some species in other host radiations.

Notably, some patterns cannot easily be explained and may be due to gaps in our knowledge or on incorrect classification of known species. It is, for instance, curious that the widely-distributed genus, *Reticulipeurus*, should occur on both Old World phasianids and New World cracids, despite all other ischnoceran lice on cracids being specific to the New World. Based on published data, there are no obvious morphological differences between the species on these host groups, although the species of cracids have not been revised in recent decades and few detailed illustrations have been published. The distribution of the genus *Megalipeurus* is also difficult to understand, but the genus is morphologically heterogeneous and a revision of the group may reveal that the current circumscription is artificial (Gustafsson et al. 2020a).

It is worth noting that elevation may influence distribution patterns. Several distinct genera and groups are known only or mainly to infest high-elevation hosts, such as *Lerwoecus* and many of the unnamed groups within the *Goniodes*-complex. In contrast, low-elevation hosts are often parasitised by more widely-distributed louse genera (e.g. *Lipeurus*, *Oulocrepis*, *Goniocotes I*).

Lice of the tragopan group

Most relevant to the taxa described here are those found in the tragopan group, all of which are high-elevation birds within Phasianidae II (Kimball et al. 2021). With the exception of an unconfirmed *Lipeurus* species occurring on one of the species of *Lophophorus*, all of the typically low-elevation groups of Ischnocera are absent from hosts in the tragopan group. However, the diversity of lice in this group is considerable. Despite comprising only ten species in three genera, the species in this group are collectively hosts to at least three *Oxylipeurus*-complex genera (Table 3), as well as a morphologically distinct group of *Lagopoecus*, four genera within the *Goniodes*-complex and almost all the known species of *Dictyocotes*. With the exception of *Dictyocotes*, all these genera and groups are unique to hosts in the tragopan group. This pattern may also be mirrored in the Amblycera. Price and Beer (1964) considered *Colpocephalum tetraophasis* Price & Beer, 1964, "rather unique", but did not detail in what way; *Amyrsidea impejani* Scharf [in Scharf and Price], 1983, was also described as having some distinct morphological characters, rare for the genus.

Possibly, the relevant factors structuring these host associations are a mixture of host phylogeny – all the hosts, except *Crossoptilon* are closely related – and habitat factors – all the hosts including *Crossoptilon* are high-elevation birds. The overlap in range varies between species pairs, but, in at least some cases, the hosts in these genera co-occur and may even forage together (Madge and McGowan 2002). More data are needed from all hosts in the genera *Lophophorus*, *Tetraophasis* and *Tragopan*, as well as from other high-altitude galliforms, to evaluate the louse community parasitising these hosts and their relationship to related lice on other galliforms.

Future collections may also help determine the extent to which the three genera of *Oxylipeurus*-complex lice on *T. temminckii* co-occur on the same host population. All three species are known from Sichuan Province, China, but from different collection events and areas within this Province. The co-occurrence of three congeneric species of lice in the *Oxylipeurus*-complex was recently reported from turkey (Gustafsson and Zou 2020b) and cases such as these could give insights into the process of microhabitat partitioning in chewing lice and potentially into the process of higher-level radiation of lice on hosts.

Emended key to the *Oxylipeurus*-complex

Here, we update the genus-level key to the *Oxylipeurus*-complex previously published by Gustafsson et al. (2020b) and emended by Gustafsson and Zou (2023) after the description of the subgenus *Reticulipeurus* (*Forcipurellus*). We here remove the genus *Afrilipeurus* from this complex, based on the justification below and include the genus *Pelecolipeurus*.

1 Broad-headed, with width of head similar to, or wider than, length of head; temples with elongated "horns" (Fig. 23) or with prominent lateral bulges (Fig. 24) 2
– Slender-headed, with head clearly longer than wide; temples generally rounded, never with prominent bulging (Fig. 25) 3
2 Temporal setae *mts1–2* macrosetae (Fig. 24) .... *Trichodomedea* Carriker, 1946
– Temporal setae *mts1–2* microsetae (Fig. 23) .... *Chelopistes* Kéler, 1939
3 Dorsal pre-antennal suture present (Fig. 25) 4
– Dorsal pre-antennal suture absent or, if present, only visible around aperture of *ads* and not extending medianly (Fig. 26) .... 10.
4 Dorsal pre-antennal suture as median, elongated oval, not expanded laterally (Fig. 27); female terminalia with marginal mesosetae distributed more or less equally around distal margin (Fig. 28); eye very large (Fig. 27) and pre-ocular nodus absent .... *Calidolipeurus* Gustafsson et al., 2020b
– Dorsal pre-antennal suture transversal, normally reaching apertures of *ads* (Fig. 25); female terminalia with marginal setae gathered in the same area (Fig. 29); eye not very large (Fig. 26) and pre-ocular nodus present 5
5 Clypeo-labral suture present (Fig. 30); stylus expanded distally, with small "hooks" on lateral margins (Fig. 31) .... *Gallancyra* Gustafsson & Zou, 2020a
– Clypeo-labral suture absent; stylus differing in shape, but never with lateral "hooks" 6
6 Dorsal pre-antennal suture with postero-lateral elongations ("epistomal suture" sensu von Kéler (1958)) extending towards preantennal nodi (Fig. 32); hyaline margin present (Fig. 32) .... *Splendoroffula* Clay & Meinertzhagen, 1941
– Dorsal pre-antennal suture without such extensions (Fig. 25); hyaline margin absent (Fig. 25) 7
7 Dorsal postantennal suture present (Fig. 33); male genitalia asymmetrical, with mesosome much reduced (Fig. 34) .... *Oxylipeurus* Mjöberg, 1910
– Dorsal postantennal suture absent (Fig. 25); male genitalia symmetrical, with prominent mesosome (variable in shape) 8

8 Coni elongated (Fig. 27); male mesosome with prominent V–.... or Y-shaped thickening in distal half (Fig. 35); proximal margin of mesosome with rounded lateral lobes (Fig. 35); frons convergent to median point in most species .... *Megalipeurus* Kéler, 1958

– Coni short (Fig. 25); male mesosome without thickening in distal half; proximal margin of mesosome variable, but never with rounded lateral lobes; frons rounded to flattened (Fig. 25)... 9

9 Male abdominal segments IX+X and XI with prominent postero-lateral extensions ("claspers" sensu Carriker (1945)) (Fig. 36)..*Eiconolipeurus* Carriker, 1945

– Male abdomen without such structures.. 12

10 Stylus of male subgenital plate about as long as rest of subgenital plate (Fig. 37); male genitalia much elongated, with mesosome comprising < 1/10 of total length (Fig. 38) ....*Pelecolipeurus* gen. nov

– Stylus of male subgenital plate < 1/4 of length of subgenital plate; male genitalia shorter, with mesosome comprising ~ 1/5 of total length 11

11 Female with prominent "claspers" formed by extensions of abdominal segment XI (Fig. 39); female vulval margin deeply emarginated, with lateral sections forming rounded lobes that have subparallel median margins and median sections convex (Fig. 39); male stylus terminal (Fig. 40)........................... *Reticulipeurus* (*Forcipurellus*) Gustafsson & Zou, 2023

– Female without such claspers (Fig. 41); female vulval margin variably concave, but either with no section of the margin forming lobes or without median section being convex (Fig. 41); male stylus subterminal (Fig. 42)..*Reticulipeurus* (*Reticulipeurus*) Kéler, 1958

12 Frons convergent to median point (similar to Fig. 33)..*Talegallipeurus* Mey, 1982

– Frons rounded to flattened (Figs 25, 26)... 13

13 Male parameres strongly S-curved (Fig. 43); stylus arising centrally on abdominal segment IX+X (Fig. 44) .... *Sinolipeurus* Gustafsson et al., 2020

– Male parameres not S-curved (Fig. 45); stylus varying in shape, but always arising terminally or subterminally on subgenital plate (Figs 40, 42) 14

14 Male genitalia simple, with parameres fused to basal apodeme and mesosome much reduced (Fig. 46) ....*Epicolinus* Carriker, 1945

– Male genitalia with parameres articulating with basal apodeme, and mesosome not reduced (Fig. 47) 15

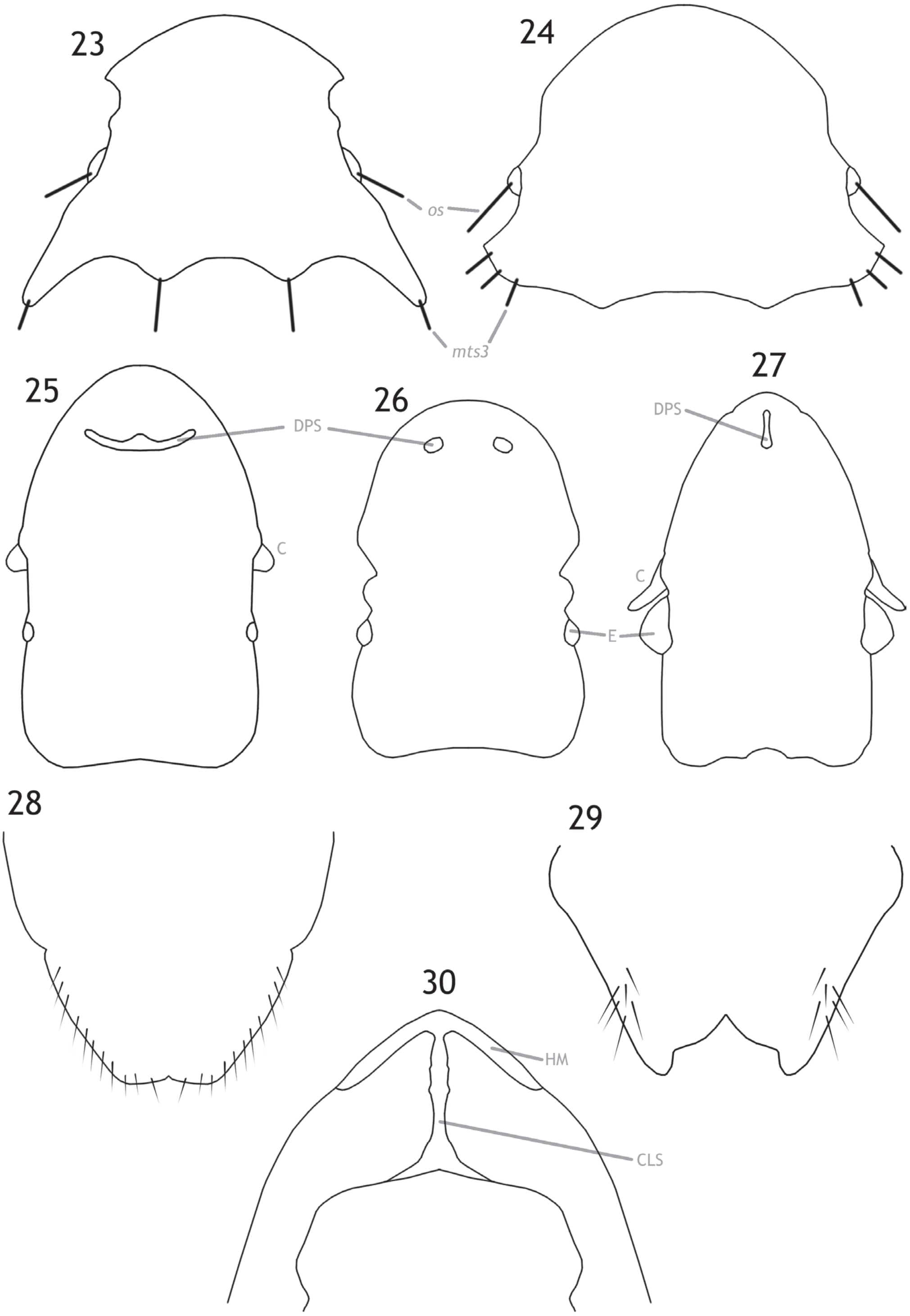
15 Lateral margins of postantennal head with secondary, ventral carina between antennal socket and site of *mts2* or *mts3* (Fig. 48); area between margin of head and secondary carina, densely reticulated, in some species, including ventral surface of eye (Fig. 48); male parameres with *pst1–2* situated close together apically (Fig. 49); female subgenital plate divided medianly and without lateral accessory vulval plates (Fig. 50)........................*Valimia* Gustafsson & Zou, 2020b

– Lateral margins of postantennal head without secondary carina and without extensive ventral reticulation; male parameres with *pst1–2* separated and only *pst2* apical (Fig. 51); female subgenital plate medianly continuous and with lateral accessory vulval plates present (Fig. 52)..*Cataphractomimus* Gustafsson et al., 2020

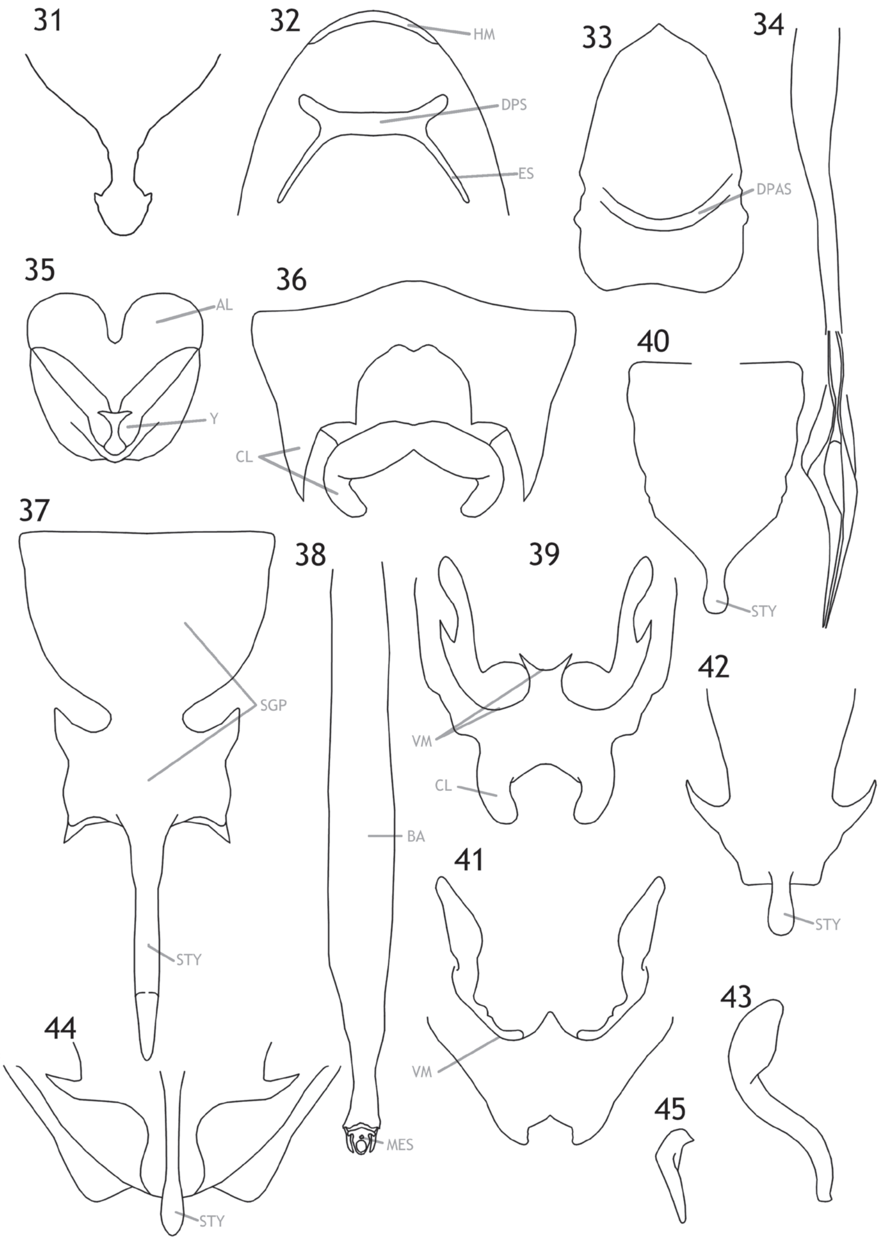
Removal of *Afrilipeurus*

We believe it is justified to remove the genus *Afrilipeurus* from the *Oxylipeurus*-complex and,instead, place it in the *Lipeurus*-complex, where it is probably closely related to *Numidilipeurus* Tendeiro, 1955, which occurs on the same host group. This is based on the following morphological comparisons:

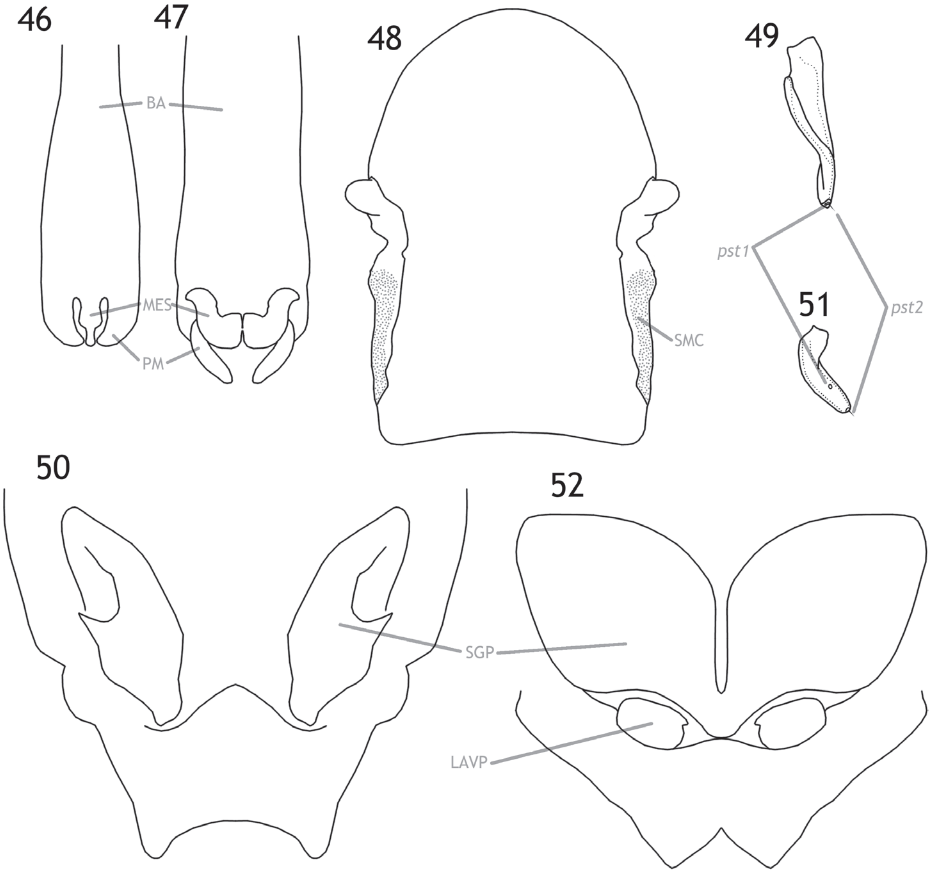
1. Amongst slender-bodied *Oxylipeurus*-complex genera, abdominal chaetotaxy consists of only *sutural setae* and *principal post-spiracular setae* dorsally and only one *sternal seta* on each side on segments II–V ventrally. In the *Lipeurus*-complex, multiple *sternal setae* per segment are the norm and, in the genus *Numidilipeurus*, both multiple *sternal setae* and *tergal posterior setae* are present on tergopleurites II–VIII. *Afrilipeurus* has multiple *sternal setae* and *tergal posterior setae* present on segments II–VIII.
2. Tergopleurites are medianly divided in all *Oxylipeurus*-complex genera except *Talegallipeurus* Mey, 1982, in which tergopleurites VII–IX+X are apparently medianly continuous; moreover, intertergal plates are absent in all *Oxylipeurus*-complex genera. In *Lipeurus* and *Numidilipeurus*, tergal plates are medianly continuous and intertergal plates are common in males, but do not occur in all species. In *Numidilipeurus*, intertergal plates are present on at least male segments III–V. *Afrilipeurus* has medianly continuous tergopleurites and intertergal plates on male segments III–IV.
3. Female genitalia lack distally convergent rows of *vulval oblique setae* in the *Oxylipeurus*-complex and this set of setae is often reduced to one or a few short setae on the posterior margin of abdominal segment VII. In *Numidilipeurus*, these setae are numerous (> 5 per side) and form roughly convergent rows on the ventral side of segments VII–IX+X, which is the same as in *Afrilipeurus*.



Figures 23–30. Key characters of the *Oxylipeurus*-complex. **23.** Outline of head and temporal macrosetae (cut off distally) of male *Chelopistes meleagridis* (Linnaeus, 1758), redrawn from Kéler (1939); **24.** Outline of head and temporal macrosetae (cut off distally) of female *Trichodomedea setosus* Carriker, 1946, redrawn from original description; **25.** Outline of head and dorsal preantennal suture of male *Reticulipeurus* (*Reticulipeurus*) *mesopelios* (Nitzsch [in Giebel], 1866), redrawn from Gustafsson et al. (2020a); **26.** Outline of head and dorsal preantennal suture of male *Cataphractomimus junae* Gustafsson et al., 2020, redrawn from original description; **27.** Outline of head, dorsal anterior suture and conus of *Calidolipeurus megalops* (Piaget, 1880), redrawn from Gustafsson et al. (2020b); **28.** Female terminalia of *Calidolipeurus megalops* (Piaget, 1880), redrawn from Gustafsson et al. (2020b); vulval margin, lateral macrosetae and subvulval plates not illustrated; **29.** Female terminalia of *Reticulipeurus* (*Reticulipeurus*) *mesopelios* (Nitzsch [in Giebel], 1866), redrawn from Gustafsson et al. (2020a); vulval margin, lateral macrosetae and subvulval plates not illustrated; **30.** ventral view of pre-antennal area in *Gallancyra dentata* (Sugimoto, 1934), redrawn from Gustafsson and Zou (2020a). Figures 23–26 and 29–30 reproduced from Gustafsson et al. (2020b), with kind permission of the European Journal of Taxonomy. Abbreviations used: C = conus; CLS = clypeo-labral suture; DPS = dorsal pre-antennal suture; E = eye; HM = hyaline margin; *mts3* = marginal temporal seta 3; *os* = ocular seta. Figures not to scale.



Figures 31–45. Key characters of the *Oxylipeurus*-complex. **31.** Outline of stylus in *Gallancyra dentata* (Sugimoto, 1934), redrawn from Gustafsson and Zou (2020a); **32.** Outline of preantennal area and dorsal pre-antennal suture of *Splendoroffula ampullacea* Kéler, 1955, redrawn from von Kéler (1958); **33.** Outline of head and dorsal post-antennal suture of *Oxylipeurus inaequalis* (Piaget, 1880), redrawn from Mey (1990); original drawing asymmetrical; **34.** Male genitalia of *Oxylipeurus inaequalis* (Piaget, 1880), redrawn from Mey (1990); some details left out for clarity; **35.** ventral view of mesosome of *Megalipeurus sinensis* Gustafsson et al., 2020a, redrawn from original description; **36.** dorsal view of male terminalia of *Eiconolipeurus melanotis* Carriker, 1945, redrawn from original description; setae not illustrated; **37.** Male subgenital plate and stylus of *Pelecolipeurus fujianensis* sp. nov., redrawn from Fig. 7 and simplified somewhat for clarity; **38.** Male genitalia of *Pelecolipeurus fujianensis* sp. nov., redrawn from Fig. 5 and simplified somewhat for clarity; **39.** Female terminalia and vulval margin of *Reticulipeurus* (*Forcipurellus*) *formosanus* (Uchida, 1917), redrawn from Gustafsson and Zou (2023); chaetotaxy and other detail omitted for clarity; **40.** Male subgenital plate of *Reticulipeurus* (*Forcipurellus*) *formosanus* (Uchida, 1917), redrawn from Gustafsson and Zou (2023); **41.** Female terminalia and vulval margin of *Reticulipeurus* (*Reticulipeurus*) *reevesi* (Clay, 1938), redrawn from Gustafsson et al. (2020a); chaetotaxy and other detail omitted for clarity; **42.** Male subgenital plate of *Reticulipeurus* (*Reticulipeurus*) *mesopelios* (Nitzsch [in Giebel], 1866), redrawn from Gustafsson et al. (2020a); **43.** Outline of male paramere of *Sinolipeurus tetraophasis* (Clay, 1938), redrawn and simplified from Gustafsson et al. (2020a); **44.** Outline of male terminalia and stylus of *Sinolipeurus tetraophasis* (Clay, 1938), redrawn and simplified from Gustafsson et al. (2020a); **45.** Outline of male paramere of *Reticulipeurus* (*Reticulipeurus*) *ithaginis* (Clay, 1938), redrawn and simplified from Gustafsson et al. (2020a). Figures 31–36 reproduced from Gustafsson et al. (2020b), with kind permission of the European Journal of Taxonomy. Abbreviations used: AL = anterior lobes; BA = basal apodeme; CL = "claspers"; DPAS = dorsal post-antennal suture; DPS = dorsal pre-antennal suture; ES = epistomal suture; HM = hyaline margin; MES = mesosome; SGP = subgenital plate; STY = stylus; VM = vulval margin; Y = Y-shaped thickening. Figures not to scale.



Figures 46–52. Key characters of the *Oxylipeurus*-complex. **46.** Distal section of male genitalia of *Epicolinus clavatus* (McGregor, 1917), redrawn from Carriker (1945); **47.** Distal section of male genitalia of *Cataphractomimus mirapelta* Gustafsson et al., 2020a, redrawn from the original description, with some simplification for clarity; **48.** Outline of male head of *Valimia polytrapezia* (Burmeister, 1838), with post-antennal ventral carina and densely reticulated area marked with grey dots; other characters omitted; **49.** Male paramere of *Valimia corpulenta* (Clay, 1938), redrawn from Gustafsson and Zou (2020b); **50.** Outline of ventral view of female terminalia of *Valimia polytrapezia* (Burmeister, 1838); **51.** Male paramere of *Cataphractomimus mirapelta* Gustafsson et al., 2020a, redrawn from the original description; **52.** Outline of ventral view of female terminalia of *Cataphractomimus impervius* Gustafsson et al., 2020a, redrawn and simplified from the original description. Figs 46, 48, 50, 52 reproduced from Gustafsson et al. (2020b), with kind permission of the European Journal of Taxonomy. Abbreviations used: BA = basal apodeme; LAVP = lateral accessory vulval plates; MES = mesosome; PM = parameres; *pst1–2* = parameral setae *1–2*; SGP = subgenital plate; SMC = secondary marginal carina. Figures not to scale.

4. *Marginal temporal seta 1* is at least a mesoseta in *Afrilipeurus* and *Numidilipeurus*, but always a microseta in the *Oxylipeurus*-complex.
5. Despite considerable variation amongst genera, the male terminalia in the *Oxylipeurus*-complex are rather uniform in their basic structure, with a generally rounded ano-genital opening, anterior to which may be a transverse sclerotisation that may be continuous with the subgenital plate; several setae of varying length are situated anterior to this opening and a maximum of one seta on each side (typically none) is situated on the ventral side of the poorly-sclerotised areas postero-lateral to the ano-genital opening. Even in genera such as *Pelecolipeurus*, where the ano-genital opening is not clearly visible, its position can be judged by the distribution of setae and the anterior sclerotisation and this structure appears to be found even in the genus *Labicotes* Kéler, 1940, in which the stylus is absent. The terminalia of the *Lipeurus*-complex males are more variable, but do not include a transverse sclerotisation and the non-sclerotised areas distal to the subgenital plate may form a longitudinal groove, with multiple setae on each side; this is, for instance, the case in some *Numidilipeurus*. In *Afrilipeurus*, there is no transverse sclerotisation and there are multiple small setae on each side lateral to a longitudinal groove.
6. The female subgenital plate is never extended much distal to the row of *sternal setae* of segment VII in the *Oxylipeurus*-complex, but is extended distal to this row in *Lipeurus*-complex and in *Afrilipeurus*.

For these reasons, we here exclude *Afrilipeurus* from the *Oxylipeurus*-complex and transfer it to the *Lipeurus*-complex, where it is probably close to *Numidilipeurus*.

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