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Two new species of *Craspedorrhynchus* Kéler, 1938, (Phthiraptera: Ischnocera: Philopteridae) from Chinese birds of prey (Accipitriformes)

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ABSTRACT

Two new species of the head louse genus *Craspedorrhynchus* Kéler, 1938 are described from specimens collected in China. They are: *Craspedorrhynchus guizhouensis* **sp. n.** ex *Accipiter soloensis* (Horsfield, 1821) and *Craspedorrhynchus obsoletus* **sp. n.** ex *Nisaetus nipalensis* Hodgson, 1836. An overview of the morphological variation within the genus is given to aid in future identifications, with an assessment of species groups delimitation.

<http://www.zoobank.org/urn:lsid:zoobank.org:pub:1F01EFCB-BF4E-4A9A-95DC-2F6421DDFD66>

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Chewing lice; new taxa; head lice; *Accipiter soloensis*; *Nisaetus nipalensis*

Introduction

The genus *Craspedorrhynchus* Kéler, 1938 comprises a relatively small group of lice parasitising the heads of many birds of prey (Accipitriformes, Falconiformes). Most species are known from larger host species, including many eagles, but hosts also include smaller birds such as some falcons (Price *et al.* 2003). The only recent overview of the genus was published by Mey (2001), but many species are poorly known and have never been adequately illustrated or described. Gállego *et al.* (1987) published illustrations of the species known from Spain, and Mey (2001) provided comparative illustrations of the heads and female tergopleurites IX+X for some species. However, no general revision has been published.

Only about 40 of the over 320 accipitriform and falconiform birds of the world are known to be parasitised by lice in the genus *Craspedorrhynchus* (Price *et al.*, 2003). However, unidentified species of the genus have been reported from many additional host species (eg Green and Palma 1991; Oyanzún-Ruiz *et al.* 2022). Most species of *Craspedorrhynchus* are known from Europe, Africa, and the Americas, and almost none have been described from the many species of birds of prey in Asia and the Australo-

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Papuan region. Here, we describe two new species of this genus from material collected in China; they constitute the first species of *Craspedorrhynchus* described from Chinese hosts. In addition, we provide a partial overview of the morphology of the known species of *Craspedorrhynchus*, to aid in the identification of specimens.

Material and methods

Previously slide-mounted specimens deposited at the Beijing Museum of Natural History, China (BMNH), were examined through a Nikon Eclipse Ni (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 were taken from images of the specimens, for the following dimensions: 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). Host taxonomy follows Clements *et al.* (2022). Terminology for chaetotaxy and other structures of the lice follows Clay (1951), Mey (1994), and Gustafsson and Bush (2017). Setal characters are italicized throughout the text.

Systematics

PHTHIRAPTERA Haeckel, 1896

Phthiraptera Haeckel, 1896: 703.

Ischnocera Kellogg, 1896

Ischnocera Kellogg, 1896: 63.

Phlopteridae Burmeister, 1838

Phlopteridae Burmeister, 1838: 422.

Phlopterus complex

Craspedorrhynchus Kéler, 1938

Craspedorrhynchus Kéler, 1938: 239.

Falcoecus Clay and Meinertzhagen, 1938: 275.

Type species

Docophorus platystomus Burmeister, 1838: 426, by original designation.

Remarks. No complete key to the species of *Craspedorrhynchus* has ever been published. Perez and Martin-Mateo (1995) published a partial key, including only the species known from Spain at the time, which can be complemented by the illustrations of the same species by Gállego *et al.* (1987). We use this key here to narrow down the potentially closest relatives of the two new species, but note that many of the other species in the genus are poorly described and illustrated. A revision of *Craspedorrhynchus* is needed; in

anticipation of such a revision, where possible we have also compared the species described here with all other well-illustrated and well-described species [see Mey (2001) for a comprehensive overview] to verify that the species described here are at least not conspecific with any of the species it is currently possible to identify.

Craspedorrhynchus guizhouensis **sp. n.**

(Figures 1–6)

Type host

Accipiter soloensis (Horsfield, 1821) – Chinese sparrowhawk.

Type locality

Guizhou Province, China.

Diagnosis. *Craspedorrhynchus guizhouensis* **sp. n.** keys to couplet 6 in the incomplete key of Perez and Martin-Mateo (1995), but the lateral margins of the dorsal anterior plate are rounded and the posterior part is long in *C. guizhouensis*, meaning that neither choice in this couplet is suitable. Judging from the illustrations of Gállego *et al.* (1987), the shape of the dorsal anterior plate appears to be an inadequate key character, as there is much variation between species. Following the first choice in couplet 6, *C. guizhouensis* keys to *Craspedorrhynchus triangularis* (Rudow, 1869), whereas if the second choice is followed and further characters of the dorsal anterior plate are ignored, *C. guizhouensis* keys to *Craspedorrhynchus subbuteonis* Gállego *et al.*, 1987. The type material of *C. triangularis* is lost (Clay and Hopkins 1955; Mey 2001), and more material is necessary to fully compare *C. guizhouensis* with *C. triangularis*.

Craspedorrhynchus guizhouensis can be separated from *C. triangularis* by the following combination of characters: preantennal area longer than postantennal area, with frons clearly concave in *C. guizhouensis* (Figure 3), but preantennal area at most as long as postantennal area and frons rounded in *C. triangularis*; lateral accessory sternal plates absent in male *C. guizhouensis* (Figure 1), but present on segments VI–VII in *C. triangularis*; dorsal anterior plate proportionately much longer, particularly in the posterior end, in *C. guizhouensis* (Figure 3) than in *C. triangularis*; dorsal side of proximal mesosome with nearly parallel, rounded antero-lateral lobes in *C. triangularis*, but with distally narrowed, anteriorly divergent lobes in *C. guizhouensis* (Figure 4); mesosomal lobes with more or less flat distal margins in *C. guizhouensis* (Figure 5), but with convex posterior margin in *C. triangularis*; parameres of different shape, with overall axis (from central base to central tip) more parallel in *C. guizhouensis* (Figure 4) than in *C. triangularis*; female vulval chaetotaxy not detailed by Gállego *et al.* (1987), but appears to be similar in the two species; however, the shape of the subgenital and subvulval plates differ between the two species (Figure 6), as does the head shape (Figure 2).

Craspedorrhynchus guizhouensis can be separated from *C. subbuteonis* by the following combination of characters: dorsal anterior plate with irregularly rounded lateral margins in *C. guizhouensis* (Figure 1; less obvious in some specimens, as in the illustrated female, Figure 2), but with parallel lateral margins in *C. subbuteonis*; male subgenital

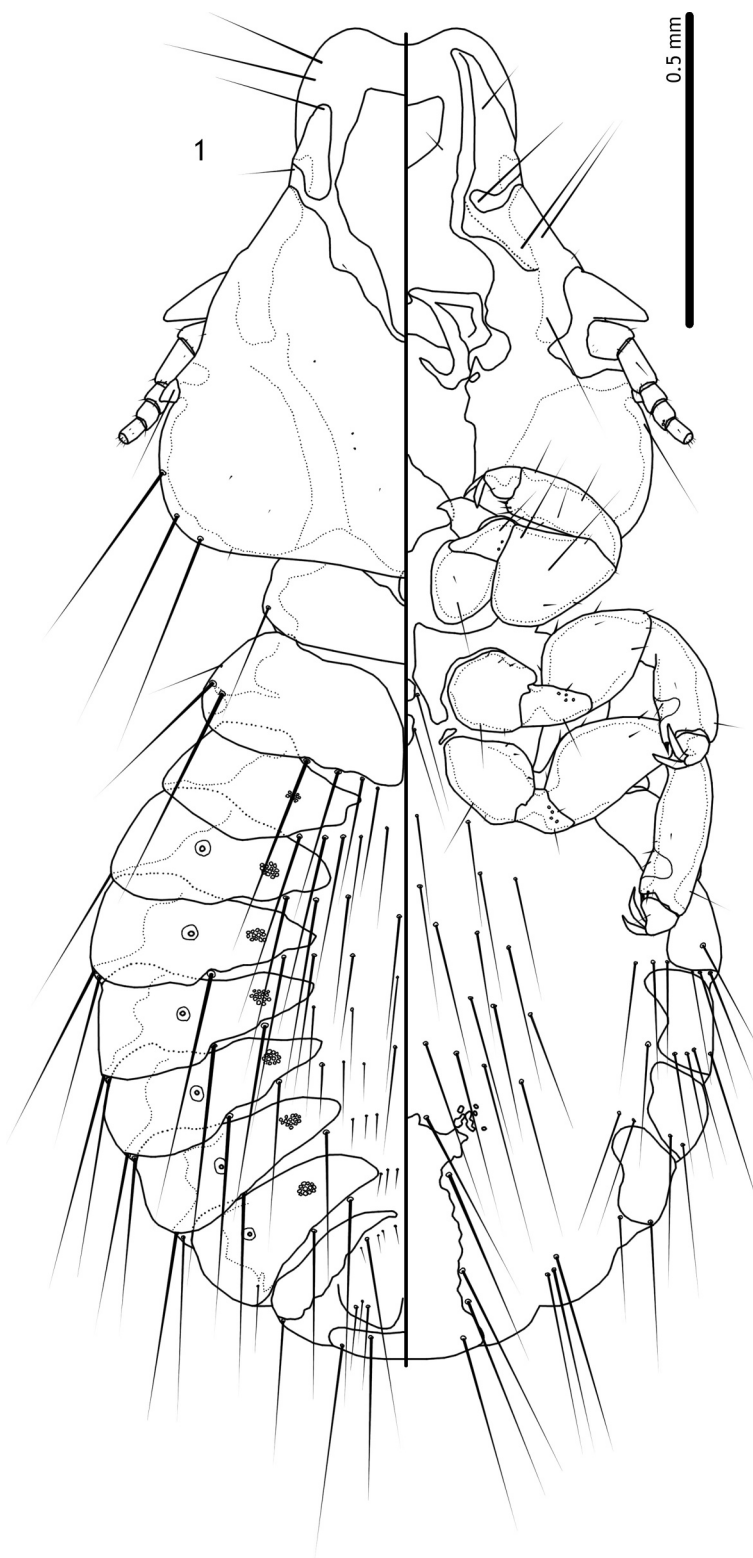


Figure 1. *Craspedorrhynchus guizhouensis* new species, male habitus, dorsal and ventral views.

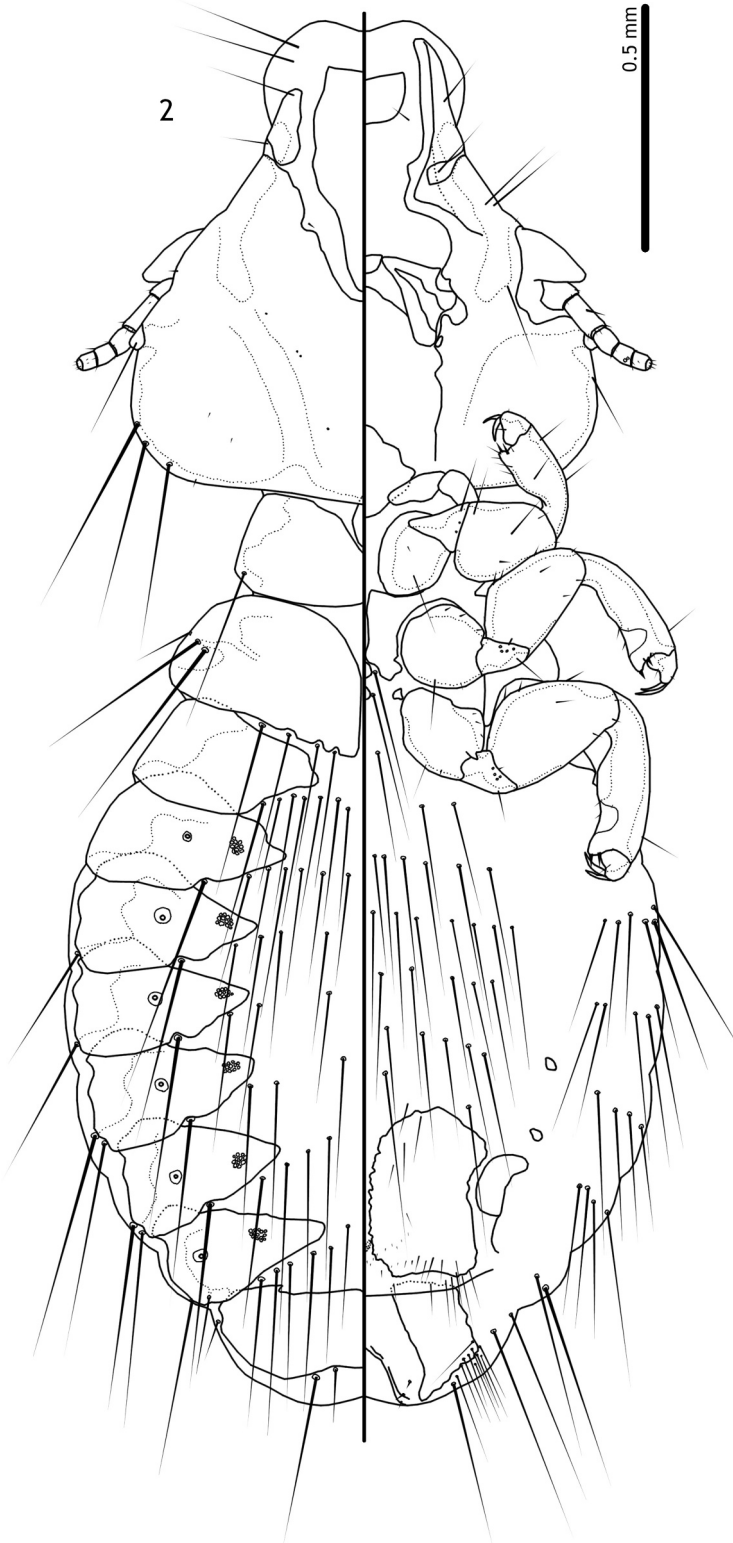


Figure 2. *Craspedorrhynchus guizhouensis* new species, female habitus, dorsal and ventral views.

plate with 4–5 macrosetae on each side in distal end in *C. subbuteonis*, but with only 3 macrosetae on each side in *C. guizhouensis* (Figure 1); *principal post-spiracular setae* absent on male tergopleurites II–III and female tergopleurite II in *C. guizhouensis* (Figures 1–2), but present on these segments in *C. subbuteonis*; the description of the male tergal chaetotaxy of *C. subbuteonis* by Perez and Martin-Mateo (1995) is not straightforward, but seems to indicate that this species has more setae than in *C. guizhouensis* on each side of at least tergopleurite II, and that *C. subbuteonis* lacks the set of very short setae median to tergopleurites VII–VIII found in *C. guizhouensis* (Figure 1); the description of the female tergal chaetotaxy by Perez and Martin-Mateo (1995) suffers the same problem, but whereas in *C. guizhouensis* there are a maximum of 7 tergal setae on each side of tergopleurite II (Figure 2), there are at least 8 on each side in *C. subbuteonis*; male parameres shorter and more strongly curved in *C. subbuteonis* than in *C. guizhouensis* (Figure 4); female vulval chaetotaxy appears to overlap, but shape of subgenital and subvulval plates set the species apart (Figure 6).

Description. Head rounded trapezoidal, preantennal head longer than postantennal head (Figure 3); frons concave. Dorsal anterior plate with almost flat anterior margin, irregularly rounded lateral margins (less obvious in female), and elongated posterior part. Head chaetotaxy as in Figure 3; *postnodal seta* present. Eye somewhat triangular, but not much extended distally. Thoracic and abdominal segments and chaetotaxy as in Figures 1–2. Lateral accessory sternal plates absent in male, but present on abdominal segments V–VIII in female. Male dorsal abdominal chaetotaxy: *principal post-spiracular setae* present on tergopleurites IV–VII; tergopleurites II–IV with 4–5 more or less equally long macrosetae on each side; tergopleurites V–VI with 4–5 mesosetae on each side, the most median and most lateral of which are clearly longer than those in between; tergopleurites VII–VIII with 3 median mesosetae and 1 more lateral meso- or macroseta on each side. Female dorsal abdominal chaetotaxy: *principal post-spiracular setae* present on tergopleurites III–VII; tergopleurites II–III with 6–7 more or less equally long macrosetae on each side; tergopleurites IV–VI with 3–4 more or less equally long macrosetae on each side, the median of which are separated from the lateral ones by a gap; tergopleurites VII–VIII with 4–6 more or less equally long macrosetae on each side. Male subgenital plate with antero-lateral corners fragmented into small plates; chaetotaxy: 1 macroseta on each side anterior to plate, 1 lateral macroseta on each side in anterior end, 3 lateral macrosetae on each side in posterior end. Basal apodeme as in Figures 4–5, with median thickening. Dorsal plates of mesosome elongated, fused proximally. Ventral mesosomal plates slender, seemingly articulating with parameral heads. Mesosomal lobes with more or less flat distal margins. Gonopore broad, proximally associated with slender curved structures. Parameres long, curved. Female subgenital plates roughly rectangular, with irregular median margins and small distal area of irregular, fragmented sclerotizations (Figure 6). Vulval margin more or less flat, with 7–8 long, slender *vms*, 6–7 slender and 3–6 thorn-like *vss*, 9–10 microsetal and (in anterior end) 5–6 slender *vos* on each side. Subvulval plates broadly rectangular with postero-median section slightly extended, and with 9 mesosetae in tufts on each side. Measurements as in Table 1.

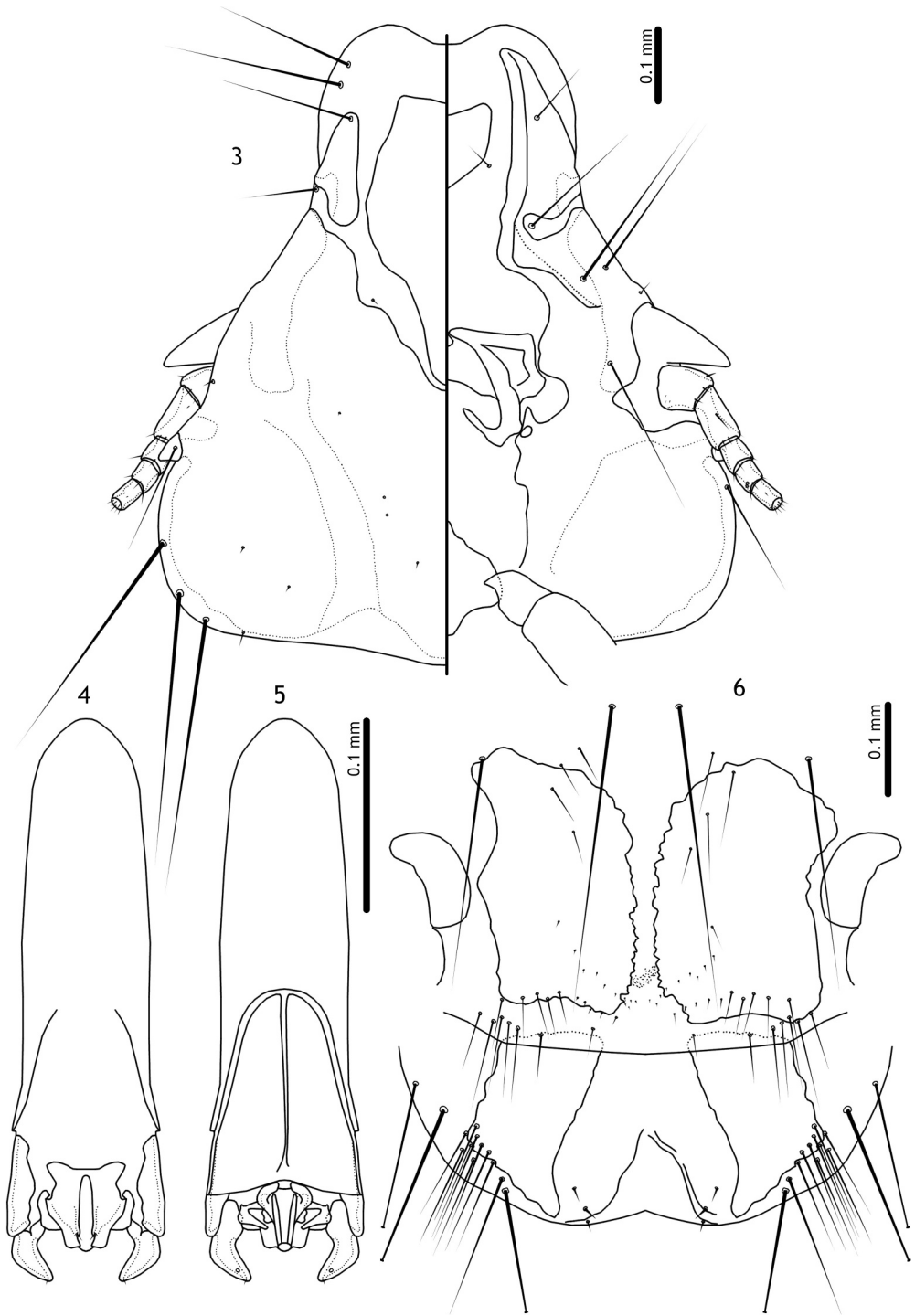


Figure 3-6. *Crapedorrhynchus guizhouensis* new species. 3, male head, dorsal and ventral views. 4, male genitalia, dorsal view. 5, male genitalia, ventral view. 6, female subgenital plates, vulval margin, and post-vulval area, ventral view.

Table 1. Measurements of the species described here. Measurements (in mm) were taken for the following dimensions: 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).

Species	Sex	N	TL	HL	HW	PRW	PTW	AW
<i>Craspedorrhynchus guizhouensis</i>	M	7 ^a	2.12–2.40	0.85–0.93	0.78–0.85	0.48–0.54	0.63–0.67	0.91–1.08
	F	7 ^b	2.56–2.85	0.94–1.01	0.88–0.96	0.54–0.59	0.67–0.80	1.02–1.28
<i>Craspedorrhynchus obsoletus</i>	M	9	1.91–2.12	0.77–0.88	0.75–0.79	0.42–0.50	0.58–0.66	0.80–1.03
	F	13 ^c	2.27–2.59 (2.43)	0.80–0.94 (0.87)	0.80–0.89 (0.85)	0.45–0.58 (0.52)	0.62–0.74 (0.68)	0.80–1.21 (1.00)

^aN for TL, PRW, PTW, AW = 6.

^bN for TL = 4, N for AW = 5, N for PRW = 6.

^cN for TL, AW = 12.

Etymology

The specific name is derived from the type locality.

Specimens examined

Holotype ♂, Guizhou [China], 22 January 1958, no collector, box E0026008, slide 40 (BNHM) [marked with black dot on slide]. **Paratypes:** 8♂, 11♀, same data as holotype, box E0026008, slides 40–42 (BNHM). **Non-types:** 3 nymphs, same data as holotype, box E0026008, slide 40 (BNHM).

Craspedorrhynchus obsoletus sp. n.

(Figures 7–12)

Type host

Nisaetus nipalensis Hodgson, 1836 – mountain hawk-eagle [uncertain].

Type locality

Jianou, Fujian Province, China.

Diagnosis. In the incomplete key of Perez and Martin-Mateo (1995), *Craspedorrhynchus obsoletus* sp. n. keys to *Craspedorrhynchus fraterculus* Eichler and Złotorzycka, 1975, based on the shape and chaetotaxy of the male subgenital plate. *Craspedorrhynchus fraterculus* has been partially illustrated by Eichler and Złotorzycka (1975), Martín Mateo and Rivas (1982), and Gállego *et al.* (1987), but all these illustrations are inadequate; for instance, the abdominal chaetotaxy and details of the male genitalia are not included. Moreover, the illustrations of Martín Mateo and Rivas (1982) and Gállego *et al.* (1987) and presumably the key of Perez and Martin-Mateo (1995) are based on specimens from a non-type host, *Aquila adalberti* Brehm, 1861. Due to the inadequate original illustrations of *C. fraterculus*, it is presently impossible to say whether the species on *A. adalberti* is conspecific with the population on the type host, *Aquila heliaca* Savigny, 1809.

The holotype of *C. fraterculus* is deposited at the Museum of Natural History, University of Wrocław, Poland (Jałoszynski *et al.* 2014), but could not be examined during the

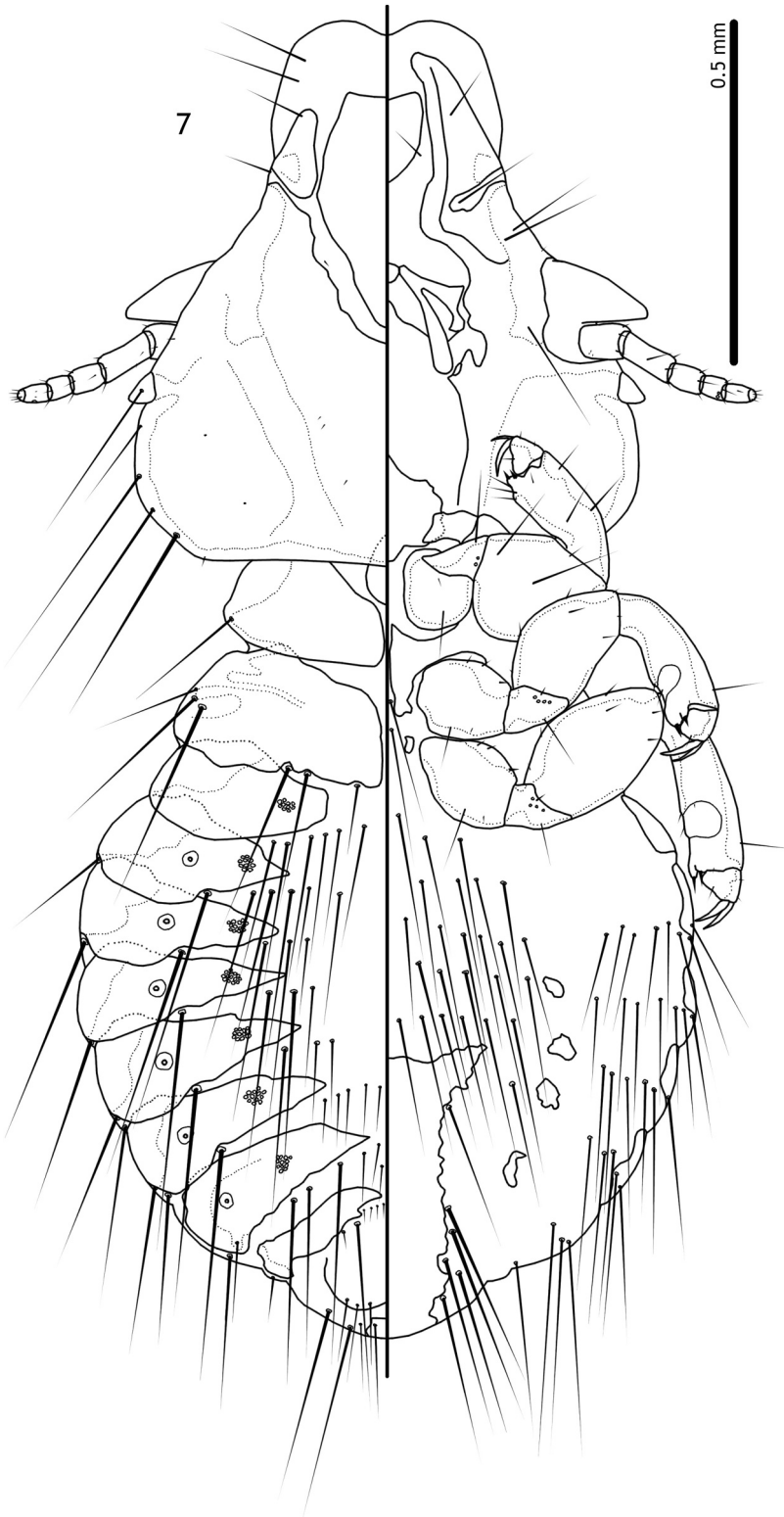


Figure 7. *Craspedorrhynchus obsolectus* new species, male habitus, dorsal and ventral views.

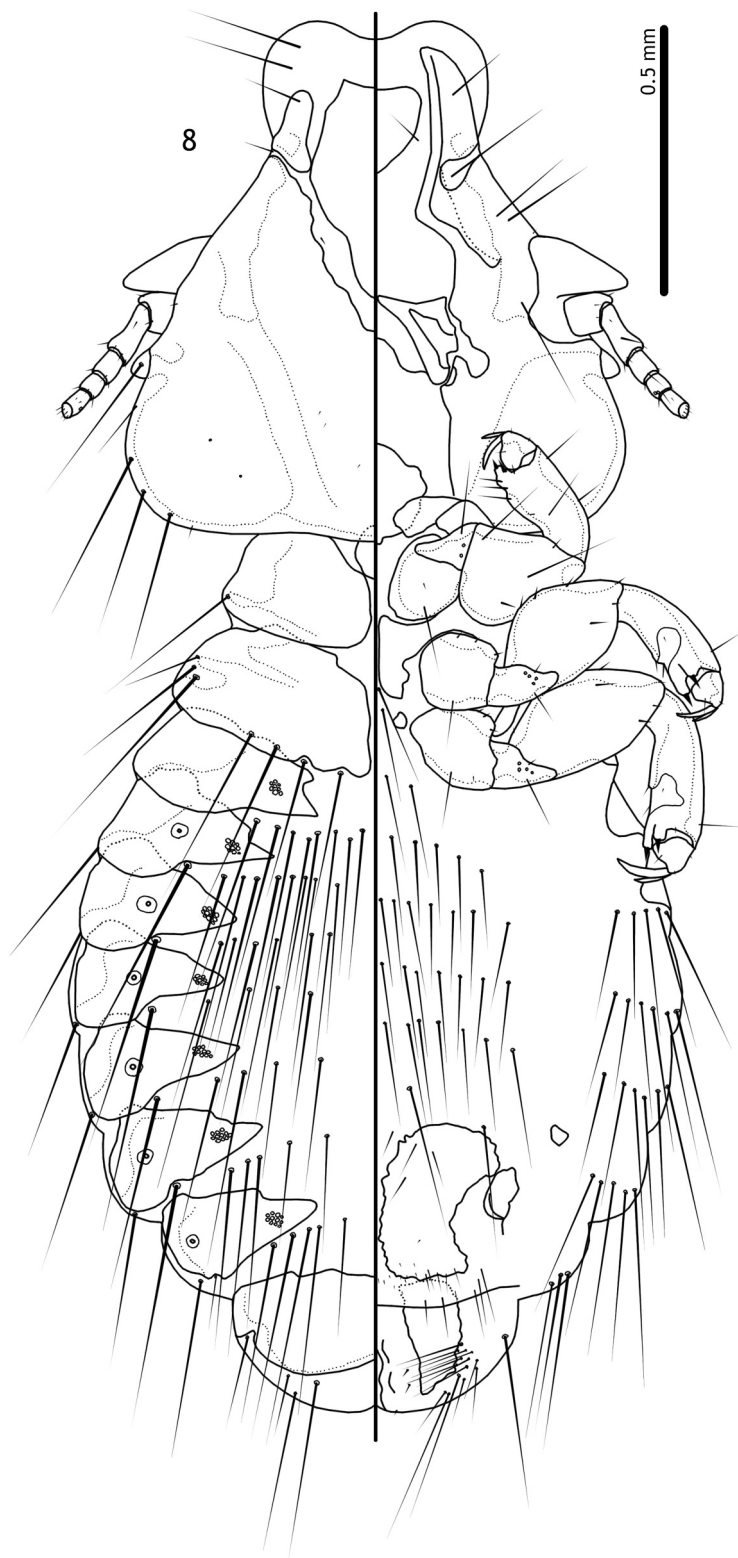


Figure 8. *Craspedorrhynchus obsoletus* new species, female habitus, dorsal and ventral views.

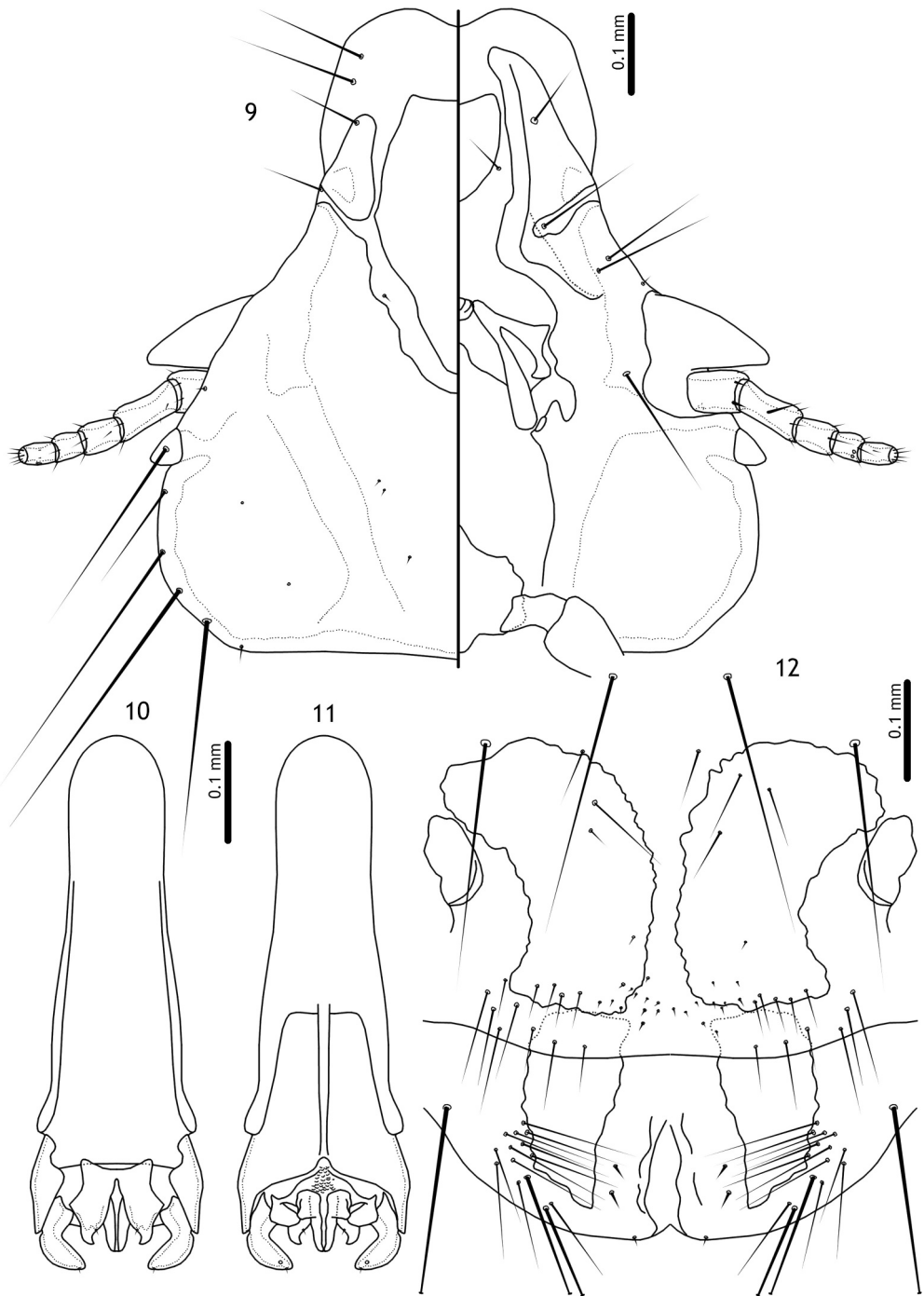


Figure 9-12. *Craspedorrhynchus obsoletus* new species. 9, male head, dorsal and ventral views. 10, male genitalia, dorsal view. 11, male genitalia, ventral view. 12, female subgenital plate, vulval margin, and post-vulval area, ventral view.

preparation of this manuscript. Mey (2001) stated that 11 paratypes were in the Museum für Naturkunde in Berlin, but as no paratypes were mentioned by Eichler and Złotorzycka (1975), these specimens have no type status. A re-examination of the type specimens is necessary to establish whether the species living on *A. adalberti* is conspecific with that on *A. heliaca*, and whether the characters listed here are sufficient to tell them apart from *C. obsoletus*. Based on the illustrations of the type series of *C. fraterculus* by Eichler and Złotorzycka (1975), this species can be separated from *C. obsoletus* by the following characters: dorsal anterior plate with different shape in *C. fraterculus* than in *C. obsoletus* (Figure 9); preantennal head probably proportionally shorter and broader in *C. fraterculus* than in *C. obsoletus* (Figure 9); dorsal plates of mesosome apparently medianly divided and with median parts near-parallel throughout, with anterior and posterior projections close together in *C. fraterculus*, but medianly continuous, with median margins distally divergent, and with proximal and distal projections widely separated in *C. obsoletus* (Figure 10).

We also compare our material of *C. obsoletus* with both the species illustrated by Martín Mateo and Rivas (1982) and Gállego *et al.* (1987), and with Sichuan specimens from the BMNH identified on the slide labels as *C. fraterculus*, with the host listed as 'eagle'. Several eagles, including *A. heliaca*, occur in Sichuan. These two sets of specimens are not conspecific, but it is unclear, based on the original description of *C. fraterculus*, which of them is conspecific with this species.

Craspedorrhynchus obsoletus can be separated from *C. fraterculus* [*sensu* Martín Mateo and Rivas (1982) and Gállego *et al.* (1987)] by the following combination of characters: preantennal head proportionately longer and narrower in *C. obsoletus* (Figure 9) than in *C. fraterculus*; male subgenital plate with antero-lateral extensions broad and somewhat triangular in *C. obsoletus* (Figure 7), but smaller, irregular, and connected to the main plate by a narrow neck in *C. fraterculus*; lateral accessory sternal plates present on male abdominal segments V–VIII in *C. obsoletus* (Figure 7), but absent in *C. fraterculus*; male subgenital plate with 1 macroseta on anterior margin on both sides in *C. fraterculus*, but apparently without such setae in *C. obsoletus* (Figure 7); male and female abdominal chaetotaxy was not clearly illustrated or discussed by either Martín Mateo and Rivas (1982) or Gállego *et al.* (1987), but at least male tergopleurites III and V, and female tergopleurites IV–VII appear to have fewer tergo-central setae in *C. fraterculus* than in *C. obsoletus* (Figs 7–8); basal apodeme with median thickening in *C. obsoletus* (Figure 11), but without such thickening in *C. fraterculus*; ventral sclerites of mesosome extended distally to overlap with projecting distal ends of dorsal sclerites in *C. fraterculus*, but shorter, blunter, and not overlapping with dorsal plates in *C. obsoletus* (Figure 11); female vulval chaetotaxy not given in detail by Martín Mateo and Rivas (1982) and Gállego *et al.* (1987), but appears to overlap at least partially with that of *C. obsoletus*.

Craspedorrhynchus obsoletus can be separated from *C. fraterculus* [*sensu* BMNH specimens] by the following combination of characters: preantennal head proportionately narrower in *C. obsoletus* (Figure 9) than in *C. fraterculus*; lateral accessory sternal plates present on male abdominal segments V–VIII and female abdominal segment VII in *C. obsoletus* (Figs 7–8), but absent in *C. fraterculus*; pronotum divided medianly in *C. obsoletus* (Figs 7–8), but undivided in *C. fraterculus*; *principal postspiracular setae* present on male tergopleurite III in *C. obsoletus* (Figure 7), but absent in *C. fraterculus*; female tergopleurite IX+X with more or less straight

anterior margin in *C. obsoletus* (Figure 8), but with strongly convex anterior margin in

C. fraterculus; basal apodeme with median thickening in *C. obsoletus* (Figure 11), but without such thickening in *C. fraterculus*; dorsal sclerites of mesosome fused at proximal end in *C. obsoletus* (Figure 10), but separate in *C. fraterculus*; distal ends of dorsal sclerites of mesosome project farther beyond margin of mesosome and whole plate has different shape in *C. obsoletus* (Figure 10) than in *C. fraterculus*; proximal ends of ventral sclerites of mesosome in *C. fraterculus* clearly separated medianly, but whole area unclear due to consistent but asymmetrical fragmentation of sclerite in *C. obsoletus* (Figure 11); parameres shorter and more strongly curved in *C. obsoletus* (Figure 10) than in *C. fraterculus*.

Description. Head rounded trapezoidal, preantennal head longer than postantennal head (Figure 9); frons concave. Dorsal anterior plate with shallowly concave anterior margin, irregularly rounded lateral margins, and broadly elongated posterior part. Head chaetotaxy as in Figure 9; *postnodal seta* absent. Eye somewhat triangular, but not much extended distally. Thoracic and abdominal segments and chaetotaxy as in Figs 7–8. Lateral accessory sternal plates present on male abdominal segments V–VIII and female abdominal segment VII. Male dorsal abdominal chaetotaxy: *principal post-spiracular setae* present on tergopleurites III–VII; tergopleurites II–III with 5–6 more or less equally long macrosetae on each side; tergopleurites IV–VI with 3 setae on each side, with wide median gap between setae; tergopleurite VII with 4–5 mesosetae centrally on each side; tergopleurite VIII with 3 mesosetae centrally on each side. Female dorsal abdominal chaetotaxy: *principal post-spiracular setae* present on tergopleurites III–VII; tergopleurites II–IV with 6–8 more or less equally long macrosetae on each side; tergopleurites V–VIII with 4–5 more or less equally long macrosetae on each side. Male subgenital plate with antero-lateral corners extended into broad-based, triangular projection; chaetotaxy: apparently no setae on anterior margin, 1 macroseta on each side in anterior end, 4–5 macrosetae on each side in posterior end. Basal apodeme narrowing proximally (Figs 10–11), with median thickening. Dorsal plates of mesosome as in Figure 10, fused proximally. Ventral mesosomal plates with broad distal recurved part, and proximal part unclear, dissolved into small scales or platelets medianly. Mesosomal lobes hooked distally. Gonopore broad, widened proximally. Parameres long, strongly curved. Female subgenital plates curved laterally, with irregular margins but no fragmented sclerotisation medianly (Figure 12). Vulval margin slightly concave with 4–6 long, slender *vms*, 5–7 slender and 3–5 thorn-like *vss*, 6–8 (one female with 9 on one side and 11 on the other) thorn-like and (in anterior end) 3–4 slender *vos* on each side. Subvulval plates broadly rectangular with postero-median section slightly extended, and with 9–12 mesosetae in tufts on each side. Measurements as in Table 1.

Etymology

The specific name is derived from '*obsoletus*', Latin for 'worn out', referring to the fragmented and unclear central part of the ventral mesosomal plates.

Specimens examined

Holotype ♂, Jianou, Fujian Province, China, 7 January 1997, no collector, box E0026206, slide 94 (BMNH) [only male on middle row of slide, marked with black dot]. **Paratypes**: 8♂, 13♀, same data as holotype, box E0026206, slides 94, 96 (BMNH). **Non-types**: 4 specimens of undeterminable sex due to partial destruction of the bodies, box E0026206, slide 96 (BMNH).

Remarks. The Chinese characters of the slide labels are not clearly legible, and the host species given here therefore needs confirmation. Price *et al.* (2003) listed *Craspedorrhynchus nipalensis* Eichler, 1944, from this host species, but according to Mey (2001), the host from which Eichler (1944) collected his samples is actually the species today called *Aquila rapax vindhiana* Franklin, 1831. Mey (2001) designated this as a type host species. As *Craspedorrhynchus nipalensis* has never been adequately described or illustrated in full, it is presently impossible to verify this by comparison with other material from *A. r. vindhiana*. However, the illustration of the head of *C. nipalensis* published by Mey (2001) shows that this species is at least not the same as *Craspedorrhynchus obsoletus*.

Yoshino *et al.* (2012) reported an unidentified species of *Craspedorrhynchus* from *Nisaetus nipalensis* (as *Spizaetus nipalensis*) from Japan. These specimens may also represent *C. obsoletus*, but cannot be identified from the published photo of the female.

Discussion

The number of accepted species of *Craspedorrhynchus* differs in recent accounts, with Mey (2001) accepting 37 species and Price *et al.* (2003) accepting 40 species; the discrepancy consists of two species Mey (2001) considered to belong to other genera, and one he suggested should be treated as a *nomen oblitum*. Naz *et al.* (2020) agreed with Mey (2001) on the status of *Craspedorrhynchus chicquerae* Ansari, 1955, and there seems to be no reason not to follow Mey (2001) regarding the other two discrepancies. A single species of the genus has been described since 2003 (Valim 2006), and as argued by Gustafsson *et al.* (2022), *Philopterus hiyodori* Uchida, 1949, also belongs to *Craspedorrhynchus*. Together with the two species described here, the genus thus presently comprises 41 species (Table 2).

Almost all species of *Craspedorrhynchus* are host-specific (Mey 2001), with only a few exceptions (eg Green and Palma 1991; Dik *et al.* 2013). However, the poor descriptions and illustrations published for many species, and the lack of a comprehensive revision of the genus, suggests that at least some of these records from non-type hosts may comprise separate species. For instance, Yudhana and Praja (2018) recorded *Craspedorrhynchus platystomus* (Burmeister, 1838) from *Spilornis cheela bido* (Horsfield, 1821), but the shape of the dorsal anterior plate in their photos suggests that this is not *C. platystomus*, and may represent an undescribed species. Unidentified species of *Craspedorrhynchus* have also been recorded from novel host species in recent years, which may represent new species (eg Oyarzún-Ruiz *et al.* 2022).

In order to facilitate identifications and descriptions of new species of *Craspedorrhynchus*, we here tabulate some of the known morphological variation in the genus (Table 2). Mey (2001) listed six morphological characters that he found helpful in

the classification of the species of *Craspedorrhynchus* into groups: shape of the male subgenital plate; structure of the male genitalia; size of the female calyx; shape and chaetotaxy of female tergopleurite IX+X; presence of tergopleurite XI in female; presence of lateral accessory sternal plates in female. These characters have all been helpful in organising the species at the BMNH, which apart from the species described here include six other species, which will be reported elsewhere (Gustafsson *in press*). In addition to the characters proposed by Mey (2001), we suggest that the following characters may warrant further attention for resolving relationships within *Craspedorrhynchus*:

- (1) Pronotum may be divided or continuous medianly; in both cases, the rhombic sclerite may be separate from it (Figure 1), but in some species with continuous pronotum the rhombic sclerite is also fused to the pronotum.
- (2) A set of distinctly shorter setae may be present submedianly on male tergopleurites VII–VIII (Figure 1). The number of setae is typically 3 on each side in species we have examined, but in some species there may be more. These are all situated median to the tergopleurite, and are generally separated from longer tergo-central setae by a clear gap.
- (3) Presence or absence of *principal postspiracular setae* (*psps*) on male tergopleurite III. Among the species we have examined, this seta is present in almost all the species that also have the short setae on tergopleurites VII–VIII, except *Craspedorrhynchus guizhouensis* (Figure 1). Conversely, specimens of *Craspedorrhynchus dilatatus* (Rudow, 1869) we have examined have *psps* on tergopleurite III, but lack the small setae of tergopleurites VII–VIII.
- (4) Presence in the male basal apodeme of a central, longitudinal thickening (Figure 5). This thickening may be associated with the seminal duct, as illustrated by Carriker (1956), but is not as broad as the duct illustrated by him, nor does it continue to the mesosome in species we have examined (eg Figure 5), and it is likely a different structure; seminal ducts as prominent as those illustrated by Carriker (1956) have not been observed in any species examined by us.
- (5) Presence or absence of a median division in the dorsal sclerites of the male mesosome. These sclerites are fused proximally in eg *Craspedorrhynchus guizhouensis* (Figure 4) but divided in *Craspedorrhynchus reichelti* Mey, 2001 (Figure 4). A separate type of sclerite is found in *C. macrocephalus* (Nitzsch [in Giebel], 1874), in which the dorsal sclerites are widely separated and fused in a different way, more distally, and the more prominent feature of the anterior mesosome is a ventral arch that connects the ventral sclerites (see eg Gallégo *et al.* 1987).

A wider survey of *Craspedorrhynchus* is needed before the utility of these characters can be evaluated, especially as many of the characters listed in Table 2 are not known for all species. Until such a revision is undertaken, the characters listed by Mey (2001) and above should be explicitly included in any descriptions or redescrptions of species of *Craspedorrhynchus*. However, the fragmentary data summarised in Table 2 indicate that these characters are not sufficient to establish useful species groups or postulate relationships within the group, as few characters seem to be correlated with each other. Presumably, as the gaps in Table 2 are

Table 2. Overview of the distribution of morphological characters in *Craspedorrhynchus*, based on the characters proposed by Mey (2001) and here. Mey (2001) also discussed the size of the calyx of the *receptaculum seminis*, but this is difficult to analyse, as measurements for these are unknown for most species, and the calyxes illustrated by Mey (2001) do not seem to fall into discrete size categories; they are undoubtedly good characters, but more data is needed. The presence and absence of lateral accessory sternal plates in females was also suggested to be a useful character by Mey (2001) but is illustrated for so few species that it has been omitted here. The characters listed here are: (1) pronotum and rhombic sclerite [A = pronotum divided medianly, separate from sclerite; B = pronotum continuous medianly, separate from sclerite; C = pronotum continuous medianly, fused to sclerite]; (2) set of smaller setae median to male tergopleurites VII–VIII [A = present; B = absent]; (3) principal post-spiracular setae on male tergopleurites III [A = present; B = absent]; (4) central longitudinal thickening of basal apodeme [A = present; B = absent]; (5) dorsal sclerites of mesosome [A = fused; B = divided; C = *C. macrocephalus* type]; (6) antero-lateral corners of male subgenital plate [A = without extensions; B = with non-fragmented extensions; C = with fragmented extensions]; (7) shape of anterior margin of female tergopleurite IX+X [A = more or less straight or concave; B = clearly convex, but median section may be concave]; (8) medio-anterior setae of female tergopleurite IX+X [A = present; B = absent]; (9) tergopleurites of female abdominal segment XI [A = present; B = absent]. BMNH under 'Data sources' refers to specimens deposited at this museum examined by us.

Species	1	2	3	4	5	6	7	8	9	Data sources
<i>C. americanus</i> Emerson, 1960	?	?	?	B	A	A	?	B	B	Emerson (1960), Mey (2001)
<i>C. aequilinus</i> (Denny, 1842) ^a	A	A	A	B	A	B/C	A/B	B	B	Gállego <i>et al.</i> (1987), Mey (2001), BMNH
<i>C. brevicapitis</i> Carriker, 1956	?	?	A	B	B?	?	?	B	B	Carriker (1956), Mey (2001)
<i>C. buteonis</i> (Packard, 1870)	?	?	?	?	?	A	?	B	B	Emerson (1960), Mey (2001)
<i>C. candidus</i> (Rudow, 1870)	?	?	?	B	B?	A	A	B	B	Carriker (1956)
<i>C. cornutus</i> (Piaget, 1880)	?	?	?	?	?	?	?	?	?	
<i>C. dilatatus</i> (Rudow, 1869)	A	B	A	B	B?	A	B	B	B	Carriker (1956), Emerson (1960), Mey (2001), BMNH
<i>C. fasciati</i> Gállego <i>et al.</i> , 1987	?	?	A	B	A	C	A	B	B	Gállego <i>et al.</i> (1987), Mey (2001)
<i>C. femoralis</i> (Giebel, 1874)	?	?	?	?	?	?	?	?	?	
<i>C. fraterculus</i> Eichler and Zlotorzyska, 1975	B	A	B	B	B	B	B	B	B	Eichler and Zlotorzyska (1975), Martín Mateo and Rivas (1982), Gállego <i>et al.</i> (1987), Mey (2001), BMNH
<i>C. genitalis</i> Carriker, 1956	?	?	?	B	B?	A?	A	B	B	Carriker (1956)
<i>C. guizhouensis</i> sp. n.	B	A	B	A	A	B	A	B	B	Present paper
<i>C. gypohieracis</i> Tendeiro, 1955	A	A	A	B	?	?	?	?	?	Tendeiro (1955)
<i>C. haematopus</i> (Scopoli, 1763)	A	A	A	B	A	B	A	A	B	Emerson (1960), Mey (2001), BMNH
<i>C. halioti</i> (Osborn, 1896)	?	?	?	?	?	?	?	?	?	
<i>C. hirsutus</i> Carriker, 1956	?	?	?	?	?	B	B	B	B	Carriker (1956), Emerson (1960), Mey (2001)
<i>C. hiyodori</i> (Uchida, 1949)	A?	?	?	?	?	?	B?	B	?	Uchida (1949)
<i>C. hopkinsi</i> Tendeiro, 1955	A	?	?	?	?	?	B	B	B	Tendeiro (1955)
<i>C. insolitus</i> Kéler, 1938	A	?	?	B	A	A	A	A	A	Kéler (1938), Mey (2001)
<i>C. intermedius</i> (Piaget, 1880)	?	?	?	?	?	?	?	?	?	
<i>C. leucogaster</i> (Giebel, 1874)	?	?	?	?	?	?	?	B	B	Mey (2001)
<i>C. linardii</i> Valim, 2006	A?	B?	A?	B	B	B	A	?	?	Valim (2006)
<i>C. macrocephalus</i> (Nitzsch [in Giebel], 1874)	C	A	A	A	C	B	B	B	A	Mey (2001), BMNH
<i>C. mellittoscopus</i> (Nitzsch [in Giebel], 1874) ^a	?	?	A	B	A	C	A/B	B	A	Gállego <i>et al.</i> (1987), Mey (2001)
<i>C. naevius</i> (Giebel, 1861)	?	?	?	?	C?	?	A	B	B	Eichler and Zlotorzyska (1975), Mey (2001)
<i>C. nipalensis</i> Eichler, 1944	?	?	?	?	?	?	?	B	B	Mey (2001)
<i>C. nisi</i> (Denny, 1842)	?	?	A	B	A	A	A	A	A	Gállego <i>et al.</i> (1987), Mey (2001)
<i>C. obscurus</i> (Giebel, 1874)	?	?	?	A	A?	A	A	B	B	Carriker (1956)
<i>C. obsoletus</i> sp. n.	A	A	A	A	A	B	A	B	B	Present paper
<i>C. pachypus</i> (Giebel, 1874)	?	?	?	?	?	?	?	?	A	Mey (2001)
<i>C. platystomus</i> (Burmeister, 1838)	C	A	B	B	A	A	A	B	B	Gállego <i>et al.</i> (1987), Mey (2001); BMNH
<i>C. ranjhae</i> Ansari, 1955	?	?	B	B	B?	C	A	B	B	Gállego <i>et al.</i> (1987), Mey (2001)

(Continued)

Table 2. (Continued).

Species	1	2	3	4	5	6	7	8	9	Data sources
<i>C. reichelti</i> Mey, 2001	?	A	A	B	B	B	B	B	B	Mey (2001)
<i>C. robustisetosus</i> Tuff, 1970	C	B?	A	B	B?	A	B	B	A	Tuff (1970)
<i>C. rotundatus</i> (Piaget, 1880)	?	?	A	A	C	B	B	B	A	Gállego <i>et al.</i> (1987), Mey (2001)
<i>C. spathulatus</i> (Giebel, 1874) ^a	A	B?	B	A/B	C	A/B	B	B	A	Tendeiro (1955), Gállego <i>et al.</i> (1987), Mey (2001)
<i>C. subbuteonis</i> Gállego <i>et al.</i> , 1987	?	?	A	B	A	C	A	B	B	Gállego <i>et al.</i> (1987), Perez and Martin-Mateo (1995)
<i>C. subhaematopus</i> Emerson, 1960	A?	?	?	B?	?	?	A	B	B	Emerson (1960)
<i>C. triangularis</i> (Rudow, 1869)	?	?	A	B	A	C	B	B	A	Gállego <i>et al.</i> (1987), Mey (2001)
<i>C. tubulus</i> Carriker, 1956	?	?	?	B	B?	A	?	?	?	Carriker (1956)
<i>C. umbrosus</i> (Carriker, 1903)	?	?	?	B	B	B	?	?	?	Carriker (1956)

^aCharacters differ between specimens and/or published descriptions, and need to be verified from type material.

filled out, and more species become known, other characters that may be useful for species group delimitation may be found, for instance in the abdominal or vulval chaetotaxy. The placement and number of setae around the male subgenital plate may also be useful, but have not been illustrated in detail for a large number of species.

The characters in Table 2 indicate that only a single species group can be delimited presently, including *C. macrocephalus*, *C. rotundatus* (Piaget, 1880), and possibly *C. spathulatus* (Giebel, 1874). This group is characterised by having male genitalia with a peculiarly shaped dorsal sclerite (see Gállego *et al.* 1987), unlike that found in all other species of *Craspedorrhynchus*, except possibly *C. naevius* (Giebel, 1861). Other characters associated with this group, but found in other species as well, include the presence of a central longitudinal thickening of the basal apodeme, presence of female tergopleurite XI, and large, usually broad-based, wing-like antero-lateral extensions of the male subgenital plate. The hosts of the three (maybe four) species included in this group are not closely related, suggesting that host associations may not be a good basis for evaluating relationships in *Craspedorrhynchus*.

Little is known about the effect of *Craspedorrhynchus*, or indeed other head lice, on their hosts. Grossi *et al.* (2023) recently showed that head lice were the only group of lice that seemed to vary in prevalence between ecologically different groups of shorebirds (Charadriiformes), suggesting that they may have a slight negative effect, but data from other groups of head lice are absent. As summarised by Ren *et al.* (2023), the host associations of head lice are often broader than expected by their presumably poor ability to spread between hosts, suggesting that we know very little about the ecology of this ecomorph. *Craspedorrhynchus* is thus something of an outlier among the head louse ecomorph, as most species are host specialists (Mey 2001; Price *et al.* 2003). However, the genus has never been comprehensively revised, and the apparent host specificity of many species may be due to the assumption that lice are host specialists (Gustafsson and Najer 2022), and thus artefactual. A general revision of the group is thus sorely needed.

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