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Separation of *Goniocotes* Burmeister, 1838, and *Dictyocotes* Kéler, 1940 (Phthiraptera: Ischnocera), with descriptions of four new species

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Abstract. The ischnoceran louse genus *Dictyocotes* Kéler, 1940, has long been considered a synonym of *Goniocotes* Burmeister, 1838, but the genus has never been revised. Here, the relationships within and between *Goniocotes* and *Dictyocotes* are discussed, and the latter genus is resurrected from synonymy. Both genera are redescribed, and four new species of lice are described and illustrated. They are: *Dictyocotes furcatus* sp. nov. ex *Lophophorus lhuysii* Geoffroy Saint-Hilaire, 1866; *Goniocotes cacumentalis* sp. nov. ex *Tetraogallus tibetanus* Gould, 1854; *Goniocotes caoi* sp. nov. ex *Chrysolophus pictus* (Linnaeus, 1758); *Goniocotes sarissa* sp. nov. ex *Tragopan caboti* (Gould, 1857). The altitudinal distribution of these two genera is discussed, and appears to indicate a division between a primarily low-altitude *Goniocotes* and an exclusively high-altitude *Dictyocotes*. The driving force behind this division is unknown, but unlikely to be based on host associations.

Keywords. Psocodea, Gonioididae, new species, *Goniocotes*, *Dictyocotes*.

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Introduction

Ischnoceran chewing lice (Phthiraptera: Ischnocera) constitute the largest radiation of parasitic lice, containing roughly 60% of the known species (Price *et al.* 2003). Different groups within this radiation have repeatedly evolved similar gross morphologies (ecomorphs), which are correlated with methods of escaping host preening (Johnson *et al.* 2012). Whereas lice in the “wing louse” and “head louse” ecomorphs are widely distributed across avian hosts, those of the “body louse” ecomorph are more restricted. Most known species in this ecomorph belong to the Gonioididae Mjöberg, 1910, which is limited to columbiform and galliform hosts (Price *et al.* 2003). Among the gonioidid lice known from galliform hosts, almost all are placed in two large, morphologically heterogeneous genera: *Goniocotes* Burmeister, 1838, and *Goniodes* Nitzsch, 1818.

The genus *Goniocotes* s. lat. contains some of the smallest ischnoceran lice known, and size differences appear to have been one of the primary characters used to separate *Goniocotes* s. lat. from *Goniodes* s. lat. over the last 150 years. As discussed by Gustafsson *et al.* (2021), no reliable morphological characters are known that can separate *Goniocotes* and *Goniodes* as currently circumscribed [e.g., Price *et al.* (2003)] other than size, as both genera include species with dimorphic and monomorphic antennae, angular and rounded temples, and solenoid and more complicated male genitalia.

Preliminary examinations of these genera (Gustafsson *et al.* in prep.) suggest that each of these two genera contain multiple distinct groups that are better considered different genera. Both groups also contain a significant undescribed diversity, which in some cases makes delimitations of groups more difficult, as some morphological characters seem to have a mosaic distribution rather than being limited to presumed monophyletic clades. For instance, the solenoid male genitalia typical of *Goniocotes* spp. are very similar to those found in the otherwise morphologically dissimilar *Goniodes eurygaster* Piaget, 1885 and *Goniodes dispar* Burmeister, 1838. However, *Goniodes dispar* also has triangular processes antero-lateral to the female vulval margin, a character otherwise primarily associated with the proposed genus *Oulocrepis* Kéler, 1940 (a synonym of *Goniodes* in Price *et al.* 2003). These processes are not found in *G. eurygaster* (type species of the proposed genus *Margaritenes* Kéler, 1940), but the modifications of the male antennae in *G. dispar* and *G. eurygaster* are near-identical. Presumably, many morphological characters have evolved independently multiple times in the Gonioididae, especially those associated with the antennae and the genitalia. More than in many other groups of ischnoceran lice, revisionary work in the Gonioididae must proceed with caution, not least due to the large number of proposed generic names in this family. It does not help that *Goniocotes* has never been revised, and *Goniodes* was last revised partially by Clay (1940) and Kéler (1940), since when 21 of the 46 species of *Goniocotes* (excepting those moved to *Pavoniocotes* by Gustafsson *et al.* 2023) and 39 of the 99 species of *Goniodes* accepted as valid by Price *et al.* (2003) have been described.

Here, we examine the proposed genus *Dictyocotes* Kéler, 1940, a group that has been considered a synonym of *Goniocotes* since Hopkins & Clay (1952) stated that the group was not separable, without justification. We find that even in a morphologically variable *Goniocotes*, *Dictyocotes* is morphologically distinct, and it is therefore here resurrected from synonymy. Together with the separation of two species of *Goniocotes* into *Pavoniocotes* by Gustafsson *et al.* (2023), this division makes *Goniocotes* less morphologically heterogeneous, and will hopefully spur future researchers into identifying and describing more species of lice in these genera.

Material and methods

Previously slide-mounted specimens deposited at the Beijing Museum of Natural History, China (BMNH) or the Natural History Museum, London, United Kingdom (NHML) were examined with 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 (all in mm; see Table 1) were made in the digital measuring software ImageJ 1.48v (Wayne Rasband; imagej.net):

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.* (2023).

Terminology for chaetotaxy and other structures of the lice, and the abbreviations thereof, follow Clay (1951), Mey (1994), Gustafsson & Bush (2017), and Gustafsson *et al.* (2020), and include:

<i>aps</i>	=	accessory post-spiracular seta
<i>as1–3</i>	=	anterior setae 1–3
<i>avs1</i>	=	anterior ventral seta 1
<i>dsms</i>	=	dorsal submarginal seta
<i>ipts</i>	=	intermediate pteronotal seta
<i>lpts</i>	=	lateral pteronotal seta
<i>mets</i>	=	metasternal seta
<i>mpts</i>	=	median pteronotal seta
<i>mss</i>	=	mesosternal seta
<i>mts1–5</i>	=	marginal temporal setae 1–5
<i>os</i>	=	ocular seta
<i>pns</i>	=	postnodal seta
<i>pos</i>	=	preocular seta
<i>ppss</i>	=	pronotal post-spiracular seta
<i>ps</i>	=	paratergal seta
<i>psps</i>	=	principal post-spiracular seta
<i>s1–6</i>	=	sensilla of the dorsal head 1–6
<i>smns</i>	=	submarginal mesometanotal seta
<i>ss</i>	=	sutural seta
<i>sts</i>	=	sternal seta
<i>tps</i>	=	tergal posterior seta
<i>vms</i>	=	vulval marginal seta
<i>vos</i>	=	vulval oblique seta
<i>vsms1–2</i>	=	ventral submarginal setae 1–2
<i>vss</i>	=	vulval submarginal seta

Table 1. Measurements of the species described herein. Measurements were taken from live 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).

Louse species	Host species	Sex	N	TL	HL	HW	PRW	PTW	AW
<i>Dictyocotes furecatus</i> sp. nov.	<i>Lophophorus lhuyssii</i>	M	2 ¹	1.128	0.35	0.49–0.51	0.23	0.48–0.49	0.65
		F	2	1.42–1.44	0.40–0.41	0.60–0.62	0.27–0.29	0.56–0.57	0.76–0.78
<i>Goniocotes cacumentalis</i> sp. nov.	<i>Tetraogallus tibetanus</i>	M	2	1.01–1.02	0.33	0.41–0.43	0.25–0.27	0.33–0.35	0.49–0.50
		F	1	1.42	0.44	0.56	0.32	0.45	0.66
	<i>T. t. aquilonifer</i>	M	1	1.04	0.35	0.44	0.25	0.37	0.54
	<i>T. t. centralis</i>	F	10	1.24–1.62 (1.42)	0.42–0.45 (0.43)	0.53–0.58 (0.55)	0.30–0.34 (0.31)	0.42–0.46 (0.44)	0.66–0.74 (0.68)
		M	1	0.98	0.35	0.43	0.22	0.31	0.49
<i>Goniocotes caoi</i> sp. nov.	<i>Chrysolophus pictus</i>	M	3	0.90–0.94	0.31–0.32	0.35–0.36	0.18–0.19	0.28–0.31	0.46–0.51
		F	8	1.16–1.27	0.37–0.40	0.43–0.47	0.22–0.24	0.32–0.38	0.56–0.62
<i>Goniocotes sarissa</i> sp. nov.	<i>Tragopan caboti</i>	M	20 ²	0.83–0.96 (0.89)	0.25–0.30 (0.28)	0.37–0.41 (0.39)	0.19–0.22 (0.21)	0.35–0.38 (0.37)	0.50–0.56 (0.54)
		F	29 ³	1.09–1.25 (1.18)	0.33–0.37 (0.35)	0.44–0.50 (0.47)	0.22–0.28 (0.25)	0.40–0.47 (0.43)	0.57–0.65 (0.62)

¹ N = 1 for TL and AW.

² N = 18 for TL and N = 19 for HL and HW.

³ N = 26 for TL and N = 28 for AW.

Results

Systematics

Class Insecta Linnaeus, 1758
Order Phthiraptera Haeckel, 1896
Superfamily Ischnocera Kellogg, 1896a
Family Gonioididae Mjöberg, 1910

Genus *Goniocotes* Burmeister, 1838

Ricinus De Geer, 1778: 69 [in partim].

Goniodes Nitzsch, 1818: 293 [in partim].

Goniocotes Burmeister, 1838: 431.

Type species

Ricinus gallinae De Geer, 1778: 79, by subsequent designation (Johnston & Harrison 1911: 326).

Diagnosis

Goniocotes is morphologically variable (see below), but all species here retained in *Goniocotes* can be separated from the species of *Dictyocotes* by the following combination of morphological characters: 1) male genitalia without mesosome in *Goniocotes* (e.g., Fig. 4), but with mesosome in *Dictyocotes* (Fig. 19); 2) female vulval margin gently rounded in *Goniocotes* (e.g., Fig. 5; except *Goniocotes chapini* Clay, 1936), but margin notched or concave medianly in *Dictyocotes* (Fig. 20; except in *D. rolandi* Gustafsson *et al.*, 2021); 3) male parameres continuous with lateral margins of basal apodeme in *Goniocotes* (e.g., Fig. 4), but with parameres separated from, and possibly articulating with, basal apodeme in *Dictyocotes* (Fig. 19).

Many additional characters are variable within *Goniocotes* as circumscribed here, which may indicate that this genus is paraphyletic or consisting of several monophyletic groups that may deserve recognition as subgenera or genera in a future revision. The following characters can separate the type species of *Goniocotes* and many morphologically similar species from *Dictyocotes*: male tergopleurites II–V with 1–2 tergoventral setae (*ss+tps*) on each side in *Goniocotes* s. str. (e.g., Fig. 1), but at least some of these segments (typically at least II–III) with >5 tergoventral setae on each side in males of *Dictyocotes* (Fig. 16); apart from abdominal segment VI, each abdominal segment has a single *sts* on each side in *Goniocotes* s. str. (e.g., Fig. 1), but at least some segments (typically III–V) have 2–4 *sts* on each side in *Dictyocotes* (Fig. 16); male lateral tergopleurite IX+X slender and small in *Goniocotes* s. str. (e.g., Fig. 1), but larger, triangular or irregular in shape in *Dictyocotes* (Fig. 16). In almost all *Goniocotes* there are a maximum of 15 short, slender *vms* on each side of the female vulval margin (e.g., Fig. 5), whereas in *Dictyocotes* there are always >20 on each side (Fig. 20); however, *Goniocotes cacumentalis* sp. nov. has >20 *vms* on each side (Fig. 10) but is otherwise morphologically similar to *Goniocotes* s. lat. and is here included in that genus.

Description

Very small lice of the body louse ecomorph (sensu Johnson *et al.* 2012). Head shape variable among species: preantennal head gently rounded to somewhat flattened at frons, temples may be parallel or slightly divergent posteriorly, typically rounded at site of *mts1*, and with a more or less pronounced posterior occipital bulge at site of *mts5*. Marginal and ventral carinae uninterrupted; marginal carina may be very narrow or very broad, with clear attendant canals connecting to apertures of many setae (e.g., *dsms*, *asl*–3, *avs1*). Dorsal preantennal suture absent, but inner dorsal curved line may be present, delimiting a less densely sclerotized central part dorsal to the mandibles and ventral carina;

typically, this line becomes obscure posteriorly and does not completely surround the less sclerotized area. Preantennal nodi variable, may be roughly square-shaped, elongated, or rather small. Antennae sexually monomorphic. Eyes often proportionately large. Marginal temporal carina typically broad, with undulating median margin and a distinct occipital nodus originating marginally median to *mts5* on each side. Head chaetotaxy: all usual head setae present; *as1–3* and *avs1* marginal or submarginal, *vsms1–2* much separated; *pns* micro- to mesoseta, *s1–6* typically all present as sensilla, but may be difficult to see or absent (particularly *s5*), and additional sensilla may be present (Fig. 3); *pts* typically mesoseta; *os* may be macroseta in male, but always microseta in female (except in *G. cacumentalis* sp. nov.); *pos* positioned far posterior to eye; *mts1* and *mts3* macrosetae, *mts5* may be thorn-like, *mts2* and *mts4* microsetae.

Prothorax wider than long, with *ppss* macroseta on postero-lateral corner. Pterothorax variable, but typically pentagonal, with 2 *lpts* macrosetae on postero-lateral corners, separated by clear gap from 2 *ipts* macrosetae; single *smns* micro- or mesoseta present submarginally, but may be difficult to see if small, or alternatively may be absent; *mpts* absent. Proepimera extensive, may be fused medianly. Meso- and metasterna absent, but *mss* and *met*s present. Legs short and stout, most notably with three stout ventral setae on tibiae II–III (likely *tbII-v3–5* and *tbIII-v3–5*, but homology uncertain). Other leg chaetotaxy variable, and many setae very short. In *G. gallinae* and similar species: *tbI-a1–2*, *fI-v2*, *cII-a1*, *tbII-a1–2*, *tbII-p1–2*, *tbIII-p4–5*, *tbII-dm3*, *cIII-a1*, *tbIII-a1–2*, *tbIII-p1–2*, *tbIII-4–5*, *tbIII-dm3* all very short microsetae or absent; *fII-p1*, *fII-dm4*, *fIII-p1*, *fIII-dm4* absent.

Abdomen broadly rounded, more elongated in female. Tergopleurites II–IX+X divided medianly, typically with posterior tergopleurites more reduced compared to anterior tergopleurites (especially in male). Male abdominal segment IX+X with lateral sclerite on each side and central sclerite anterior to dorsal ano-genital opening. Female tergopleurites IX+X fused medianly. Paratergal plates may be indistinct, absent, or clearly visible and broad. Sternal plates generally absent, but reticulated, lightly sclerotized areas may be visible on ventral side of female abdominal segments II–VI (Fig. 12), or on segments II–VI in both sexes (not shown). Male subgenital plate variable, may be divided medianly; female subgenital plate absent. Subvulval plates may be present, but indistinct in many species. Abdominal chaetotaxy variable among species; anterior seta of tergopleurite II present. In *G. gallinae* and similar species, chaetotaxy is much reduced: *ss* present on tergopleurites II–VII (male; typically mesosetae in anterior segments and microsetae in posterior segments) or II–VIII (female; typically of uniform length); *tps* absent (female and males of some species) or present only on tergopleurites II, II–III, or II–IV (males of some species); *psps* typically present on tergopleurites II–VII (male) or V–VII (female; but sensilla may be visible on II–IV), but variable and may be absent more anteriorly in males, or be associated with a single shorter more median seta (*tps?*) in some segments. In other groups the dorsal abdominal chaetotaxy is much more extensive. Ventral side with 1 *sts* on each side of segments II–V, and 2 *sts* on each side on segments VI. Macrosetae present on ventral side of abdominal segments VII–VIII in both sexes.

Male genitalia solenoid, consisting of slender, elongated (anterior end may reach abdominal segment II) basal apodeme fused distally with simple parameres. Distal to male genitalia are often diaphanous, irregular structures of uncertain homologies, which in rare cases may have visible sensilla. In some species, parameral sensilla are visible, but these are easily overlooked if the male genitalia are pale or the specimen is poorly clearer; often, the sites of these sensilla are visible only because the parameres are swollen. Distal margin of basal apodeme may be indistinct median to parameres, or may be clearly delimited. In a few species, a vague, slightly reticulated structure which may be a genital sac is visible.

Female vulval margin typically gently rounded to somewhat flattened medianly, with a small number (<15) *vms* microsetae and 2–4 (in most species 3) *vss* thornlike setae on each side; *vos* microsetae variable in number and location, and may form distally convergent rows, but rarely numerous.

Host and geographical distribution

Goniocotes is only known from hosts in the order Galliformes Temminck, 1820, but distribution is somewhat scattered. Species of *Goniocotes* are known from at least some of the hosts in each of the three divisions of Phasianidae Horsfield, 1821 by Kimball *et al.* (2021), as well as on Numididae de Selys Longchamps, 1842 and Megapodiidae Lesson, 1831. However, the genus is largely absent on more boreal hosts, almost all New World hosts (except *Meleagris gallopavo* Linnaeus, 1758, which has acquired *G. gallinae* probably as stragglers in domestic settings), and many alpine hosts (Price *et al.* 2003). The presence of this genus on megapodiid hosts also appears to be limited (Mey 1997), and the *Goniocotes* species from numidid hosts, as well as many other species, are morphologically aberrant and may warrant separation into different genus. No species are known from cracid or odontophorid hosts.

Included species

In anticipation of a broader revision of the genus, all species placed in *Goniocotes* by Price *et al.* (2003: 181–182) are here retained in this genus, with the exception of the species listed under *Dictyocotes* below and those separated into the genus *Pavoniocotes* by Gustafsson *et al.* (2023).

Goniocotes afer Tendeiro, 1989: 70.

Goniocotes afropavo (Clay, 1938: 9) [in *Goniodes*]

Goniocotes albidus Giebel, 1874: 189.

Goniocotes homocerus Kéler, 1940: 151.

Goniocotes phasiani Kéler, 1940: 151.

Goniocotes cacumentalis sp. nov.

Goniocotes caoi sp. nov.

Goniocotes castaneicollis Tendeiro, 1965: 79.

Goniocotes chapini (Clay, 1938: 7) [in *Goniodes*].

Goniocotes chrysocephalus Giebel, 1874: 189.

Goniocotes clayae Tendeiro, 1954a: 316.

Goniocotes congolensis Tendeiro, 1989: 82.

Goniocotes coxatus Piaget, 1885: 43.

Goniocotes crassicauda Tendeiro, 1989: 82.

Goniocotes creber Kellogg, 1896b: 519.

Goniocotes diasi Tendeiro, 1954b: 81.

Goniocotes diplogonus Nitzsch in Giebel, 1866: 389.

Goniocotes eurygaster Piaget, 1885: 43.

Goniocotes gallinae (De Geer, 1778: 79) [in *Ricinus*].

Goniocotes hologaster (Nitzsch, 1818: 294).

Goniocotes gregarius (Nitzsch in Giebel, 1866: 388) [in *Goniodes*].

Goniocotes ictiorhynchi Tendeiro, 1989: 76.

Goniocotes ignitus Eichler, 1947: 12.

Goniocotes ignitus rufus Eichler, 1947: 13.

Goniocotes irregularis Rudow, 1869: 23 [unidentifiable].

Goniocotes jifrufti Ansari, 1947: 298.

Goniocotes keleri Tendeiro, 1989: 73.

Goniocotes keniensis Tendeiro, 1989: 75.

Goniocotes kivuensis Tendeiro, 1960: 119.

Goniocotes kristinae Gustafsson, Tian & Zou, 2021: 301.

- Goniocotes laticeps* Piaget, 1885: 41 [unidentifiable].
Goniocotes maculatus Taschenberg, 1882: 76.
 Goniocotes nigromaculatus Mjöberg, 1910: 106.
 Goniocotes numidae Kéler, 1940: 147.
 Goniocotes valdezi Tendeiro, 1954a: 327.
Goniocotes megalcephalus Uchida, 1916: 86.
 Goniocotes macrocephalus Uchida, 1916: 86.
Goniocotes microcephalus Uchida, 1917: 177.
Goniocotes microthorax (Stephens, 1829: 333) [in *Goniodes*].
 Goniocotes alatus Piaget, 1885: 45.
 Goniocotes simillimus Kéler, 1937: 128.
Goniocotes nahanii Tendeiro, 1989: 67.
Goniocotes obscurus Giebel, 1874: 188.
Goniocotes pallidiflavus Piaget, 1890: 235.
Goniocotes pallidomaculatus Piaget, 1880: 227.
Goniocotes plumiferae Tendeiro, 1989: 81.
Goniocotes pternistis Tendeiro, 1965: 74.
Goniocotes pucherani Tendeiro, 1989: 79.
Goniocotes punctatus Neumann, 1891: 91.
Goniocotes pusillus (Nitzsch in Giebel, 1866: 387) [in *Goniodes*].
Goniocotes rectangulatus Nitzsch in Giebel, 1866: 389.
 Goniocotes rectangulus Giebel, 1874: 185.
Goniocotes reticulatus Kéler, 1940: 142.
Goniocotes rotundiceps Piaget, 1880: 223.
Goniocotes sarissa sp. nov.
Goniocotes schraderi Tendeiro, 1989: 74.
Goniocotes shelleyii Tendeiro, 1989: 66.
Goniocotes vulturini Tendeiro, 1989: 78.

Remarks

Goniocotes as circumscribed here is undoubtedly morphologically variable, and several groups may deserve recognition as at least subgenera. However, adequate illustrations and descriptions of most species in the genus have never been published, and a general revision is sorely needed. From published descriptions and the specimens we have examined from various East Asian hosts, it is clear that the following character sets may be especially useful for separating species groups or future genera in the *Goniocotes*-group:

Ocular seta – in *G. gallinae* and many other species this seta is sexually monomorphic, but the *os* are macrosetae in males of, e.g., *G. albidus*, *G. pusillus*, and *G. cacumentalis* sp. nov. (Fig. 6).

Pterothoracic setae – in almost all species, there is only a single *smns* on each side submedianly (e.g., Fig. 6), but in *G. kristinae* and *G. sarissa* sp. nov. there is a patch of several setae in this area (Fig. 11). In some other species the *smns* may be absent, but as these setae may be sensillous they may have been overlooked in the specimens we have examined.

Male abdominal chaetotaxy – in *G. gallinae* and many other species this is reduced, with at most 1 *tps* on each side on some or all of tergopleurites II–IV. However, in many other species the number of *tps* is substantially higher (e.g., Fig. 11), with setal rows that may reach *psps* in species like *G. albidus* and *G. pusillus*. Moreover, the distribution of *psps* on male tergopleurites varies among species, and these

Table 2. Some morphological variation between *Goniocotes* Nitzsch, 1818, and *Dictyocotes* Kéler, 1940. *Goniocotes* s. str. as used here refers only to the type species of this genus and some presumably closely related species (likely including *G. caoi* sp. nov.), and much variation remains to be explored and understood within this genus. As an example, we have included two other species here retained in *Goniocotes*, which likely warrant recognition as separate genera. These two species are in need of redescription. For examples of other morphological variation within *Goniocotes* as circumscribed here, see the other two new species described here.

Character	<i>Goniocotes</i> s. str.	<i>Goniocotes afropavo</i> Clay, 1936	<i>Goniocotes chapini</i> Clay, 1936	<i>Dictyocotes Kéler</i> , 1940
Antennae	Sexually monomorphic	Sexually monomorphic	Sexually dimorphic	Sexually monomorphic
Occipital bulge at base of <i>mts5</i>	Present, large	Absent	Absent	Present, but may be small
Tergoventral setae (<i>ss+tps</i>) of male tergopleurites II–V	1–2 per side	2 per side	2–3 per side	> 5 per side
Male lateral tergopleurite IX+X	Slender	Broad?	Broad?	Broad
<i>Sternal setae</i> on abdominal segments II–VI	1–2 on each side	1–2 on each side	1–2 on each side	2–4 on at least some segments (typically III–V)
Mesosome	Absent	Present?	Absent	Present
Parameres	Fused to basal apodeme	Fused to basal apodeme	Separate from basal apodeme?	Separate from basal apodeme, possibly articulating
Female vulval margin	Rounded or flat	Narrowly rounded	Medianly notched	Medianly notched
<i>Vulval marginal setae</i>	Typically < 15 on each side	13 illustrated	19 (?) illustrated	> 20 on each side

setae may be absent in more anterior segments (e.g., in *G. pusillus*). In *G. maculatus*, there are single *tps* macrosetae roughly equidistant between the *psps* and *ss*.

Abdominal plates – sternal plates are absent in almost all species of *Goniocotes*, but present in the form of reticulated but poorly sclerotized plates in females of *G. kristinae* and *G. sarissa* sp. nov. (Fig. 12), and as small reticulated plates in *G. albidus*. In *G. maculatus*, there are small nodi lateral to spiracle openings on abdominal segments II–V. Moreover, whereas reticulation patterns are indistinct or absent in most *Goniocotes*, they are clear and extensive in *G. kristinae*, *G. sarissa* (Figs 11–12), *G. albidus*, and some other species.

Some of the morphological variation within *Goniocotes*, and the corresponding characters in *Dictyocotes*, are summarized in Table 2.

***Goniocotes caoi* sp. nov.**

[urn:lsid:zoobank.org:act:8FAA858F-FDEA-4BA9-A925-987158128D42](https://zoobank.org/act:8FAA858F-FDEA-4BA9-A925-987158128D42)

Figs 1–5

Diagnosis

Goniocotes caoi sp. nov. is most similar to *Goniocotes chrysocephalus*, with which it shares the following morphological characters: preantennal head with inner curved line separating median less sclerotized region and lateral and anterior more sclerotized region (Figs 1–3); proepimera fused medianly (Figs 1–2); *smns* absent (Figs 1–2); *psps* present on male tergopleurites II–IV (Fig. 1); *tps* absent on male tergopleurites III–VII (Fig. 1); male tergopleurites IV–VII with narrowed inner part that reaches at least halfway between edge of abdomen and midline on each side (Fig. 1).

Goniocotes caoi sp. nov. can be separated from *G. chrysocephalus* by the following combination of characters: occipital bulge at site of *mts5* less pronounced in *G. caoi* (Fig. 3) than in *G. chrysocephalus*; *tps* absent on male tergopleurite II in *G. caoi* (Fig. 1), but present in *G. chrysocephalus*; *ss* absent on male tergopleurites VI–VII in *G. caoi* (Fig. 1), but present in *G. chrysocephalus*; *ps* absent on male abdominal segment III in *G. caoi* (Fig. 1), but present in *G. chrysocephalus*; female vulval margin with small patch of *vms* microsetae near lateral corners in *G. chrysocephalus*, but without such patch in *G. caoi* (Fig. 5).

Etymology

Goniocotes caoi sp. nov. is named after the classical Chinese author Cao Xueqin, who wrote *Hongluo Meng* (Dream of the Red Chamber), considered one of the Four Great Classics of Chinese literature. This is in reference to this new species being Chinese, and living amongst the mainly red body feathers of its host.

Type material

Holotype (ex *Chrysolophus pictus*)

CHINA • ♂; location unknown; 23 Jan. 1989; collector unknown; box E0026203, slide 57; BMNH [male vertical, marked with black dot on slide].

Paratypes (ex *Chrysolophus pictus*)

CHINA • 2 ♂♂, 10 ♀♀; location unknown; 23 Jan. 1989; collector unknown; box E0026203, slides 55–59; BMNH • 1 ♂, 4 ♀♀; Shaanxi Province, Qinling Mountains; 15 Nov. 199; collector unknown; box E0026198, slide 39; BMNH.

Type host

Chrysolophus pictus (Linnaeus, 1758) – golden pheasant.

Type locality

China; more detailed locality unknown.

Description

Frons rounded, in some specimens appearing slightly pointed (Fig. 3). Marginal carina broad, with clear attendant canals of preantennal setae. Internal line separating median, less densely sclerotized area from

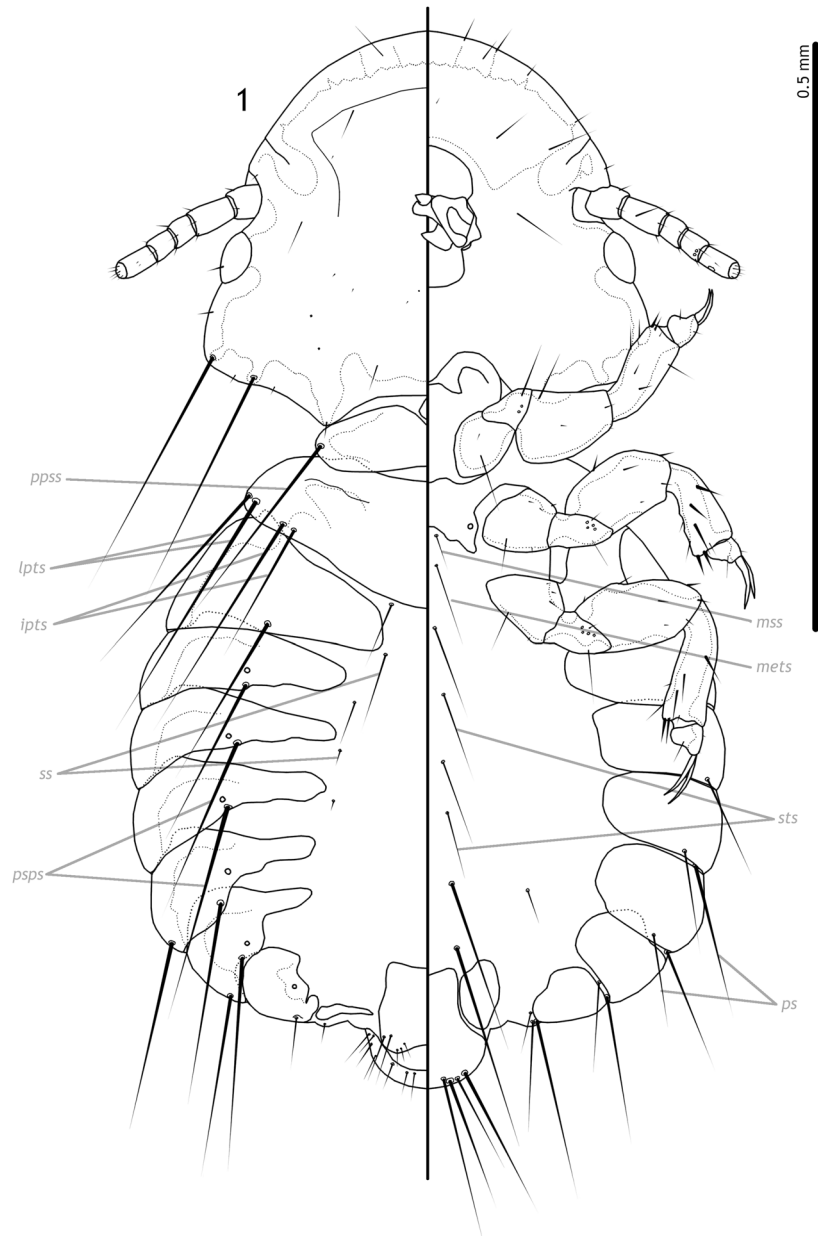


Fig. 1. *Goniocotes caoi* sp. nov., holotype, ♂ (BMNH, slide 57, box E0026203). Habitus, dorsal and ventral views. Abbreviations: *ipts* = intermediate pteronotal seta; *lpts* = lateral pteronotal seta; *mets* = metathoracic seta; *mss* = mesothoracic seta; *ppss* = pronotal post-spiracular seta; *ps* = paratergal seta; *psps* = principal post-spiracular seta; *ss* = sutural seta; *sts* = sternal seta.

lateral and anterior more densely sclerotized area; in at least some females this line is also visible in the post-antennal head (Fig. 2). Preantennal nodi elongated, rounded in male, more square-shaped in female. Male *os* microsetae, may be slightly thorn-like. Lateral temporal margins rounded, divergent posteriorly. Occipital bulge present, not very prominent; *mts* situated apically. Occipital nodi prominent.

Thoracic and abdominal segments and chaetotaxy as in Figs 1–2. Rhombic sclerite not fused to pronotum. Pronotum with rounded to slightly extended postero-lateral corners. Proepimera fused medianly. Postero-lateral corner of pteronotum not extended laterally; posterior margin gently rounded; *smns* absent. Male tergopleurites much reduced on more posterior segments; tergopleurite VIII with no visible median extension; lateral tergopleurite IX+X small, slender, not reaching median sclerite.

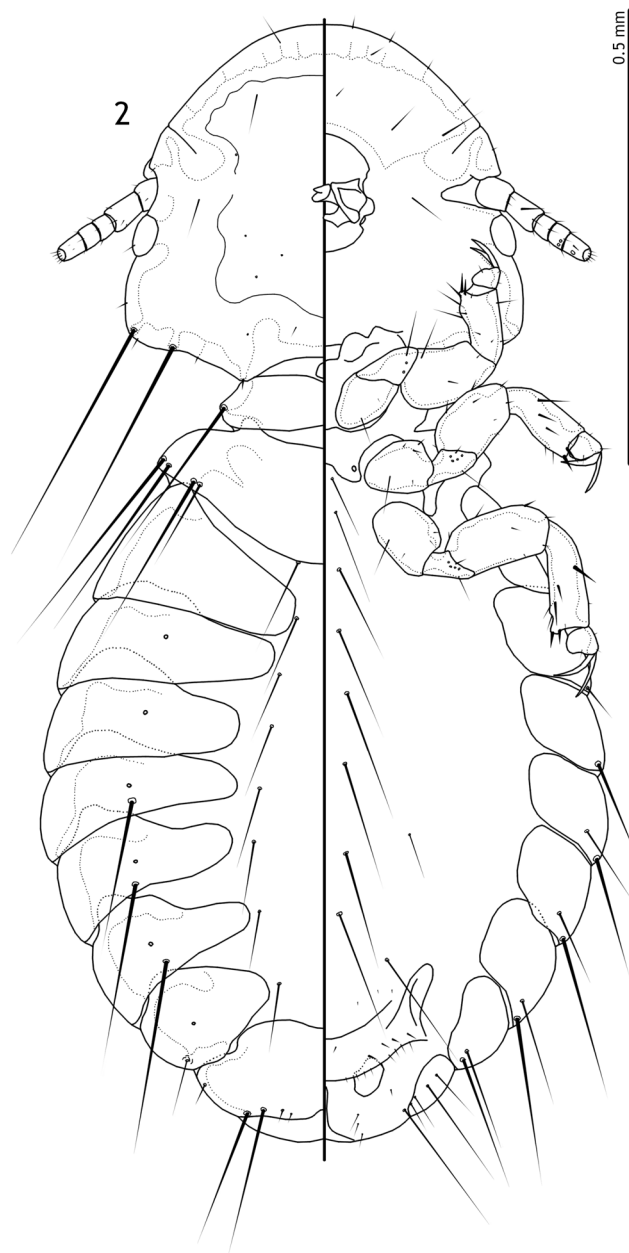
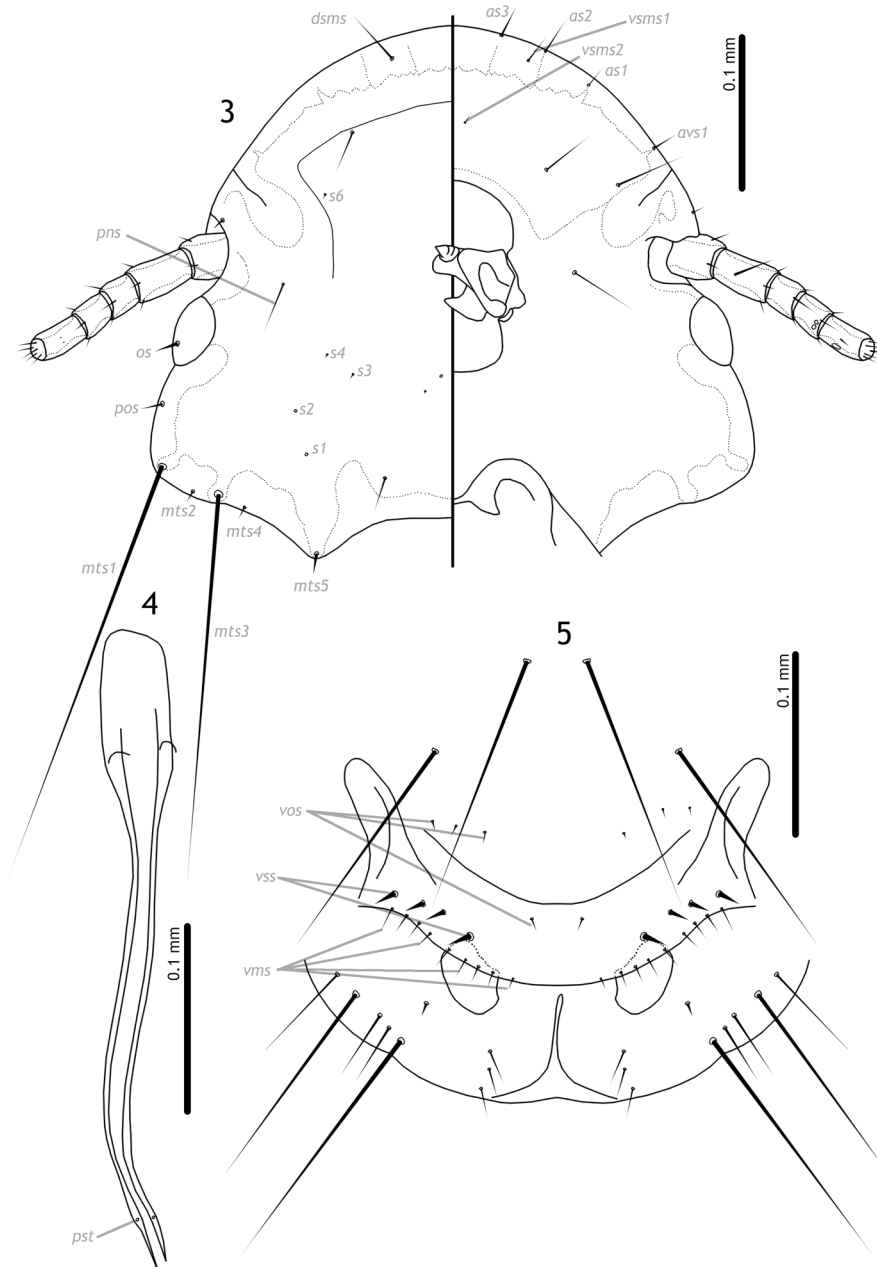


Fig. 2. *Goniocotes caoi* sp. nov. Female habitus, dorsal and ventral views.

Lateral accessory sternal plates absent. Male abdominal chaetotaxy: *ss* present on tergopleurites II–V; *tps* and *aps* absent; *psps* present on tergopleurites II–VII; *ps* present on abdominal segments IV–VIII. Female abdominal chaetotaxy: *ss* present on tergopleurites II–VIII; *tps* and *aps* absent; *psps* present on tergopleurites V–VI; *ps* present on abdominal segments III–VIII.



Figs 3–5. *Goniocotes caoi* sp. nov. **3–4.** Holotype, ♂ (BMNH, slide 57, box E0026203). **3.** Head, dorsal and ventral views. **4.** Genitalia, dorsal view. **5.** Female genitalia, ventral view. Abbreviations: *as1–3* = anterior setae 1–3; *avs1* = anterior ventral seta 1; *dsms* = dorsal submarginal seta; *mts1–5* = marginal temporal setae 1–5; *os* = ocular seta; *pns* = postnodal seta; *pos* = preocular seta; *pst* = parameral seta; *s1–6* = sensilla of dorsal head 1–6; *vms* = vulval marginal seta; *vos* = vulval oblique seta; *vsms1–2* = ventral submarginal setae 1–2; *vss* = vulval submarginal seta.

Male genitalia as in Fig. 4; solenoid, with no clear distal margin; *pst* visible as sensilla and parameres widening at site of *pst*.

Female genitalia as in Fig. 5; subgenital plate absent, but section of ventral surface nearest vulval margin marginally more densely sclerotized than other parts (symbolized by a curved line in Fig. 5). Vulval margin somewhat flattened medianly, with 8–10 short, slender *vms* and 3–5 longer, thorn-like *vss* on each side; 2–4 short, slender *vos* on each side, the distalmost of which is near *vss*. Subvulval plates present, roughly oval.

Measurements as in Table 1.

***Goniocotes cacumentalis* sp. nov.**

[urn:lsid:zoobank.org:act:8669F58C-2D3B-4DC6-A9E1-B27B9CDCA28D](https://zoobank.org/act:8669F58C-2D3B-4DC6-A9E1-B27B9CDCA28D)

Figs 6–10

Diagnosis

The following combination of characters makes *G. cacumentalis* sp. nov. unique among all known species of *Goniocotes*: marginal carina very narrow (Fig. 8); *os* macroseta in both male and female (Figs 6–7); male tergopleurites II–III with 3–4 *tps* mesosetae on each side (Fig. 6); female tergopleurites II–IV with *psps* macrosetae (Fig. 7); *smns* present (Figs 6–7); female with > 20 *vms* microsetae on each side of vulval margin (Fig. 10); *mts4–5* both situated on occipital bulge (Fig. 8; this is more clear in the male where the bulge is more prominent).

Two of these characters are especially important, and are to our knowledge unique within *Goniocotes*: the female *os* being macrosetae, and the *mts4* being situated on the occipital bulge, and much closer to *mts5* than to *mts3*. In all other species of the genus we have examined (either as specimens or from illustrations and drawings), female *os* are microsetae. As such, *G. cacumentalis* sp. nov. may have some of the best characters to separate females of all known species in *Goniocotes*.

The placement of *mts4* close to *mts3* on a relatively flat part of the posterior head margin, and *mts5* apically on the occipital bulge is constant throughout most of the Gonioididae, including all other *Goniocotes*. However, in the *Goniodes* from peacocks (*Pavo* Linnaeus, 1758), both *mts4–5* are on the occipital bulge, and Kéler (1940) illustrated the female of *G. gregarius* with *mts5* on the median margin of the occipital bulge, not apically. This character is thus variable within the family, and requires further study.

The presence of *psps* on female tergopleurites II–V is also rare in *Goniocotes*, and otherwise only known from *G. diplogonus*, *G. kristinae*, and *G. sarissa* sp. nov. There are no other characters that suggest any close relationship between *G. cacumentalis* sp. nov. and these species.

Etymology

The specific epithet is constructed from ‘*cacumen*’, Latin for ‘peak’ or ‘summit’. This refers to the high altitudinal range of the host and its louse, which extends to almost 6000 m (Madge & McGowan 2002), the highest by far of all known *Goniocotes*. To this is arbitrarily added the ending ‘*-talis*’.

Type material

Holotype (ex *Tetraogallus tibetanus*)

CHINA • ♂; Tibet; 1877; collector unknown; Brit. Mus. 1974-240, NHMUK010676049; NHML [male closest to the female on the slide, marked with a black dot].

Paratypes (ex *Tetraogallus tibetanus*)

CHINA • 1 ♂, 1 ♀; same data as for holotype; NHML.

(ex *Tetraogallus tibetanus aquilonifer*)

INDIA • 1 ♂, 10 ♀♀; Sikkim; date unknown; R. Meinertzhagen leg.; 13400, NHMUK010676048; NHML • 2 ♀♀; Ladakh; Jun. 1925; R. Meinertzhagen leg.; 248, NHMUK010676047; NHML.

Type host

Tetraogallus tibetanus Gould, 1854 – Tibetan snowcock.

Type locality

Tibet, China.

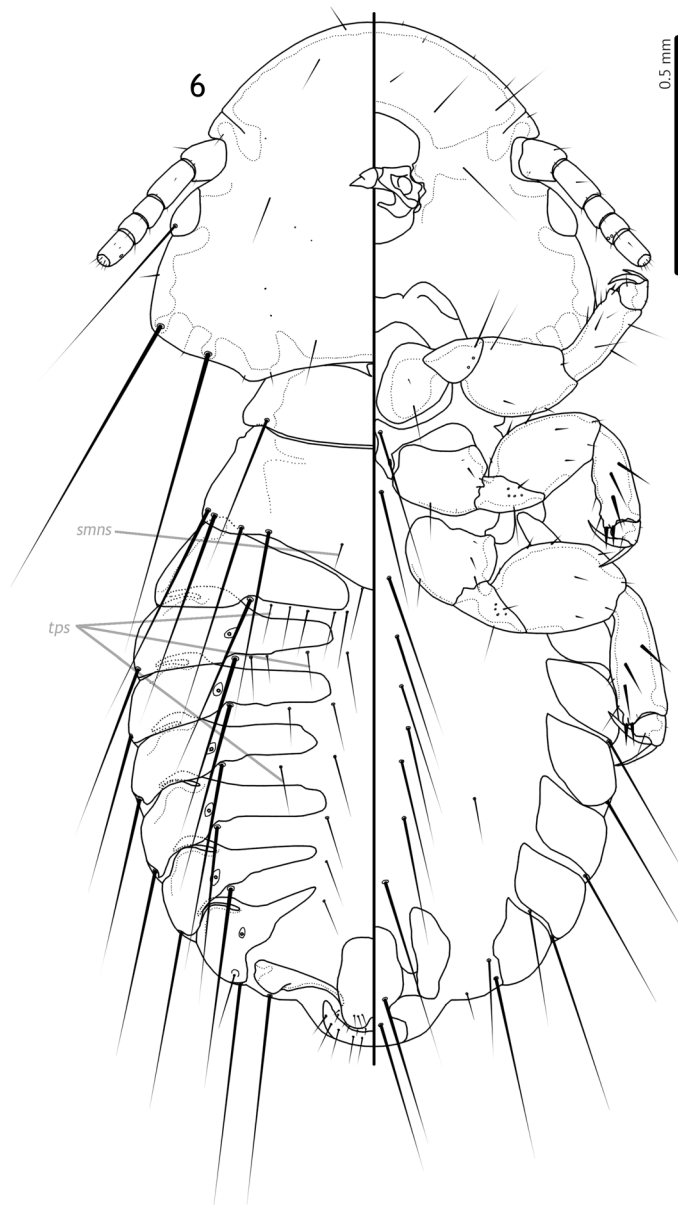


Fig. 6. *Goniocotes cacumentalis* sp. nov. Male habitus, dorsal and ventral views. Abbreviations: *smns* = submarginal mesometanotal seta; *tps* = tergal posterior seta.

Other host

Tetraogallus tibetanus aquilonifer Meinertzhagen & Meinertzhagen, 1926.

Description

Frons broadly rounded (Fig. 8). Marginal carina very narrow, attendant canals not clear. No internal line. Preantennal nodi narrowed basally and expanded medianly, but shape differs among specimens. Male *os* macrosetae; *mts*4–5 both situated on occipital bulge, which is slight. Lateral temporal margins convex, divergent. Occipital nodi slender.

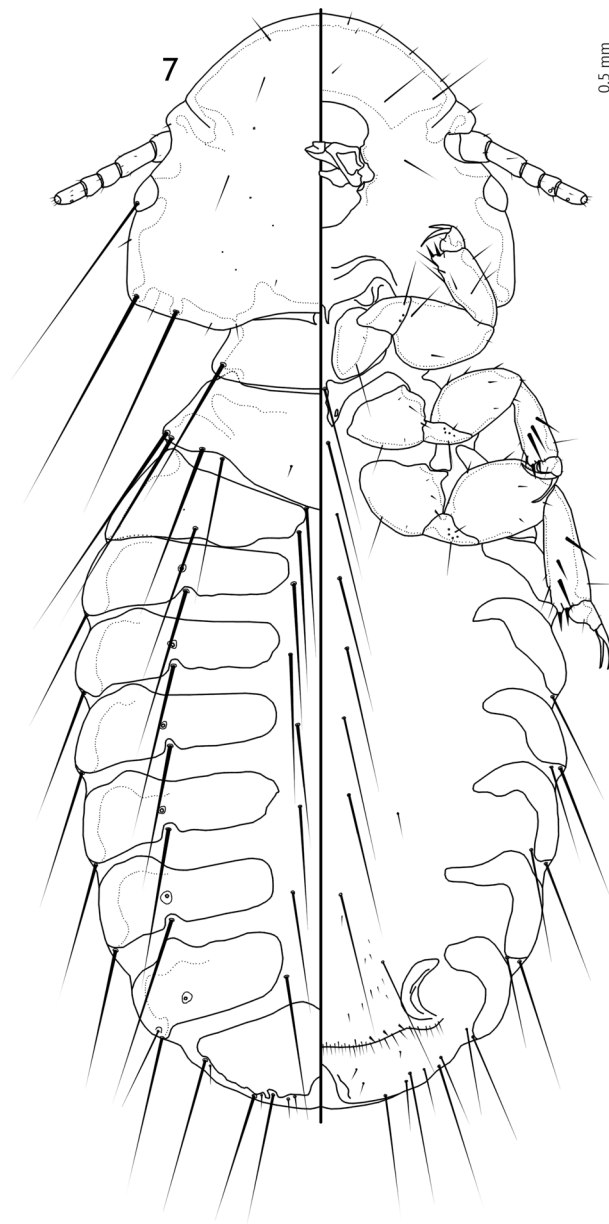
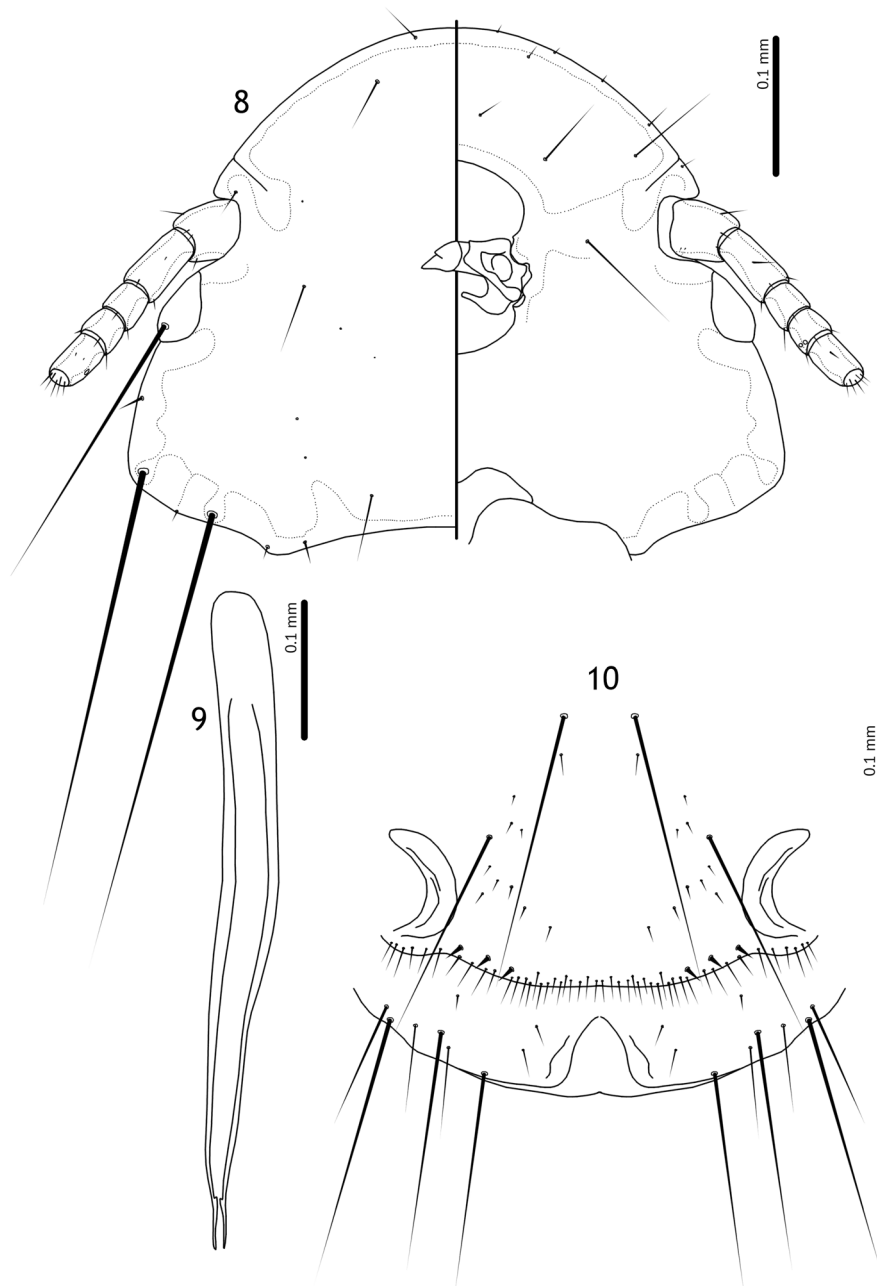


Fig. 7. *Goniocotes cacumentalis* sp. nov., ♀ (NHML, slide NHMUK010676049). Habitus, dorsal and ventral views.

Thoracic and abdominal segments and chaetotaxy as in Figs 6–7. Rhombic sclerite fused to pronotum. Pronotum with rounded postero-lateral corners. Proepimera not fused medianly. Postero-lateral corner of pteronotum not extended laterally; posterior margin gently rounded; single *smns* present. Male tergopleurites reduced on more posterior segments, but tergopleurites II–VIII are extended medianly to reach near site of *ss*; lateral tergopleurite IX+X slender, curved, reaching median sclerite IX+X, with which it may overlap slightly. Lateral accessory sternal plates absent. Male abdominal chaetotaxy: *ss* present on tergopleurites II–VIII; *tps* present on tergopleurites II–V, numbers decreasing on more posterior segments; *psps* present on tergopleurites II–VII; *aps* absent; *ps* present on segments III–VIII.



Figs 8–10. *Goniocotes cacumentalis* sp. nov. **8–9.** Holotype, ♂ (NHML, slide NHMUK010676049). **8.** Head, dorsal and ventral views. **9.** Genitalia, dorsal view. **10.** Paratype, ♂ (NHML, slide NHMUK010676049). Genitalia, ventral view.

Female abdominal chaetotaxy: *ss* present on tergopleurites II–VIII; *tps* and *aps* absent; *psps* present on tergopleurites II–VII; *ps* present on segments III–VIII.

Male genitalia as in Fig. 9; solenoid, with no clear distal margin; *pst* not visible.

Female genitalia as in Fig. 10; subgenital plate absent. Vulval margin flattened medianly, with 21–28 short, slender *vms* and 3–4 longer, thorn-like *vss* on each side; 5–7 (one specimen with 1–0) short, slender *vos* on each side. Subvulval plates absent.

Measurements as in Table 1.

Remarks

Goniocotes cacumentalis sp. nov. is the first species in the genus to be described from a truly high-elevation host, which typically is found at an altitude of 5000–6000 meters (Madge & McGowan 2002). Almost all other known species of *Goniocotes* parasitizing hosts that occur at altitudes >4000 m (Table 3) are here transferred to the genus *Dictyocotes*. This suggests that species of *Goniocotes* s. lat. may be found in many more host species, including those of boreal and alpine environments, and that the lack of records from such hosts may be more an effect of the difficulty of sampling than an actual absence.

Goniocotes sarissa sp. nov.

[urn:lsid:zoobank.org:act:CFD6B564-DC4E-44FA-B2D1-3586CCCA76E6](https://doi.org/10.21203/rs.3.rs-4171111/v1)

Figs 11–15

Diagnosis

Goniocotes sarissa sp. nov. is most similar to *Goniocotes kristinae*, with which it shares the following characters: most sclerotized plates densely reticulated (Figs 11–12); male *os* macrosetae, but female *os* microsetae (Figs 11–12); male pteronotum with patch of multiple *smns* centrally (Fig. 11); male tergopleurites II–IV with *tps* (Fig. 11); *ss* absent on male tergopleurites VI–VIII (Fig. 11); female tergopleurites II–IV with *psps* (Fig. 12); female but not male with reticulated lateral accessory sternal plates on abdominal segments II–VI (Fig. 12).

Goniocotes sarissa sp. nov. can be separated from *G. kristinae* by the following characters: male tergopleurites II–III with more numerous *tps* in *G. sarissa* (Fig. 11) than in *G. kristinae*; male tergopleurites VI with *ss* in *G. sarissa* (Fig. 11), but without *ss* in *G. kristinae*; proepimera fused medianly in *G. sarissa* (Figs 11–12), but medianly separated in *G. kristinae*; temples more flaring posteriorly in *G. sarissa* (Figs 11–12) than in *G. kristinae*; rhombic sclerite separate from pronotum in *G. sarissa* (Figs 11–12), but fused to pronotum in *G. kristinae*.

Reticulated lateral accessory sternal plates are also known in *Goniocotes albidus*, where they are found in both male and female. However, in *G. albidus* the plates are small and rounded or oval, whereas in *G. sarissa* sp. nov. they are elongated. Moreover, *G. albidus* has a rounded, not flaring, temporal corner, males have dense rows of *tps* on all of tergopleurites II–VI and only a single *smns* on each side, and females lack *psps* on tergopleurites II–III.

Goniocotes diplogonus is probably also closely related to *G. sarissa* sp. nov. and *G. rolandi*, and share the reticulated lateral accessory sternal plates. No specimens of this species were examined. Kéler (1940: fig. 88) illustrated the male and female, but noted that his male was morphologically aberrant. Based on Kéler's illustrations, *G. sarissa* can be separated from *G. diplogonus* by the following characters: temples more flaring and frons more flattened in *G. sarissa* (Fig. 13) than in *G. diplogonus* (but temples drawn differently on each side of the head of the male by Kéler 1940); male pteronotum with patch of *smns* in *G. sarissa* (Fig. 11), but this is apparently lacking in *G. diplogonus*; male tergopleurites V–VI

with *ss* in *G. sarissa* (Fig. 11), but these apparently lacking in *G. diplogonus*; *tps* present on male tergopleurite IV in *G. sarissa* (Fig. 11), but apparently absent in *G. diplogonus*. However, *G. diplogonus* needs to be redescribed to confirm these characters.

Etymology

The specific name is derived from ‘*sárisa*’, Greek for the long pikes used in traditional phalanx formations. This refers to the patch of *smns* on the male pteronotum combined with the rows of *tps* on male tergopleurites II–IV, which are reminiscent of a loose, small phalanx.



Fig. 11. *Goniocotes sarissa* sp. nov., holotype, ♂ (BMNH, slide 95, box E0026011). Habitus, dorsal and ventral views.

Type material

Holotype (ex *Tragopan caboti*)

CHINA • ♂; Fujian Province; 30 Oct. 1990; collector unknown; box E0026011, slide 95; BMNH [second male from right in top row, marked with black dot on slide].

Paratypes (ex *Tragopan caboti*)

CHINA • 17 ♂♂, 21 ♀♀; same data as for holotype; BMNH • 5 ♂♂, 4 ♀♀; Fujian Province; 29 Sep. 1990; collector unknown; box E0026136, slides 24–25; BMNH • 2 ♂♂, 2 ♀♀; Fujian Province, Jianou; 7 Jan. 1997; collector unknown; box E0026195, slide 4; BMNH • 5 ♂♂, 7 ♀♀; Guangxi Province; 10 Jan. 1995; collector unknown; box E0026136, slides 20–22; BMNH.

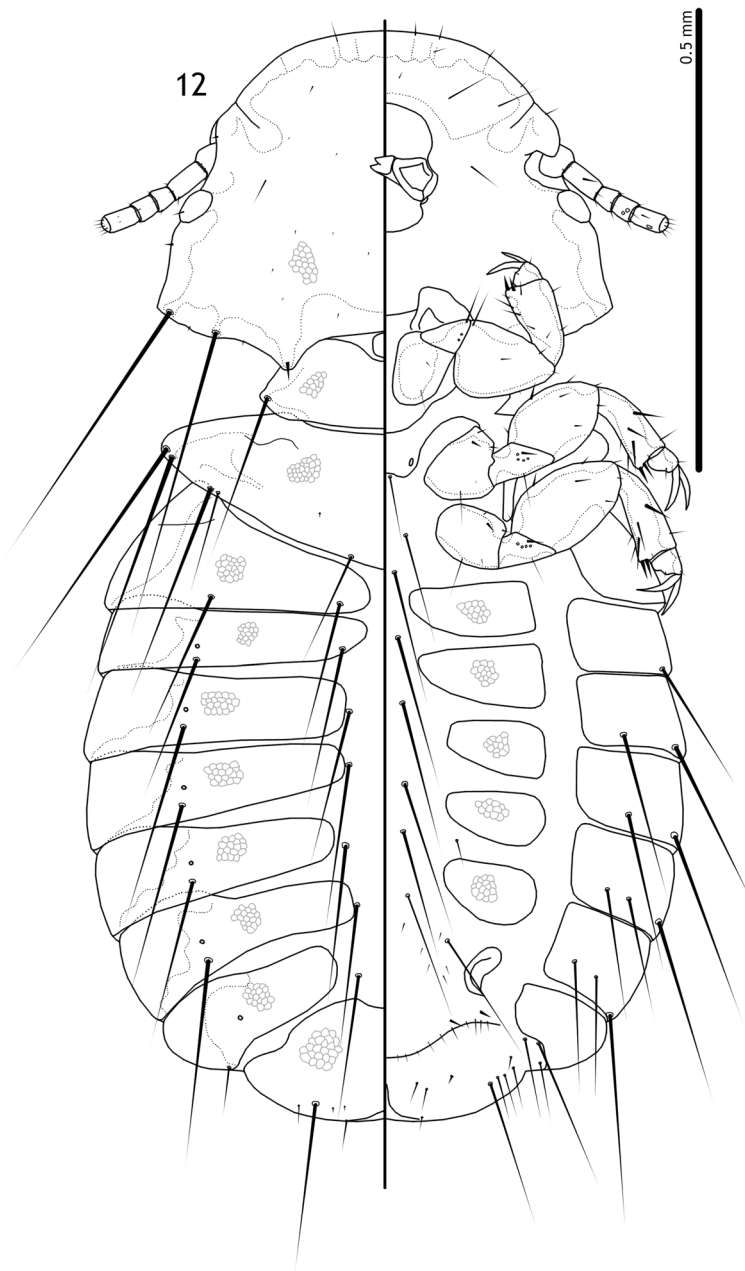


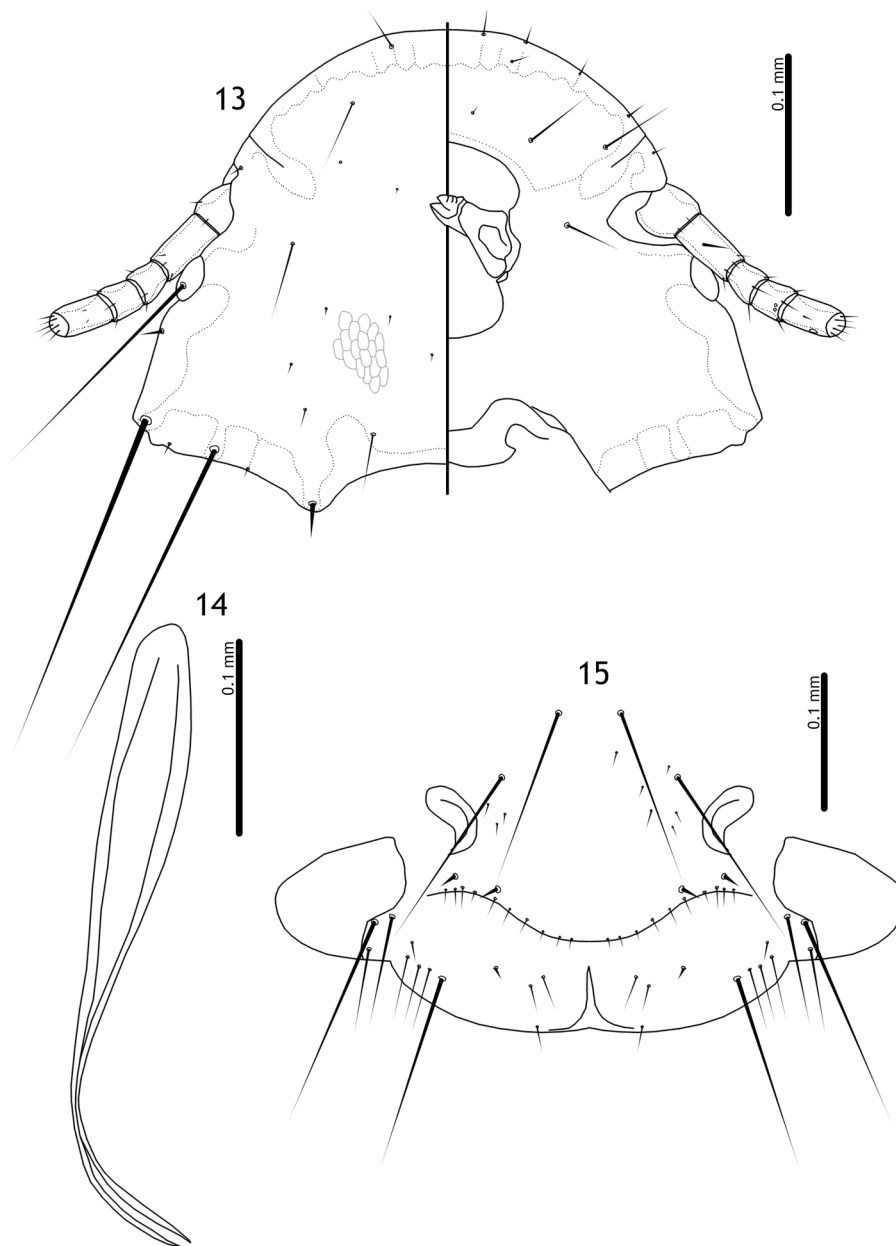
Fig. 12. *Goniocotes sarissa* sp. nov. Female habitus, dorsal and ventral views.

Type host

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

Type locality

Fujian Province, China; no more detailed locality given on slides.



Figs 13–15. *Goniocotes sarissa* sp. nov. **13–14.** Holotype, ♂ (BMNH, slide 95, box E0026011). **13.** Head, dorsal and ventral views. **14.** Genitalia, dorsal view. **15.** Female genitalia, ventral view.

Description

Frons slightly flattened (Fig. 13). Marginal carina broad, with clear attendant canals of preantennal setae. No internal line present. Preantennal nodi elongated, narrowed at base, broader in female than in male. Male *os* macrosetae, female *os* microsetae. Lateral temporal margins slightly concave, divergent posteriorly. Occipital bulge present, prominent; *mts5* situated apically. Occipital nodi large.

Thoracic and abdominal segments and chaetotaxy as in Figs 11–12. Rhombic sclerite not fused to pronotum. Postero-lateral corners of pronotum slightly extended laterally. Proepimera fused medianly. Postero-lateral corner of pteronotum not extended laterally; posterior margin gently rounded; *smns* as patch of 4–5 setae on each side in male, but as single seta on each side in female. Male tergopleurites extensive on segments II–VI, but much reduced on segments VII–VIII, with that of segments VIII lacking median extension; lateral tergopleurite IX+X small, arched, not reaching median sclerite IX+X. Lateral accessory sternal plates present in female, as large reticulated plates on segments II–VI. Male abdominal chaetotaxy: *ss* present on tergopleurites II–VI; *tps* present on tergopleurites II–IV; *psps* present on tergopleurites II–VII; *aps* absent; *ps* present on segments III–VIII. Female abdominal chaetotaxy: *ss* present on tergopleurites II–VIII; *tps* and *aps* absent; *psps* present on tergopleurites II–VII; *ps* present on segments III–VIII.

Male genitalia as in Fig. 14; solenoid, with no clear distal margin; *pst* not visible.

Female genitalia as in Fig. 15; subgenital plate absent. Vulval margin somewhat flattened medianly, with 8–11 short, slender *vms* and 3 longer, thorn-like *vss* on each side; 3–6 short, slender *vos* on each side. Subvulval plates absent.

Measurements as in Table 1.

Remarks

A single female of a second, larger species of *Goniocotes* has also been seen from the same host (box E0026011, slide 95 at BMNH). More specimens are needed to identify this species, and verify that it occurs on *T. caboti*.

Genus *Dictyocotes* Kéler, 1940

Goniocotes Burmeister, 1838: 431 [in partim].

Dictyocotes Kéler, 1940: 153.

Type species

Goniocotes haplogonus Nitzsch in Giebel, 1866: 390, by original designation.

Diagnosis

Dictyocotes can be separated from *Goniocotes* s. lat. by the following combination of characters: male mesosome present in *Dictyocotes* (Fig. 19), but absent in *Goniocotes* (e.g., Fig. 4); male parameres fused to basal apodeme in *Goniocotes* (e.g., Fig. 4), but separate from, and possibly articulating with, basal apodeme in *Dictyocotes* (Fig. 19); female vulval margin notched medianly in *Dictyocotes* (Fig. 20; not in *D. rolandi*), but rounded or flattened in *Goniocotes* (e.g., Fig. 5); male lateral tergopleurite IX+X slender and small in *Goniocotes* s. str. (Fig. 1), but larger, triangular or irregular in shape in *Dictyocotes* (Fig. 16).

For other characters that separate *Dictyocotes* from *Goniocotes* s. str., but which are variable within *Goniocotes* s. lat., see above.

Description

Very small lice of the body louse ecomorph (sensu Johnson *et al.* 2012). Head shape roughly semicircular or semioval, but may be flattened at frons, temples divergent posteriorly, typically somewhat angular at site of *mts1*, and with a slight to pronounced occipital bulge at site of *mts5*. Marginal and ventral carinae uninterrupted; marginal carina moderately wide, may have clear attendant canals connecting to apertures of many setae (e.g., *dsms*, *as1–3*, *avs1*). Dorsal preantennal suture absent. Preantennal nodi variable, in most species elongated. Antennae sexually monomorphic. Eyes often proportionately large. Marginal temporal carina typically broad, with undulating median margin and a distinct occipital nodus originating marginally median to *mts5* on each side. Head chaetotaxy: all usual head setae present; *as1–3* and *avs1* marginal or submarginal; *vsms1–2* much separated; *pns* micro- to mesoseta; *s1–6* typically all present as microsetae or in some species as sensilla, and additional sensilla are present in some species; *os* macrosetae in males, mesosetae in females; *pos* positioned far posterior to eye; *mts1* and *mts3* macrosetae, *mts5* may be thorn-like, *mts2* and *mts4* microsetae. Dorsal head densely reticulated.

Prothorax wider than long, with *ppss* macroseta on postero-lateral corner, which may be extended laterally at site of *ppss*. Pterothorax variable, but typically pentagonal, may be extended laterally which gives a slightly ‘winged’ appearance; 2 *lpts* macrosetae on postero-lateral corners, separated by clear gap from 2 *ipts* macrosetae; single *smns* meso- or macroseta present submarginally; *mpts* present or absent. Proepimera extensive, not fused medianly. Meso- and metasterna absent, but *mss* and *met5* present. Legs short and stout, most notably with three stout ventral setae on tibiae II–III (likely *tbII-v3–5* and *tbIII-v3–5*, but homology uncertain). Other leg chaetotaxy variable, and many setae very short.; typically: *tbI-a1*, *cII-a1*, *tbII-a1*, *tbII-p1–2*, *tbII-p4–5*, *tbII-v3*, *cIII-a1*, *tbIII-a1*, *tbIII-p1–2*, *tbIII-p4–5*, *tbIII-v3* very short or absent; *fII-v2*, *fII-p1*, *fIII-v2*, *fIII-p1* absent. Most sclerotized plates densely reticulated.

Abdomen rounded, more elongated in female. Tergopleurites II–IX+X divided medianly, typically with posterior tergopleurites more reduced compared to anterior tergopleurites in male. Male abdominal segment IX+X with lateral sclerite on each side and central sclerite anterior to dorsal ano-genital opening; lateral tergopleurite large, roughly rectangular or triangular, but generally irregular. Postero-laterally, tergopleurites may be extended to produce small posterior points, particularly in males and often more prominent in posterior segments; postero-lateral corner of tergopleurite VIII may be bifurcated. Paratergal plates prominent. Sternal plates absent in both sexes. Male subgenital plate variable, may be divided submedianly; female subgenital plate absent. Subvulval plates absent. Abdominal chaetotaxy variable among species; anterior seta of tergopleurite II present; rows of *tps* present on at least tergopleurites II–III in male, and single *tps* (homology uncertain) may be present on female tergopleurites III–VII just median to *psps*; *psps* present on tergopleurites II–VII in both sexes, typically markedly larger than other setae, but may be similar to *tps* on tergopleurite II. Ventral side with 2–4 *sts* on each side of segments II–VI, and 2 *sts* on each side on segments VI. Macrosetae present on ventral side of abdominal segments VII–VIII in both sexes. Most sclerotized plates densely reticulated.

Male genitalia with long, slender basal apodeme (anterior end may reach abdominal segment II), which may have central arched thickening in distal third; postero-lateral corners of basal apodeme may have rugose distal extensions. Mesosome present, reduced are seemingly fused to basal apodeme. Dorsally, mesosome typically as small, transverse gonopore bearing 1–2 visible sensilla on each side (number may be 4 in all species, but difficult to see). Distal to gonopore is typically an elongated thickening on each side, converging towards distal margin of mesosome. Ventral structures of mesosome typically unclear, but may include a single central sclerite or paired lateral sclerites. Parameres not fused to basal apodeme, and may be articulating with postero-lateral corners of apodeme; *pst1–2* not visible in any examined species.

Table 3. Approximate altitudinal range of the known lice in *Goniocotes* Burmeister, 1838 s. lat. and *Dictyocotes* Kéler, 1940, based on known altitudinal ranges of their hosts. Altitude range of hosts primarily derived from Madge & McGowan (2002), with altitudes given as exceptional not included. Species for which no clear altitudes were given by Madge & McGowan (2002) are not included. Altitudes are given in ranges. For domesticated hosts, only the ranges of their wild populations are given. Note that as altitude data or detailed collection data is normally not given in older louse descriptions and for many of the slide-mounted specimens we have examined, it is possible that lice only occur within parts of the host ranges given here, but more data is needed to establish whether this is the case. For louse species that occur on multiple host species, the total altitudinal range of all hosts is given.

Lice	0–1000 m	1000–2000 m	2000–3000 m	3000–4000 m	4000–5000 m	5000–6000 m
<i>Goniocotes pucherani</i>	X					
<i>Goniocotes afropavo</i> , <i>G. caoi</i> sp. nov., <i>G. chapini</i> , <i>G. gallinae</i> , <i>G. ictiorhynchi</i> , <i>G. ignitus</i> , <i>G. rectangularis</i> , <i>G. sarissa</i> sp. nov.	X	X				
<i>Goniocotes albidus</i> , <i>G. creber</i> , <i>G. gallinae</i> , <i>G. jifrufti</i> , <i>G. kristinae</i> , <i>G. obscurus</i> , <i>G. pternistis</i> , <i>G. rotundiceps</i>	X	X	X			
<i>Goniocotes congolensis</i> , <i>G. eurygaster</i> , <i>G. maculatus</i> , <i>G. microcephalus</i> , <i>G. reticulatus</i> , <i>G. shelleyi</i>	X	X	X	X		
<i>Goniocotes microthorax</i> , <i>G. pallidomaculatus</i> , <i>G. pusillus</i>	X	X	X	X	X	
<i>Goniocotes kiviensis</i>		X	X	X		
<i>Goniocotes diplogonus</i>		X	X	X	X	
<i>Goniocotes schraederi</i>			X	X		
<i>Dictyocotes haplogonus</i>			X	X	X	
<i>Dictyocotes furcatus</i> sp. nov., <i>D. rolandi</i> , <i>D. tetraophasis</i>			X	X	X	
<i>Dictyocotes crossoptiloni</i>				X	X	X
<i>Goniocotes cacumentalis</i> sp. nov.						X

Female vulval margin strongly convex medianly, but notched or concave at midline, with numerous (>15, often much more than 20) long, slender *vms* and 2–5 short, thorn-like *vss* on each side; *vos* microsetae variable in number and position, typically not approaching vulval margin, but may form roughly convergent rows.

Host and geographical distribution

All known species parasitize mid-to-high-altitude hosts in East Asia (Table 3), occurring on hosts in the genera *Lophophorus* Temminck, 1813, *Tetraophasis* Elliot, 1871, and *Crossoptilon* Hodgson, 1838.

Included species

Dictyocotes crossoptiloni (Liu, 1990: 120) [in *Goniocotes*] comb. nov.

Dictyocotes furcatus sp. nov.

Dictyocotes haplogonus (Nitzsch in Giebel, 1866: 390) [in *Goniocotes*].

Dictyocotes rolandi (Gustafsson, Tian & Zou, 2021: 310) [in *Goniocotes*] comb. nov.

Dictyocotes tetraophasis (Liu, 1990: 119) [in *Goniocotes*] comb. nov.

Remarks

Four of the five known species of *Dictyocotes* appear to fall into two distinct groups, with species from *Crossoptilon* spp. having rounded postero-lateral corners of tergopleurite VIII in both sexes, no *tps* just median to the *psps* on female tergopleurites II–VII, and rugose postero-lateral extensions to the basal apodeme, and species from *Lophophorus* spp. having extended and bifurcated (at least in male) postero-lateral corners of tergopleurite VIII, *tps* present on female tergopleurites II–VII, and no rugose postero-lateral extensions to the basal apodeme. However, in the single known species from *Tetraophasis* spp. the postero-lateral corner of tergopleurite VIII is as in the *Crossoptilon*-infesting group, whereas the female abdominal chaetotaxy and basal apodeme are as in the *Lophophorus*-infesting group.

As more species of *Dictyocotes* become known, it may be possible to divide the species into 2–3 species groups, but due to the intermediary morphology of *D. tetraophasis* we do not here consider these characters to have even informal taxonomic value.

Dictyocotes furcatus sp. nov.

[urn:lsid:zoobank.org:act:A69C962E-67B2-4865-A0F6-426AC84AAF66](https://zoobank.org/urn:lsid:zoobank.org:act:A69C962E-67B2-4865-A0F6-426AC84AAF66)

Figs 16–20

Diagnosis

Dictyocotes furcatus sp. nov. is most similar to *Dictyocotes haplogonus*, with which it shares the bifurcated and elongated postero-lateral corner of male tergopleurite VIII (Fig. 16). The *tps* just median to the *psps* on female tergopleurites II–VII is also found in *D. haplogonus* and *D. tetraophasis*, but the latter lacks the poster-lateral extensions of tergopleurites VII–VIII (male) and VI–VIII (female).

Dictyocotes furcatus sp. nov. can be separated from *D. haplogonus* by the following characters (see Kéler 1940 for illustrations of *D. haplogonus*): male tergopleurite VI with only one *tps* on each side in *D. furcatus* (Fig. 16), but with multiple *tps* on each side in *D. haplogonus*; male tergopleurite VIII with 1 *tps* on each side in *D. furcatus* (Fig. 16), but without *tps* in *D. haplogonus*; male tergopleurite VIII extended further medianly in *D. furcatus* (Fig. 16) than in *D. haplogonus*; head proportionately broader in *D. furcatus* (Fig. 18) than in *D. haplogonus*; female *os* reaches approximately to site of *pos* in *D. furcatus* (Fig. 17), but approximately to posterior end of head in *D. haplogonus*; postero-lateral corner of female tergopleurite VIII bifurcated in *D. furcatus* (Fig. 17), but not bifurcated in *D. haplogonus*; female tergopleurite IX+X differently shaped in the two species, with that of *D. furcatus* (Fig. 17) having a clear notch submedianly, which is absent in *D. haplogonus*.

Etymology

The specific name is derived from ‘*furcatus*’, Latin for ‘forked’, referring to the double-pointed postero-lateral corner of tergopleurite VIII in both sexes.

Type material

Holotype (ex *Lophophorus lhuysii*)

CHINA • ♂; Sichuan Province, Baoxing; 29 Jun. 1983; collector unknown; box E0026136, slide 29; BMNH [male with everted genitalia, marked with black dot on slide].

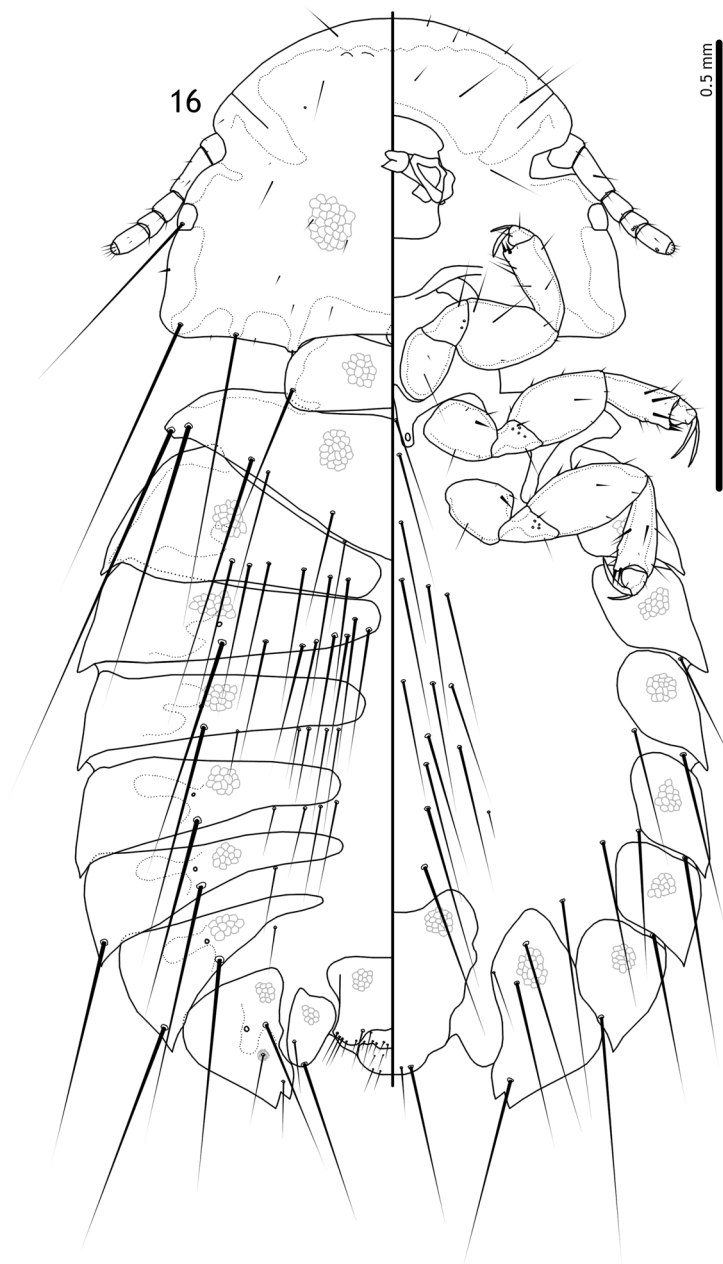


Fig. 16. *Dictyocotes furcatus* sp. nov., holotype, ♂ (BMNH, slide 29, box E0026136). Habitus, dorsal and ventral views.

Paratypes (ex *Lophophorus lhuysii*)

CHINA • 1 ♂, 2 ♀♀; same data as for holotype; BMNH.

Type host

Lophophorus lhuysii Geoffroy Saint-Hilaire, 1866 – Chinese monal.

Type locality

Baoxing, Sichuan Province, China.

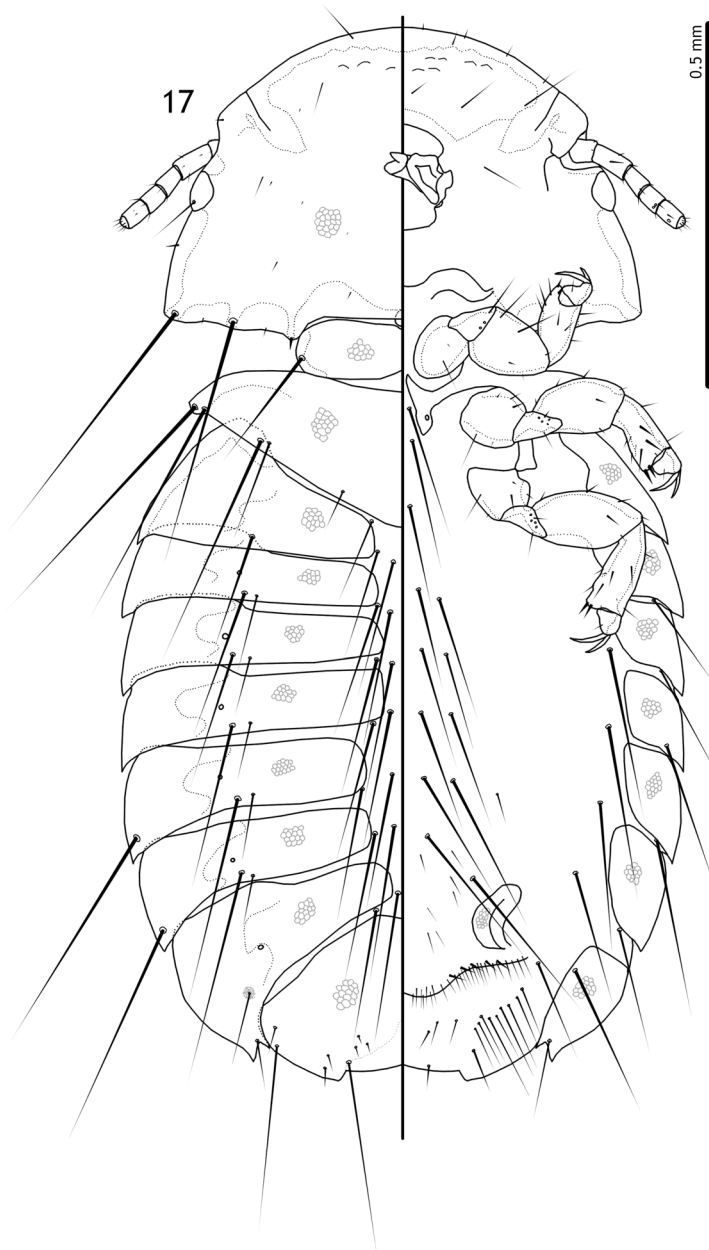
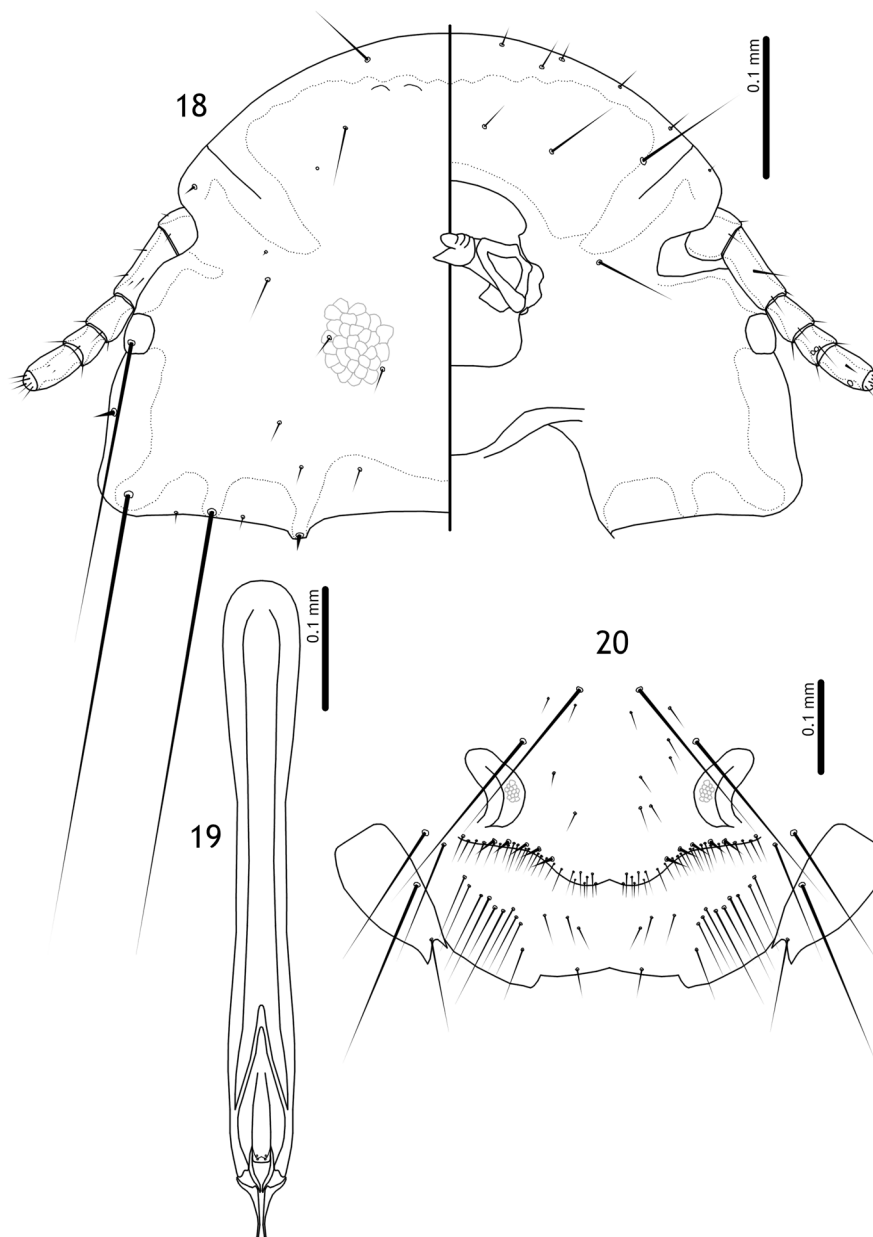


Fig. 17. *Dictyocotes furcatus* sp. nov. Female habitus, dorsal and ventral views.

Description

Frons broadly rounded (Fig. 18). Marginal carina broad, with no prominent attendant canals. No internal line; entire dorsal surface of head densely reticulated. Preantennal nodi elongated, broad. Male *os* macrosetae; female *os* mesosetae. Lateral temporal margins somewhat convex posteriorly, only slightly divergent. Occipital bulge slight, with *mts5* apical. Occipital nod prominent.

Thoracic and abdominal segments and chaetotaxy as in Figs 16–17. Rhombic sclerite not fused to pronotum. Pronotum with rounded postero-lateral corners. Proepimera separate medianly. Postero-lateral corners of pteronotum extended slightly laterally, giving “winged” appearance; posterior margin



Figs 18–20. *Dictyocotes furcatus* sp. nov. **18–19.** Holotype, ♂ (BMNH, slide 29, box E0026136). **18.** Head, dorsal and ventral views. **19.** Genitalia, dorsal view. **20.** Female genitalia, ventral view.

convergent to rounded median section; *smns* present as single seta on each side. Male tergopleurites not reduced much, except tergopleurite VIII which is not extended medianly; lateral tergopleurite IX+X semi-oval, not overlapping with median sclerite IX+X. Lateral accessory sternal plates absent. Male abdominal chaetotaxy: *ss* present on tergopleurites II–V; *tps* present on tergopleurites II–VII; *psps* present on tergopleurites II–VII; *aps* absent; *ps* present on segments III–VIII. Female abdominal chaetotaxy: *ss* present on tergopleurites II–VIII; *tps* present medianly on tergopleurites II–VIII and setae here interpreted as lateral *tps* present just median to *psps* on tergopleurites III–VII; *psps* present on tergopleurites II–VII; *aps* absent; *ps* present on segments III–VIII. All dorsal thoracic and all abdominal plates densely reticulated.

Male genitalia as in Fig. 19. Basal apodeme long, slender, may reach to segment II; arched thickening present in distal third of basal apodeme; postero-lateral rugose extensions not present. Mesosome dorsally as slight, transversal thickening bearing 2 visible sensilla on each side, and distally as curved, distally convergent, submedian thickenings. Parameres somewhat curved, structure typical for genus.

Female genitalia as in Fig. 20; subgenital and subvulval plates absent. Vulval margin bilobed with median notch, with 22–24 short, slender *vms* (median 3–4 in inner rows) and 3–5 short, thorn-like *vss* on each side; 3–7 short, slender *vos* on each side in roughly parallel rows that do not reach level of *vss*.

Measurements as in Table 1.

Remarks

Holotype with one abdominal segment broken, and this has been illustrated based on the tergopleurite of the other side of the body.

Discussion

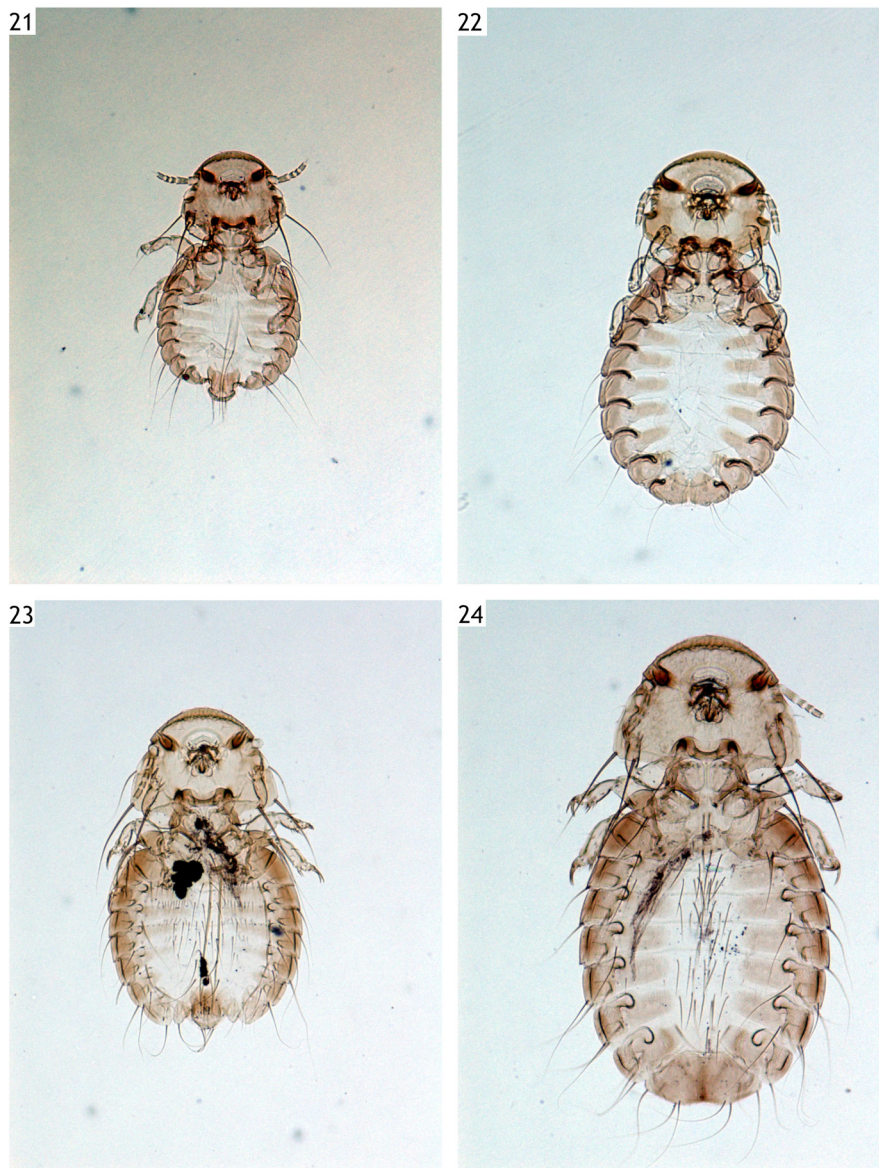
Based primarily on differences in the structure of the male genitalia, we here recognize the genus *Dictyocotes*, as separate from *Goniocotes*. A comparison of the gross morphology of representatives of these genera can be found in Figs 21–24 and Table 2. Separating *Dictyocotes* from *Goniocotes* makes the latter genus morphologically more homogeneous, as almost all species retained in *Goniocotes* here have the same solenoid type of male genitalia without a mesosome. The exceptions are the two species known from *Afropavo congensis* Chapin, 1936, as well as possibly some species from guineafowl. In *G. chapini*, the parameres are not fused to the basal apodeme, whereas in *G. afropavo* there appears to be a central structure between the parameres in the original illustrations (Clay 1938: fig. 15), but the homology of this structure is unclear. Species like *G. pucherani* and *G. crassicauda* also appear to have broader parameres that may be different from the typical male genitalia found in *Goniocotes*, but the original photos of these species (Tendeiro 1989: pl. xxi photo 1, and pl. xxvi photo 2) are unclear. These species are in need of redescription, and likely do not belong in *Goniocotes*.

However, even if the species from *A. congensis* and guineafowl are removed from *Goniocotes*, there is considerable morphological variation within the genus, particularly in the chaetotaxy and the abdominal plates (see above). Even the three species of *Goniocotes* described here are morphologically very different, and may represent three different subgenera or species groups. In the absence of a more thorough revision of the genus, we do not propose any species groups or subgenera here.

Moreover, the division of *Goniocotes* and *Dictyocotes* does not solve the problem of *Goniocotes* being inseparable from *Goniodes* sensu Price *et al.* (2003). This problem was recognized already by Clay (1951), who suggested that the two genera “grade into each other” if sufficient species were examined. As Price *et al.* (2003) synonymized the genera from megapodiid hosts discussed and described by Mey (1997) with *Goniodes*, even a *Goniocotes* in which all species have simple solenoid male genitalia

would be inseparable from *Goniodes* s. lat. Based on our preliminary survey of ~50% of the species in *Goniodes* and *Goniocotes*, the best way forward seems to be to abandon the idea of keeping *Goniodes* and *Goniocotes* sensu Price *et al.* (2003) intact, and divide each genus into smaller, morphologically homogeneous groups, as suggested by Mey (2009).

Johnson *et al.* (2011) published the only large-scale phylogeny of the Gonioididae to date but focused mainly on the genera parasitizing columbiform hosts. Most of the deep divisions within their phylogeny had no statistical support, including the placement of the three specimens of *Goniocotes*. Taking their tree at face value, the three included specimens of *Goniocotes* did not form a monophyletic clade together, with the single specimen from a megapodiid host being distantly related to the other two specimens.



Figs 21–24. Comparison of gross morphology of *Goniocotes* Burmeister, 1838, and *Dictyocotes* Kéler, 1940. **21–22.** *G. gallinae* (De Geer, 1778) (NHML). **21.** Male. **22.** Female. **23–24.** *D. rolandi* (Gustafsson *et al.*, 2021) (NHML). **23.** Male. **24.** Female.

However, this specimen was identified as *Goniocotes (Aurinirmus) talegallae* (Tendeiro, 1983), which was placed in *Goniodes* by Price *et al.* (2003). The other two specimens included were *Goniocotes chrysocephalus*, here retained in *Goniocotes*, and an unidentified species from a francolin; two different species of *Goniocotes* are known from this host species, both of which are here retained in *Goniocotes*. Thus, published genetic data is insufficient to test relationships within *Goniocotes*, and between this genus and *Dictyocotes*.

The hosts of *Goniocotes* as circumscribed here span most of the Phasianidae, but they are rare on megapodiid hosts and are probably absent on cracid and odontophorid hosts (Gustafsson *et al.* 2024). There appear to be no clear patterns in host associations, as *Goniocotes* are known from all three major radiations of the Phasianidae (sensu Kimball *et al.* 2021), including both large- and small-bodied hosts (Price *et al.* 2003), although they are presently not recorded from some of the smallest-bodied hosts. The known hosts also include species living in drier savannah and humid rainforests, and the humidity-dependent patterns seen in some other louse genera thus appears absent in *Goniocotes* (Bush *et al.* 2009; Gustafsson & Zou 2020). However, such patterns may be obscured by the relatively few species known, and a revision of the species here placed in *Goniocotes* is needed. At present, the only tentative pattern in distribution we can find is related to altitude.

Altitude

With the exception of the morphologically aberrant *G. cacumentalis* sp. nov., there appears to be a rough altitudinal division between *Goniocotes* and *Dictyocotes* (Table 3). Known species of *Dictyocotes* are all found on high-altitude hosts, whereas the known species of *Goniocotes* are primarily found on low-altitude hosts. This could partially be an effect of host phylogeny, as the host genera *Lophophorus* and *Tetraophasis*, parasitized by *Dictyocotes*, are closely related (Kimball *et al.* 2021). However, *Dictyocotes* is not known from hosts in the closely related genus *Tragopan* Cuvier, 1829, but is known from the more distantly related genus *Crossoptilon*. Future collections from other high-altitude galliforms (e.g., *Lerwa* Hodgson, 1837, *Ithaginis* Wagler, 1832) are needed to examine this possible altitudinal variation further.

The altitudinal variation of louse communities is poorly known. Gustafsson *et al.* (2022) suggested that the *Resartor*-group within the *Brueelia*-complex may be high-altitude specialists, as many of the species in this group parasitize high-altitude hosts from a variety of families, but are unknown from relatives of these hosts at lower altitudes. Gustafsson *et al.* (2019) suggested that differences in ambient humidity between different altitudes may influence prevalence of lice, and Sychra *et al.* (2024) suggested that perhaps ecological differences in the hosts at different altitudes may also affect prevalence. Much more data is needed from high-altitude birds before any conclusions can be drawn on the effect of altitude on either the prevalence or the community structure of lice. However, it is notable that many high-altitude hosts have markedly different louse species or genera than related birds at lower altitudes (e.g., Mey 2006), although the effects of altitude and host phylogeny may be difficult to disentangle in host groups where high-altitude species are closely related.

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