

**Feather mites of the genus *Pterotrogus* Gaud 1981  
(Analgoidea: Pteronyssidae) from New World woodpeckers  
(Piciformes: Picidae)**

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**Abstract**

A review of the feather mite genus *Pterotrogus* is given, including a new diagnosis of the genus, description of 14 new species, cladistic analysis of the genus and a brief discussion of host associations. New species are described as follows: *Pterotrogus borealis* sp. n. from *Picoides borealis*, *P. colapti* sp. n. from *Colaptes punctigula guttatus*, *P. oconnori* sp. n. from *Dryocopus pileatus*, *P. veniliornis* sp. n. from *Veniliornis cassini* (type host) and *V. kirkii*, *P. leucopogon* sp. n. from *Campephilus leucopogon*, *P. robustus* sp. n. from *C. robustus*, *P. lanceolatus* sp. n. from *C. guayaquilensis*, *P. melanoleuci* sp. n. from *C. melanoleucos*, *P. rubricolli* sp. n., *P. quadratus* sp. n., and *P. sinusoidus* sp. n. from *C. rubricollis*, *P. guatemalensis* sp. n., *P. iron* sp. n., and *P. macrosinusoidus* sp. n. from *C. guatemalensis*. Four morphological species groups (*simplex*, *lanceolatus*, *sinusoidus*, and *iron*) are recognized within the genus.

Maximum parsimony cladistic analysis of phylogenetic relationships between *Pterotrogus* species shows that three derived groups (*iron*, *lanceolatus*, and *sinusoidus*) are monophyletic, while the *simplex* species group is paraphyletic, including species characterised by plesiomorphic features, and forms the core of the genus. Based on relationships between mite species and host associations it is hypothesized that the genus *Pterotrogus* originated on the ancestors of the New World genus-group that now includes *Colaptes*, *Campephilus*, *Dryocopus*, and *Melanerpes*, and in the course of subsequent cospeciation and specialisation has formed three lineages of derived species groups within the genus *Campephilus*.

**Keywords:** Astigmata, Pteronyssidae, *Pterotrogus*, systematics, phylogeny, host associations.

### Introduction

The feather mite family Pteronyssidae (Astigmata: Analgoidea) currently includes about 130 species in 22 genera (FACCINI & ATYEO, 1981; GAUD & ATYEO, 1996; MIRONOV, 2001, 2003). They are mainly associated with Passeriformes and Piciformes, and only a few species are known from Coraciiformes. Mites of this family are typical representatives of the feather mite morphotype adapted to inhabit vanes of large feathers and they are commonly located on the ventral surfaces of flight feathers and the large upper covert feathers of wings.

Pteronyssid mites associated with woodpeckers (Picidae) have been extensively investigated in the Old World, including Eurasia (ČERNÝ & SHUMILO, 1973; MIRONOV, 1989; 2002, 2003) and Africa (GAUD, 1989, 1990a, 1990b, 1991), but only a few records from picid hosts have been made in the New World (FACCINI & ATYEO, 1981; ATYEO *et al.*, 1987). Nine pteronyssid genera are currently known from Picidae, five of which (*Neopteronysus* MIRONOV, 2003, *Pteronyssus* ROBIN, 1877, *Pterotrogus* GAUD, 1981, *Stenopteronysus* FACCINI & ATYEO, 1981, and *Zygepigynia* GAUD & CORPUZ-RAROS, 1985) are restricted to this host family.

Among pteronyssid genera associated exclusively with woodpeckers, the genus *Pterotrogus* is most clearly characterised by the derived feature of complete fusion of prodorsal and hysteronotal shields into a single dorsal shield that covers almost the entire dorsal surface of the idiosoma (FACCINI & ATYEO, 1981; MIRONOV *et al.*, 2005) (Figs 1, 2, 5). Up to now, this genus included only two species from woodpeckers of North America. The type species is known from the widely distributed Red-headed Woodpecker *Melanerpes erythrocephalus* (LINNAEUS, 1758), and the other is described from a museum specimen of the Ivory-billed Woodpecker *Campephilus principalis* (LINNAEUS, 1758) (FACCINI & ATYEO, 1981; MIRONOV *et al.*, 2005). In a generic revision of the pteronyssids, FACCINI & ATYEO (1981) noted that five undescribed congeneric species are also distributed on the New World Picidae; however, these authors listed neither species nor genera of woodpeckers from which they collected *Pterotrogus*.

In the course of a long-term investigation into the systematics and biodiversity of pteronyssid mites associated with piciforms (MIRONOV, 1989, 2002, 2003; MIRONOV *et al.*, 2005), fourteen new species of the genus *Pterotrogus* have been found on New World woodpeckers.

The present paper gives an improved diagnosis of the genus, descriptions of new species, cladistic analysis of the genus and a brief discussion of host associations of *Pterotrogus* species.

### Material and methods

#### Specimens

The main part of the material used in the present study was borrowed in a loan from the University of Georgia (Athens, USA). A smaller proportion of examined material is from the feather mite collection deposited in the

Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia).

A new diagnosis of the genus and descriptions of new species are given in the standard formats used for pteronyssid taxa of respective ranks (FACCINI & ATYEO, 1981; MIRONOV, 1992, 2001, 2003). The general morphological terms, leg and idiosomal chaetotaxy follow GAUD & ATYEO (1996). All measurements in the descriptions are given in micrometers ( $\mu\text{m}$ ). A full set of standard measurements is given only for the holotype (male) and one paratype (female); the range of idiosomal size (length, width) is displayed for other paratype specimens of the type series. The measurements implying the distance between different pairs of setae represent the shortest distance between the transverse levels formed by setae of respective pairs.

Scientific names of birds follow "The Howard and Moore Complete Checklist" (DICKINSON, 2003). Specimen depositories and reference accession numbers are cited using the following abbreviations: AMNH - American Museum of Natural History, New York, USA; BMOC or MZUM - Museum of Zoology, University of Michigan, Ann Arbor, USA; NU - Nebraska University, Lincoln, USA; UGA - University of Georgia, Athens, USA; UBR - Übersee Museum, Bremen, Germany; ZISP - Zoological Institute, Saint Petersburg, Russia. Where the collection number consists of two sections, the first section refers to the collection number of the mite specimens and the second is the collection number of the respective host specimen.

### Phylogenetic analysis

Qualitative morphological characters such as the presence/absence of a structure or form of morphological structure were used in the parsimony-based cladistic analysis (Table 1). A few rare autapomorphic characters were also included; although these characters do not help with elucidation of cladistic relationships, they are very important in the evolutionary sense, are helpful for future research, and are necessary for taxonomic diagnoses (YEATES, 1992).

Six species of three other pteronyssid genera also restricted to woodpeckers were used as outgroups to test monophyly of the genus: *Neopteronysus gecinuli* MIRONOV, 2003 from *Gecinulus grantia* (HORSFIELD, 1840), *N. pici* (SCOPOLI, 1763) from *Dendrocopus major* LINNAEUS, 1758, *N. picinus* (KOCH, 1841) from *Dryocopus martius* (LINNAEUS, 1758), *Stenopteronysus spathuliger* (TROUESSART, 1885) from *Celeus elegans* (STATIUS MULLER, 1776), and *Zygepigynia acosmetura* GAUD & CORPUZ-RAROS, 1985 and *Z. rhytidura* GAUD & CORPUZ-RAROS, 1985, both from *Chrysocolaptes lucidus* (SCOPOLI, 1786). In total, 21 taxa and 48 characters, 2 of which represented autapomorphies, were included in the analysis (Tables 1, 2). Construction and editing of the data matrix was done using NEXUS Data Editor 0.5.0 (PAGE, 2001). All characters were treated as unordered; characters having multiple states were interpreted as polymorphic and not modified into binary characters. Reconstruction of phylogenetic relationships was performed with PAUP 4.0 beta version for Windows 95/NT (SWOFFORD, 1998). The branch

Table 1. List of characters used in the phylogenetic analysis.

No	Character
1.	Prodorsal shield: not extending beyond scapular setae (0), extending beyond scapular setae (1)
2.	Anterior end of hysteronotal shield: not extending to prodorsal shield (0), extending to prodorsal shield (1)
3.	Prodorsal and hysteronotal shields: not fused to each other (0), fused to each other (1)
4.	Idiosoma in male: normal, elongated (0), widened (1)
5.	Opisthosoma in male: narrower than body, with small lobes (0), widened, with extending bases of terminal setae on posterior margin (1), widened, semi-ovate (2), widened, with truncate posterior end (3)
6.	Lateral incisions of prodorsal shield in male: absent or extending to setae <i>se</i> (0), extending to setae <i>si</i> (1)
7.	Lateral prodorsal ridges of prodorsal shield in male: absent (0), present (1)
8.	Longitudinal lateral furrows on hysteronotal shield in male: absent (0), present (1)
9.	Ornamentation of hysteronotal shield in male: absent (0), longitudinal sinusoid ridges (1), transverse striation (2), numerous irregular lacunae (3)
10.	Coxal fields III in male: widely open (0), closed (1)
11.	Ventral sclerotisation in male: sclerotized areas along epimerites are narrow or absent (0), wide sclerotized area around epimerites (1), total ventral sclerotisation of idiosoma (2)
12*	Transventral sclerite in male: present (0), absent (1)
13.	Genital shield in male: absent (0), present (1)
14.	Idiosoma in female: normal, parallel-sided in medial part of the body (0), ovate (1)
15.	Size of hysteronotal shield in female: developed in median part of hysterosoma (1), covering almost dorsal surface of hysterosoma (1)
16.	Heavily sclerotized ridges on hysteronotal shield in female: absent (0), present (1)
17.	Posterolateral parts of prodorsal shield of female: sclerotized as other shields (0), with weakly sclerotized areas (1)
18.	Epygium: not connected with coxosternal elements (0), touching epimerites IIIa (1)
19.	Sclerotized folds of oviporus in female: short (0), long, extending to level of epimerites IV (1)
20.	Position of openings <i>gl</i> in male: equidistant from levels of setae <i>d2</i> and <i>e2</i> , or closer to <i>d2</i> (0), closer to setae <i>e2</i> (1)
21.	Setae <i>e1</i> and openings <i>gl</i> in male: setae <i>e1</i> anterior to level of openings <i>gl</i> (0), setae <i>e1</i> at the same level or posterior to <i>gl</i> (1)
22.	Setae <i>c3</i> in male: lanceolate (0), setiform (1)
23.	Setae <i>cp</i> in males: setiform or rod-like with filiform apical end (0), thickened, rod-like, with acute apex (1)
24.	Setae <i>f2</i> in male: setiform (0), lanceolate (1)
25.	Setae <i>ps1</i> in male: setiform (0), lanceolate (1)
26.	Setae <i>ps2</i> in male: setiform, thin (0), lanceolate (1), setiform, thickened (2)
27.	Bases of setae <i>h2</i> in male: rounded (0), cup-shaped (1)
28.	Bases of setae <i>h3</i> in male: rounded (0), cup-shaped (1)
29.	Ratio of setae <i>f2</i> to <i>ps1</i> in male: setae <i>f2</i> subequal or shorter than <i>ps1</i> (0), <i>f2</i> 1.2-2 times longer than <i>ps1</i> (1)
30.	Position of setae <i>e1</i> and openings <i>gl</i> in female: setae <i>e1</i> anterior to <i>gl</i> (0), <i>e1</i> posterior to <i>gl</i> or at the same level (1)
31*	Setae <i>c3</i> in female lanceolate (0), setiform (1)
32.	Setae <i>f2</i> in female: setiform (0), lanceolate (1)
33.	Setae <i>ps1</i> in female: setiform (0), lanceolate (1)
34.	Setae <i>ps2</i> in female: setiform (0), lanceolate (1)
35.	Bases of setae <i>h3</i> in female: rounded (0), cup-shaped (1)
36.	Retrograde spine of femur I: absent (0), present (1)
37.	Dorsal crest on femur I: absent (0), present (1)
38.	Dorsal crest on femur II: absent (0), present (1)
39.	Solenidion <i>ol</i> of genu I: longer than tarsal solenidion <i>ol</i> (0), shorter than tarsal solenidion <i>ol</i> (1)
40.	Tooth on dorsal crest of femur II in male: absent (0), present (1)
41.	Basiventral crest of femur II in male: absent (0), present (1)
42.	Form of dorsal crest on femur II in male: rounded anteriorly (0), with acute angle (1)
43.	Lateral crest of femur II in male: absent (0), present (1)
44.	Legs III in male: long, extending by tibia and tarsus beyond lobar apices (0), short, extending by tarsus (1)
45.	Apical spine of tarsus III in male: present (0), absent or greatly reduced (1)
46.	Legs IV in male: extending to or slightly beyond lobar apices (0), not extending to level of setae <i>ps2</i> (1)
47.	Two dorsobasal spines on tarsus IV in male: absent (0), present (1)
48.	Tooth in dorsal crest of femur II in female: absent (0), present (1)

(\*) Uninformative character

Table 2. Data matrix.

	1	1111111112	2222222223	3333333334	44444444
	1234567890	1234567890	1234567890	1234567890	12345678
<i>Stenopteronysus spathuliger</i>	0100000000	0000000000	0000000000	0000000000	00000000
<i>Neopteronysus gecinuli</i>	10000-0020	010001-000	0000000000	0000000000	00000010
<i>N. pici</i>	10000-0000	010001-000	0000000000	0000000000	00000010
<i>N. picinus</i>	0000000030	0100010000	0000000000	0000000000	00000010
<i>Zygepyginia acosmetura</i>	0100000000	0100100100	0000000000	0000010010	00011000
<i>Z. rhytidura</i>	0100000000	0100100100	0000000000	0000010010	00011000
<i>Pterotrogus borealis</i>	0110010000	0100100010	0100000000	1000000010	00010000
<i>P. colapti</i>	0110001000	0100100010	0000020000	0000000010	00010000
<i>P. guatemalensis</i>	0111100100	0110100011	1001111111	0111101110	01011101
<i>P. iron</i>	0111300001	0101100011	1000000001	0000001111	10010101
<i>P. lanceolatus</i>	0111100100	0110100011	1001111101	0111101110	01011101
<i>P. leucopogon</i>	0111100000	0100100011	1000110001	0111001110	00110101
<i>P. macrosinusoidus</i>	0111200010	21071?7011	111001000?	?????01110	0011010?
<i>P. melanoleuci</i>	0111100100	0110100011	1001111111	0111101110	00111101
<i>P. oconnori</i>	0110000000	0100100011	1000000000	0000000010	00010000
<i>P. principalis</i>	0110000000	0100101011	1000000001	0000000010	00010000
<i>P. quadratus</i>	0111300001	0101100011	1000000001	0100001111	10010101
<i>P. robustus</i>	0111100000	0110100011	1001111111	0111101110	00111101
<i>P. simplex</i>	0110010000	0100101010	0000000000	0000000010	00010000
<i>P. sinusoidus</i>	0111200010	2101100011	1110010101	0111001110	00110101
<i>P. veniliornis</i>	0110001000	1100100010	0000000000	0000000010	00010000

(?) Character state unknown, (-) character inapplicable.

and bound algorithm was used for the maximum parsimony analysis and reconstruction of phylogeny. For *a posteriori* optimization of characters states, I used the DELTRAN option (delayed transformation), which favours parallelism over reversal when the choice is equally parsimonious. Bremer indices used for estimating support for branches were calculated with the program Autodecay (ERIKSSON, 1998). Drawing and editing of tree was made with Winclada, version 1.0 (NIXON, 1999).

### Systematic part

#### Family Pteronyssidae OUDEMANS, 1941

#### Genus *Pterotrogus* GAUD, 1981

GAUD in: FACCINI & ATYEO, 1981: 58; MIRONOV *et al.*, 2005: 13.

**Type species:** *Pteronyssus simplex* HALLER, 1882.

**Both sexes.** Epimerites I fused in a Y, sternum about 1/2 of total length of epimerites or less. Unpaired vertical seta *vi* present. Prodorsal and hysteronotal shield fused to form single idiosomal shield covering almost the entire dorsal surface of idiosoma, traces of fusion between these shields rarely visible; scapular shields fused with prodorsal shield or free from it; scapular setae *se*, *si* on prodorsal shield or in its lateral incisions. Setae *c2* setiform, short. Setae *c3* lanceolate, or spiculiform, or hair-like. Setae *dp2* of palpa simple, hair-like. Setae *ba* of tarsi I, II hair-like. Solenidion *o1* of genu I shorter than solenidion *o1* of tarsus I. Ventral membrane of tarsus I about 1/2 of tarsal length or shorter.

**Male.** Idiosoma variously shaped, elongated, ovate or sub-cuneiform (shaped like a laundry iron) (Figs 1, 7, 8, 29, 39, 48). Opisthosomal lobes small and short or widened, and their terminal margins either smooth or with extensions bearing setae of the terminal complex - *f2*, *ps2*, *h2*, *h3* (*lanceolatus* species group) (Figs 25, 29, 34, 35). Terminal cleft small, commonly semicircular or shallowly concave. Lateral and terminal margins of opisthosomal lobes without membranes, narrow interlobar membrane present or absent. Supranal concavity weakly expressed, open into cleft. Setae *c2* on inner margins of humeral shields. Setae *ps1* anterior to setae *h3* (except *P. robustus*). Hysteronotal shield usually uniformly punctured, without any ornamentation, or bearing a pair of sinusoidal longitudinal ridges (*sinusoidus* group) (Fig. 48). Humeral shields commonly fused with anterolateral parts of hysteronotal shield, rarely free. Coxal fields III open (Figs 2, 30) or closed (Fig. 40) (in *iron* group). Transventral sclerite absent; epiandrium and pregenital sclerite absent (except *P. veniliornis*). Genital shield present or absent. Anal discs circular. Adanal apodemes and adanal membranes absent. Adanal shields absent (present in *iron* group). Setae *f2*, *ps1*, *ps2* setiform or lanceolate; macrosetae *h2*, *h3* setiform or lanceolately enlarged in basal part. Tarsus III slightly elongated, commonly with small apical claw; seta *r* shorter than length of this segments (Fig. 3). Setae *e*, *d* of tarsus IV cone-shaped, weakly sclerotized (Fig. 4).

**Female.** Idiosoma cigar-shaped or ovate (Figs 5, 27, 41). Opisthosoma with smoothly rounded margin or with extension bearing the setae of terminal complex (*f2*, *h2*, *h3*, *ps2*). Surface of dorsal idiosomal shield without ornamentation. Hysteronotal gland openings *gl* on hysteronotal shield. Epigynium arch-shaped; sclerotized folds of oviporus long, extending at least to midlevel of epimerites IV. Adanal sclerites situated lateral to setae *ps3* usually present (absent in *simplex* group).

**Hosts.** Woodpeckers (Piciformes: Picidae) of the genera *Campephilus* GRAY, 1840, *Colaptes* VIGORS, 1825, *Dryocopus* BOIE, 1826, *Picoides* LACEPEDE, 1799, and *Veniliornis* BONAPARTE, 1824.

**Remark.** The genus includes 16 species arranged into 4 morphological groups (*iron*, *lanceolatus*, *simplex*, and *sinusoidus*) based on the general form of the idiosoma and structure of the terminal complex of setae in both sexes and ornamentation of the dorsum in males.

#### Key to species of *Pterotrogus*

(*P. rubricollis*, known only from females, is not included)

1. In both sexes, setae *ps1*, *ps2* setiform or spiculiform; macrosetae *h2*, *h3* always setiform (Figs 1, 2, 5, 6, 39-42) ..... 2
- In both sexes, setae *ps2* lanceolate, macrosetae *h2*, *h3* with lanceolate basal enlargement or setiform (Figs 23, 24, 29, 30); in females setae *ps1* lanceolate, in males, setae *ps1* lanceolate or setiform (Figs 27, 28, 36-38) ..... 9

2. In both sexes, femora II with longitudinal dorsal crest having acute tooth. In males, idiosoma greatly widened, sub-cuneiform (iron-shaped); opisthosoma as wide as sejugal region of the body; posterior margin of opisthosoma with scarcely marked lobes; tarsus I wider than long (Figs 39, 40, 44, 45). In females, idiosoma ovate (Figs 41, 42) (*iron* group) ..... 3
  - In both sexes, femora II without crests. In males, idiosoma elongated, opisthosoma narrower than sejugal region of idiosoma, with pair of small opisthosomal lobes; tarsus I normal, longer than wide (Figs 1, 2, 5-8). In females, idiosoma parallel-sided, cigar-shaped (Figs 3, 4) (*simplex* group) ..... 4
3. In males, coxal fields III completely closed, setae *ps3* situated on small unpaired sclerite at the anterior end of anal slit (Fig. 43); in females, setae *f2* lanceolate (Fig. 47) ..... *P. quadratus* sp. n.
  - In males, anterior border of coxal fields III interrupted by several longitudinal striae, setae *ps3* on soft integument (Fig. 40); in females, setae *f2* are short setiform (Fig. 41) ..... *P. iron* sp. n.
4. In both sexes, epimerites I, II with wide sclerotized areas (Fig. 19), scapular shield fused with prodorsal shield and any traces of fusion indistinct. In males, longitudinal pregenital sclerite present (Fig. 20). In females, dorsal surface of opisthosoma with heavily sclerotized longitudinal patch (Fig. 21) ..... *P. veniliornis* sp. n.
  - In both sexes, epimerites I, II without sclerotized areas; scapular shields free from prodorsal shield or fused but traces of fusion are clearly visible. In males, pregenital sclerite absent. In females, dorsal surface of hysterosoma uniformly sclerotized ..... 5
5. In males setae *e1* situated at the level of setae *e2*. (Fig. 7). In females, setae *e1* posterior to the level of setae *e2* (Fig. 15) ..... *P. principalis* MIRONOV, DABERT & EHRSBERGER, 2005
  - In both sexes, setae *e1* between the levels of setae *d2* and *e2*. (Figs 1, 8, 9, 10) ..... 6
6. In males, idiosoma longer than 300, setae *ps2* longer than distance between bases of setae *ps1* (Fig. 8). In females, pygidial area of opisthosoma with irregular transverse striae between levels of setae *e2* and *f2*, length of idiosoma over 450 (Fig. 16) ..... *P. oconnori* sp. n.
  - In males, idiosoma less than 280, setae *ps2* shorter or equal to distance between setae *ps1*. In female, dorsal idiosomal shield monotonously punctured, length of idiosoma less than 430 ..... 7
7. In both sexes, setae *c3* spiculiform (Figs 13, 17). In males, ambulacral disc of leg IV not extending beyond the level of lobar apices (Fig. 9) ..... *P. borealis* sp. n.
  - In both sexes, setae *c3* lanceolate (Figs 2, 14). In males, ambulacral disc of leg IV extending beyond the level of lobar apices (Fig. 1) ..... 8
8. In both sexes, scapular shields separated from prodorsal shield, postero-

- lateral areas of prodorsal shield weakly sclerotized (Figs 1, 5). In males, prodorsal shield with deep lateral incisions, scapular setae *si* and *se* on soft integument; setae *ps1* and *ps2* short setiform, subequal in length (Fig. 2) . . . . . *P. simplex* (HALLER, 1882)
- In both sexes, scapular shields fused with prodorsal shield, traces of fusion usually visible (Figs 10, 18). In males, prodorsal shield with short lateral incisions extending only to base of setae *se*; setae *ps2* thickened and twice as long as setae *ps1* (Fig. 14) . . . . . *P. colapti* sp. n.
9. In males, ventral surface of opisthosoma almost completely sclerotized, dorsal surface with pair of longitudinal sinusoid ridges; setae *f2*, *ps1* short setiform (Figs 48, 52). In females, humeral setae *cp* rod-like, with acute apex (*sinusoidus* group) . . . . . 10
- In males, ventral surface with sclerotization only along epimerites I-IV, dorsal surface monotonously punctured without ornamentation; setae *ps1* lanceolate, setae *f2* lanceolate or setiform (Figs 23, 29). In females, humeral setae *cp* setiform (*lanceolatus* group) . . . . . 11
10. In males, sinusoid ridges narrow, about 5 in width, width of terminal cleft less than 25 (Fig. 48) . . . . . *P. sinusoidus* sp. n.
- In males, sinusoid ridges wide, about 10, width of terminal cleft more than 30 (Fig. 52) . . . . . *P. macrosinusoidus* sp. n.
11. In males, setae *f2* short setiform, setae *ps2* narrowly lanceolate, not wider than 5 (Figs 23, 24). In both sexes, setae *ps2*, *h2*, *h3* on short stump-like extensions. In females, setae *ps1* thin, about 5 in width (Fig. 27) . . . . . *P. leucopogon* sp. n.
- In males, setae *f2* lanceolate, *ps2* widely lanceolate, 7-12 in width. In both sexes, setae *ps2*, *h2*, *h3* situated on cup-like extensions. In females, setae *ps1* 10-13 in width . . . . . 12
12. In males, terminal cleft short and wide, with heavily sclerotized membrane; setae *ps1* are most caudal setae of opisthosoma, widely separated from each other by 70 (Figs 25, 26). In females, setae *f2* about 65 in length (Fig. 28) . . . . . *P. robustus* sp. n.
- In males, posterior margin with small terminal cleft, setae *ps1* sitting on its margin situated anterior to level of setae *h2*, *h3* and their bases separated by 10-15. In females, setae *f2* less than 50 in length . . . . . 13
13. In males, dorsal crest of femur II with acute angle (Fig. 32), setae *f2* about 30-46 in length and approximately twice as long as setae *ps1* (Figs 29, 30, 35). In females, greatest width of setae *ps2*, *h2*, *h3* 12-14, length of setae *ps2* 80-86 (Figs 36, 38) . . . . . 14
- In males, dorsal crest of femur II with rounded anterior end (Fig. 33), setae *f2* about 17 in length, approximately equal to setae *ps1* (Fig. 34). In females, greatest width of setae *ps2*, *h2*, *h3* about 9-10, setae *ps2* about 110 in length (Fig. 37) . . . . . *P. melanoleuci* sp. n.
14. In males, setae *ps1* approximately two times shorter than setae *f2* (about

23 versus 44 in length); in females, length of idiosoma 445-455 (Figs 29, 30, 36) ..... *P. lanceolatus* sp. n.

- In males, setae *ps1* similar in size to setae *f2* (about 33 in length), in females, idiosoma less than 420 in length (Figs 35, 38) .....

..... *P. guatemalensis* sp. n.

### Species group *simplex*

**Diagnosis.** In both sexes, setae *f2*, *h2*, *h3*, *ps1*, *ps2* setiform, femora and genua I, II without dorsal crests. In males, idiosoma elongated, parallel-sided in scapular and humeral regions, opisthosoma posterior to legs III narrower than sejugal part of the body, with a pair of small rounded or trapezoidal lobes, dorsal surface of idiosoma without ornamentation, epimerites I, III, IIIa in most species without sclerotized areas, remaining ventral surface soft and striated, coxal fields III open, tarsus I wider than long. In females, idiosoma elongated, parallel-sided, posterior margin rounded.

#### 1. *Pterotrogus simplex* (HALLER, 1882) (Figs 1-6)

**Material examined.** 1 male, 1 female from *Melanerpes erythrocephalus* (BMOC 83-0923-2, UMMZ 206 308) USA, Michigan, Benzie Co., near Honor, 20.V.1983, R. CARR; 1 male (BMOC 88-0524-1, UMMZ 227 574), same host, USA, Michigan, Wayne Co., Plymouth, 23.V.1988, R. SMITH; 1 female (NU 4414), same host, USA, Michigan, Barry Co., Sheffield Road near Noonan Road, 29.VIII.1960, D. CLARK.

This species is known only from the type host, the red-headed woodpecker *M. erythrocephalus*, in the USA and Canada (HALLER, 1882; FACCINI & ATYEO, 1981).

#### 2. *Pterotrogus principalis* MIRONOV, DABERT & EHRNSBERGER, 2005 (Figs 7, 11, 15)

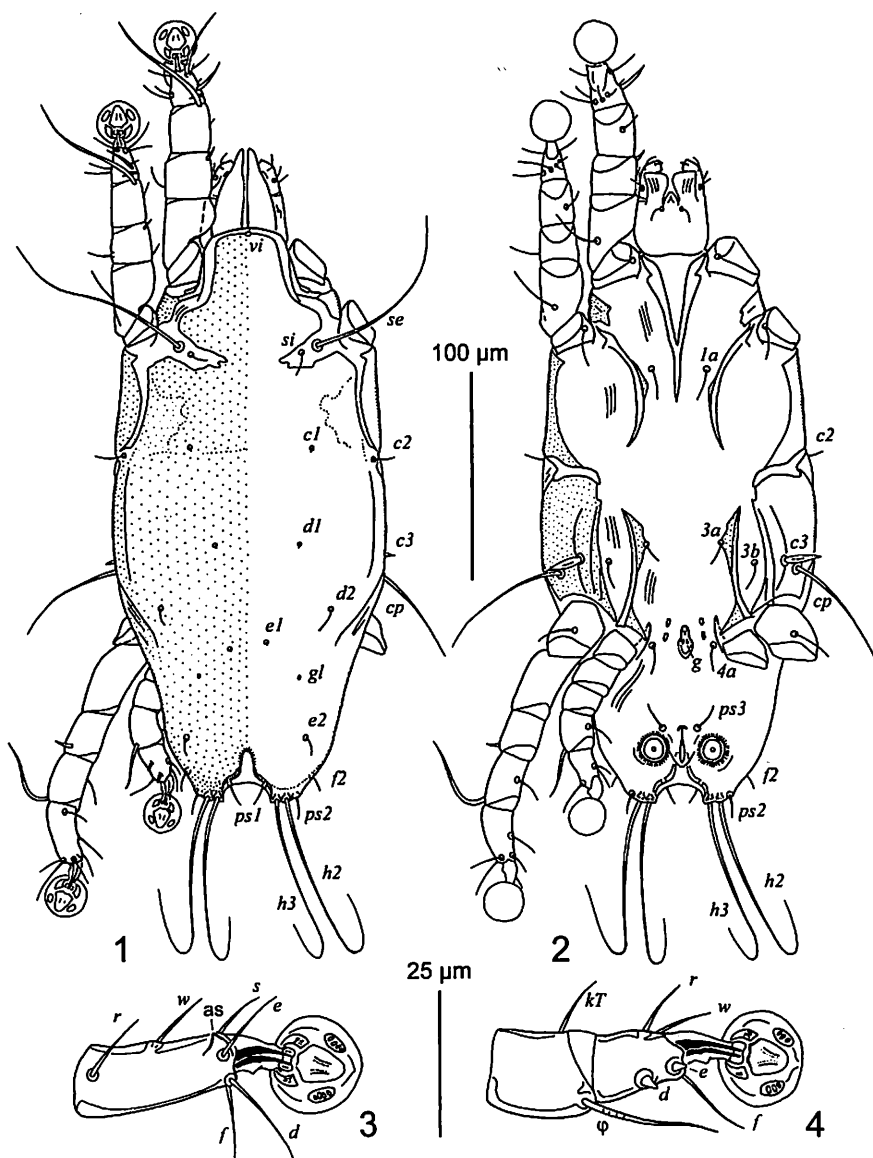
**Material examined.** Holotype male, 2 male and 2 female paratypes (ZISP BR-145, UBR 6165) from *Campophilus principalis* (LINNAEUS, 1758), North America, no other data.

This species has been recently described from a museum specimen of the ivory-billed woodpecker *C. principalis* in North America (MIRONOV *et al.*, 2005). This woodpecker inhabited mature forests of southeastern areas in the USA and in Cuba, but at present is close to extinction (FITZPATRICK *et al.*, 2005).

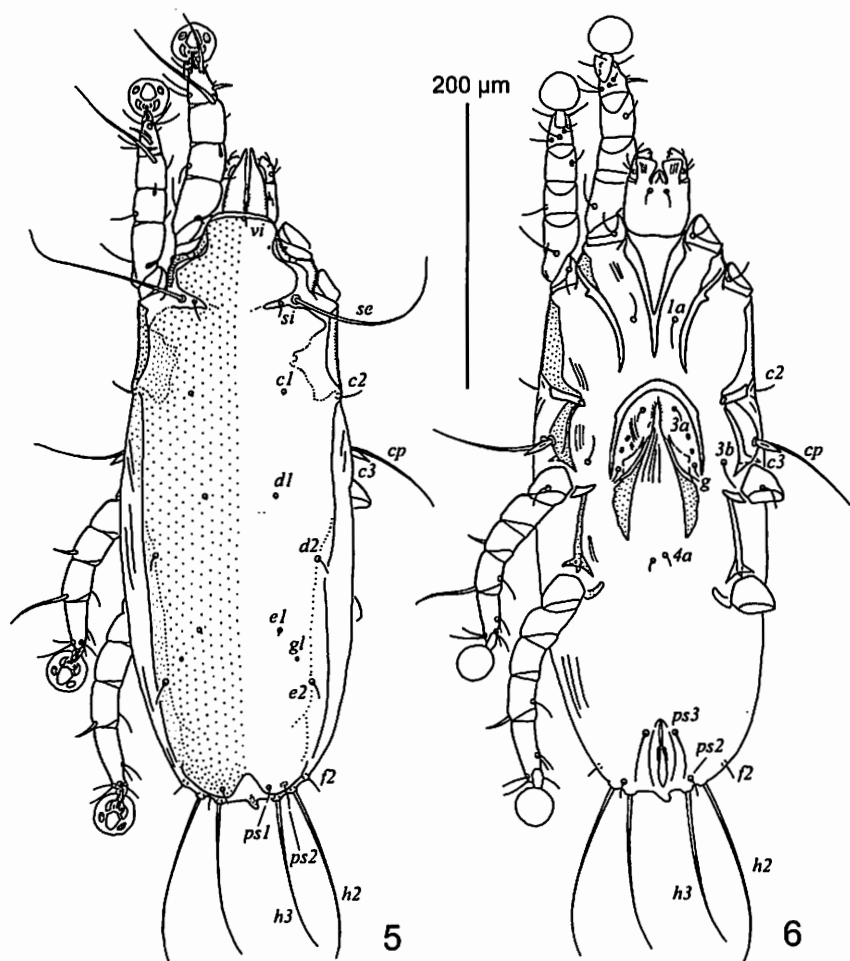
#### 3. *Pterotrogus oconnori* MIRONOV sp. n. (Figs 8, 12, 16)

**Type material.** Holotype male, 2 male and 2 female paratypes (BMOC 88-1202-2, UMMZ 227 333) from *Dryocopus pileatus* (LINNAEUS, 1758), USA, Kentucky, McCreary Co., 3 mi SW Cumberland Falls State Park, Indian Creek, 6.V.1986, W.S. MOORE. Holotype, 1 male and 1 female paratypes - UMMZ, other paratypes - ZISP.

**Additional material.** 1 male, 1 female (NU 1578) from *D. pileatus*, USA, Texas, Lake Walker Co., 3 mi E Thomas, 2.VIII.1936, W.P. TAYLOR; 1 female (NU 2029), same host, USA Louisiana, W. Baton Rouge Parish, 11.V.1941, G.H. LOWRY.



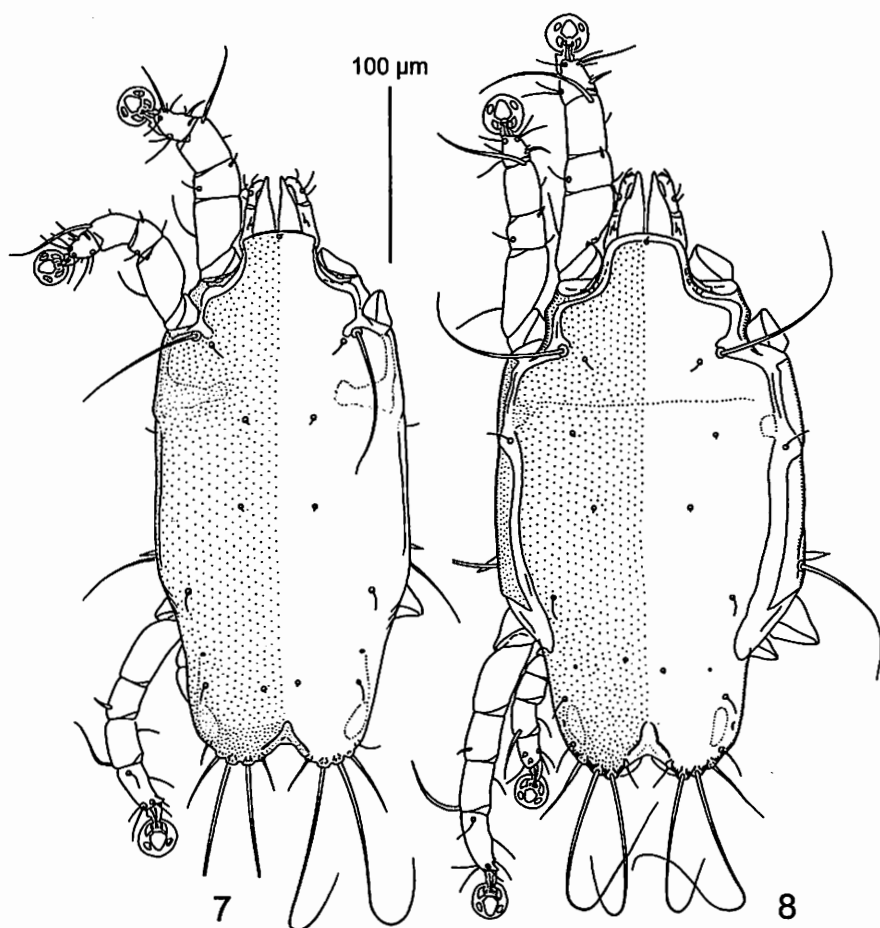
Figs 1-4. *Pterotrogus simplex*, male. 1: dorsal view, 2: ventral view, 3: tarsus III, 4: tarsus IV. as - apical claw of tarsus III.



Figs 5-6. *Pterotrogus simplex*, female. 5: dorsal view, 6: ventral view.

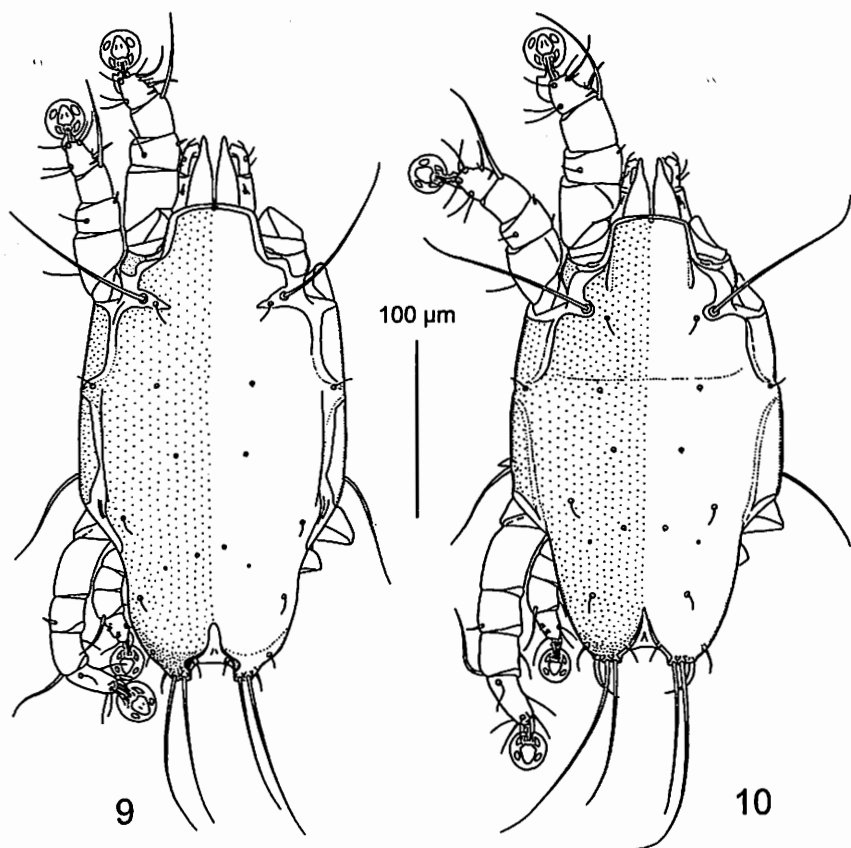
### Description

**Male** (holotype). Length of idiosoma 303, greatest width of idiosoma 170 (idiosomal size in 2 paratypes 305-310 x 155-165). Transverse trace between fused prodorsal and hysteronotal shields visible, scapular and humeral shields separated from complex dorsal shields, respectively; dorsal surface of hysteronotum without ornamentation (Fig. 8), lateral margins of prodorsal shield with small incisions extending to bases of scapular setae *se*; distance between these setae 75. Length of hysterosoma from level of setae *c2* to lobar apices 174. Setae *c3* lanceolate, with acute apex, 20 in length. Dorsal setae *e1* situated anterior to the level of lateral setae *e2*. Opisthosoma over half as wide



Figs 7-8. Males of the genus *Pterotogus*, dorsal view of idiosoma. 7: *Pterotogus principalis*, 8: *P. oconnori*.

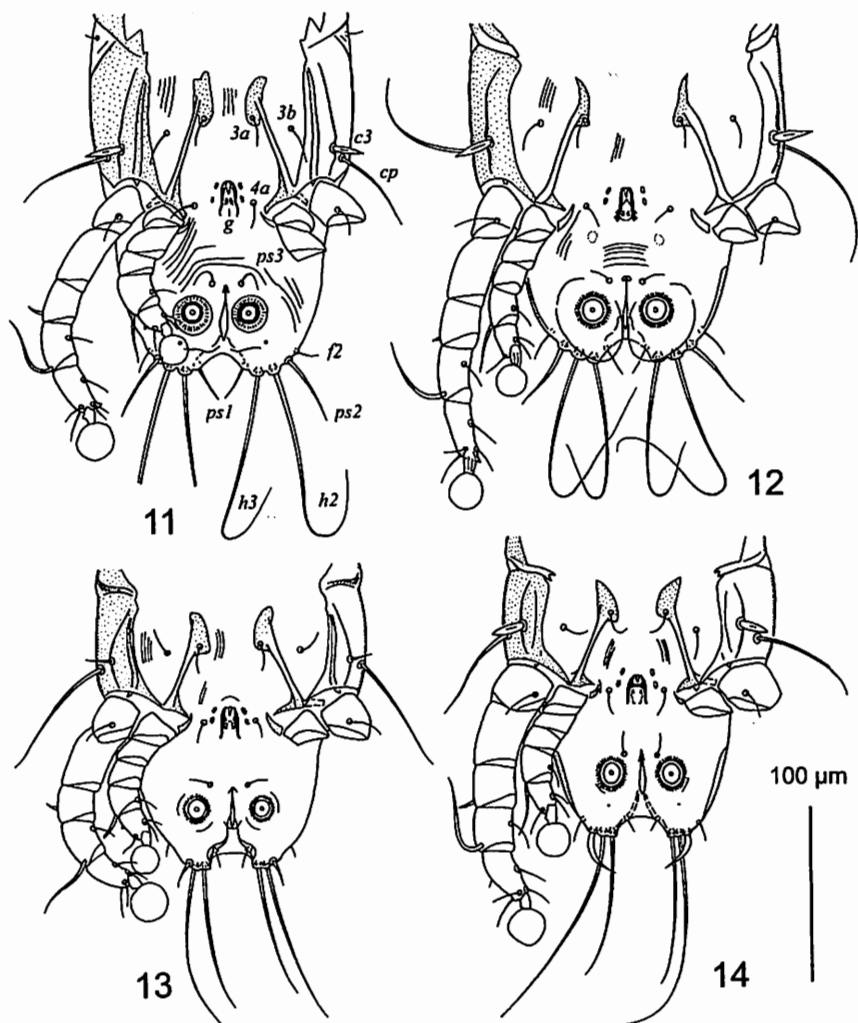
as greatest body width, with small and widely rounded opisthosomal lobes; terminal cleft shallowly concave, 11 in length. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform; length of setae: *ps1* 12, *ps2* 46, *f2* 11. Dorsal measurements: *c2-d2* 82, *d2-e2* 58, *d2-g1* 37, *e1-e2* 18-22, *e2-h3* 40, *h2-h2* 43, *h3-h3* 35, *ps1-ps1* 24, *ps2-ps2* 71. Epimerites I, II with narrow sclerotized areas. Inner ends of epimerites IIIa form an oblique L; epiandrium absent. Setae *3a* and *3b*, at the same transverse level. Genital arch 20 in length, 12 in width, aedeagus about one third of arch length, coxal setae *4a* at midlevel of genital arch. Genital shield absent. Adanal shields absent. Diameter of anal discs 16. Tarsus I longer than wide. Genua and femora I, II without crests. Tarsus III with small apical claw, 33 in length; seta *r* short, about half-length



Figs. 9-10. Males of the genus *Pterotrogus*, dorsal view of idiosoma. 9: *Pterotrogus borealis*, 10: *P. colapti*.

of the segment. Legs IV extending beyond lobar apices by length of ambulacral disc.

*Female* (paratype). Length of idiosoma 464, width of idiosoma 209 (idiosomal size in other paratype 455 x 196). Transverse trace between fused prodorsal and hysteronotal shields visible, scapular shields free, lateral margins of prodorsal shield as in the male, bases of setae *se* separated by 102; posterior end of opisthosoma between levels of setae *e1* and *f2* with wavy transverse striation. Length of hysterosoma from level of setae *c2* to posterior end 312. Setae *c3* lanceolate with acute apex, 22 in length. Posterior margin of opisthosoma rounded, without lobes. Setae *d1* posterior to setae *cp*, setae *e1* anterior to the level of setae *e2*. External copulatory tube as small weakly sclerotized cone-like extension. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform; length of setae: *ps1* 20, *ps2* 10, *f2* 10. Dorsal measurements: *c2-d2* 122, *d2-e2* 123, *e2-f2* 42, *e1-e2* 28-29, *h2-h2* 71, *ps1-ps1* 22. Epimerites I, II



Figs 11-14. Males of the genus *Pterotrogus*, ventral view of hysterosoma. 11: *Pterotrogus principalis*, 12: *P. oconnori*, 13: *P. borealis*, 14: *P. colapti*.

as in the male. Epigynum as long arch, 63 in length, 73 in width; sclerotized folds of oviporus extending to midlevel of epimerites IV. Adanal sclerites absent. Genua and femora I, II without crest.

**Differential diagnosis.** The new species is most similar to the type species, *Pterotrogus simplex*. Both sexes of the new species differ from it by having shorter incisions in lateral margins of the prodorsal shield extending to setae *se* only and monotonous sclerotization of this shield; males are distinguished

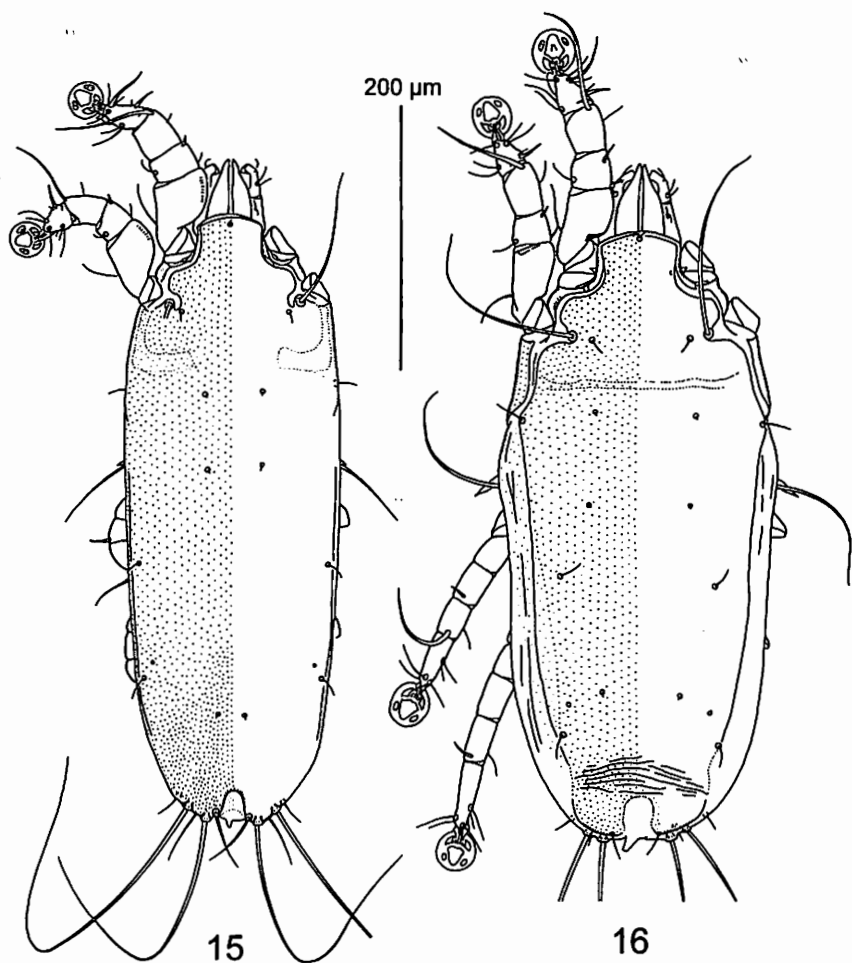


Fig. 15-16. Females of the genus *Pterotrogus*, dorsal view of idiosoma, 15: *Pterotrogus principalis*, 16: *P. oconnori*.

by humeral shields separated from the hysteronotal shield; females differ by transverse striation in the pygidial area. In *P. simplex*, both scapular setae (*se*, *si*) are in lateral incisions of prodorsal shields, posterolateral areas of the prodorsal shield are sclerotized much more weakly than the remaining area of this shield; in males the humeral shields are fused with hysteronotal shield; in females, the pygidial area is monotonously punctured.

**Etymology.** Species is named in a honour of the prominent acarologist, Dr. Barry M. OConnor (The University of Michigan, Ann Arbor, USA).

#### 4. *Pterotrogus borealis* MIRONOV sp. n. (Figs 9, 13, 17)

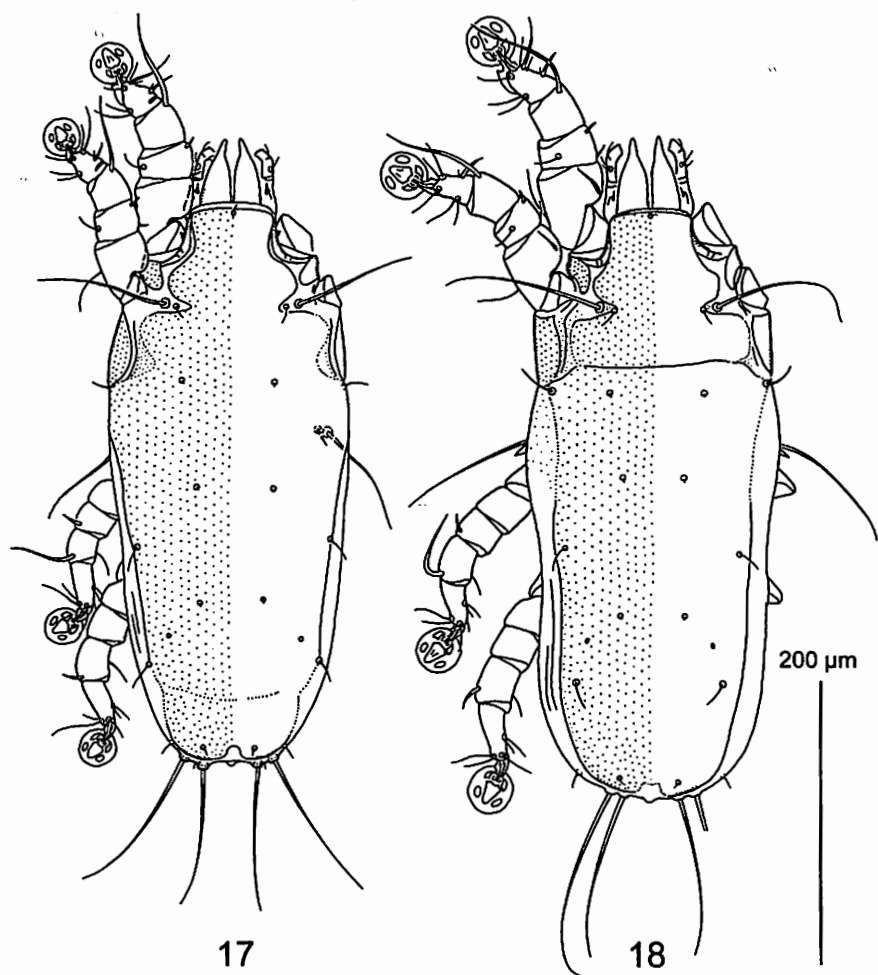
**Type material.** Male holotype (NU1564) from *Picoides borealis* (VIEILLOT, 1809), USA, Texas, Harris Co., 4 mi N Huffman, 9.VIII.1938, coll. unknown; 1 female paratype (NU 1565), same host, USA, Texas, Trinity Co., 2 mi W Trinity, 3.IV.1936, W.P. TAYLOR. Holotype and paratypes – UMMZ.

**Additional material.** 1 male, 2 females (UGA 9389, AMNH 363 783) from *Picoides borealis*, USA, Mississippi, 5.VIII.1919, A.P. SMITH; 1 male (UGA 7577, AMNH 229 483), same host, USA, Missouri, Shannon Co., 30.IV.1907, L.B. WOODRUFF; 1 male, 1 female (UGA 9388, AMNH 96427), same host, USA, Virginia, Cobham Bay, 30.XII.1887, coll. unknown.

#### Description

**Male** (holotype). Length of idiosoma 270, greatest width of idiosoma 146. Trace between fused prodorsal and hysteronotal shields indistinct, scapular and humeral shields free; dorsal surface of hysteronotum without ornamentation; lateral margins of prodorsal shield with angular incisions around scapular setae *si* and *se*; bases of setae *se* separated by 75. Length of hysterosoma from level of setae *c2* to lobar apices 156. Setae *c3* spiculiform, 11 in length. Dorsal setae *e1* anterior to the level of setae *e2*. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform; length of setae: *ps1* 10, *ps2* 14, *f2* 7 (Fig. 9). Opisthosoma wide, over half of greatest body width, with very short opisthosomal lobes having clear posteromedian angle; terminal cleft small, shorter than wide, with almost straight anterior margin, 11 in length. Dorsal measurements: *c2-d2* 71, *d2-e2* 44, *d2-gl* 31, *e1-gl* 7-11, *e1-e2* 16-22, *e2-h3* 42, *h2-h2* 37, *h3-h3* 26, *ps1-ps1* 17, *ps2-ps2* 46. Epimerites I, II with narrow sclerotized areas. Inner ends of epimerites IIIa form an oblique T; epiandrium absent. Setae *3a* and *3b* approximately at the same transverse level. Genital arch 17 x 13, aedeagus much shorter than arch, coxal setae *4a* at midlevel of genital arch. Genital shield absent. Adanal shields absent. Diameter of anal discs 12. Tarsus I longer than wide. Genua and femora I, II without crest. Tarsus III with small apical claw, 26 in length; seta *r* very short, about half-length of the segment. Ambulacral discs of legs IV not extending beyond lobar apices.

**Female** (paratype). Length of idiosoma 398, width of idiosoma 192. Transverse trace between fused prodorsal and hysteronotal shields; scapular shields free (Fig. 17), lateral incisions in this shield as in the male; bases of setae *se* separated by 86. Length of hysterosoma from level of setae *c2* to posterior end 266. Setae *c3* spiculiform, with acute apex, 20 in length. Posterior margin of opisthosoma rounded, slightly concave between setae *h3*. Setae *d1* posterior to the level of humeral setae *cp*, setae *e1* equidistant from levels of setae *d2* and *e2*. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform; length of setae: *ps1* 7, *ps2* 8, *f2* 7. External copulatory tube as very small tubercle-like terminal extension. Dorsal measurements: *c2-d2* 122, *d2-e2* 77, *e2-f2* 60, *e1-e2* 49-50, *h2-h2* 58, *ps1-ps1* 25. Epimerites I, II as in the male. Epigynium 58 x 60; sclerotized folds of oviporus extending to midlevel of epimerites IV. Adanal sclerites absent. Genua and femora I, II without crest.



Figs 17-18. Females of the genus *Pterotrogus*, dorsal view of idiosoma, 17: *Pterotrogus borealis*, 18: *P. colapti*.

**Differential diagnosis.** This species is similar to *Pterotrogus simplex* (Figs 1-6). Both sexes of *P. borealis* clearly differ from that species by having spiculiform setae *c3*. This character differentiates the new species from all other known species of the *simplex* group. In addition, males of the new species are distinguished from *P. simplex* by having legs IV not extending beyond the level of lobar apices, and short distance between the levels of setae *d2* and *e2*, that is twice as short as the distances between members of each pair (Figs 9, 13); the females differ by having the external copulatory tube as a small tubercle-like extension (Fig. 17). In both sexes of *P. simplex*, setae *c3*

are lanceolate; in males, ambulacral discs of legs IV reach beyond the lobar apices, and the distance between levels of setae *d2* and *e2* are approximately equal to the distance between members of each setal pair.

**Etymology.** Specific epithet is taken from the name of the type host.

### 5. *Pterotrogus colapti* MIRONOV sp.n. (Figs 10, 14, 18)

**Type material.** Male holotype, 1 male and 2 female paratypes (UGA 9404, AMNH 278 652) from *Colaptes punctigula guttatus* (SPIX, 1824), Brazil, Amazonas, Villa Bella Imperatriz, 17.XI.1930, OLALLA Brothers; 1 male and 1 female paratype (UGA 9406, AMNH 278 649), same data except date, 5.XI.1930. Holotype, 1 male and 2 female paratypes – UMMZ, other paratypes – ZISP.

#### Description

**Male** (holotype). Length of idiosoma 255, greatest width of idiosoma 148 (idiosomal size in 2 paratypes 258-268 x 147-151). Trace between fused prodorsal and hysteronotal shields weakly visible; scapular and humeral shields fused with complex idiosomal shield, traces of fusion visible (in some paratypes poorly distinct); dorsal surface of hysteronotum without ornamentation (Fig. 10). Anterior part of prodorsal shield with lateral longitudinal ridges, lateral margins of this shield with small incisions reaching scapular setae *se*; bases of these setae separated by 68. Length of hysterosoma from level of setae *c2* to lobar apices 156. Setae *c3* lanceolate, with acute apex, 15 in length. Dorsal setae *e1* anterior to the level of setae *e2*, hysteronotal gland openings *gl* poorly developed. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform, setae *ps2* thickened, hook-shaped (Fig. 14); length of setae *ps1* 10, *ps2* 19, *f2* 7. Opisthosoma wide, about 2/3 of greatest body width, with short and widely rounded opisthosomal lobes; terminal cleft shallowly concave, 12 in length. Dorsal measurements: *c2-d2* 64, *d2-e2* 55, *d2-gl* 24, *e1-gl* 15, *e2-e1* 40, *e2-h3* 37, *h2-h2* 40, *h3-h3* 33, *ps1-ps1* 15, *ps2-ps2* 51. Epimerites I, II with narrow sclerotized areas; inner ends of epimerites IIIa form an oblique T; epiandrium absent. Setae *3a* anterior to *3b*. Genital arch 15 x 9, aedeagus much shorter than arch, coxal setae *4a* at midlevel of genital arch. Genital shield absent. Adanal shields absent. Diameter of anal discs 13. Tarsus I longer than wide. Femora I, II with poorly developed lateral crest, genua I, II without crest. Tarsus III with small apical claw, 31 in length; seta *r* about half length of the segment. Legs IV extending by ambulacral disc beyond lobar apices.

**Female** (paratype). Length of idiosoma 423, width of idiosoma 178 (idiosomal size in other 2 paratypes 414-420 x 183-188). Trace of fusion between prodorsal and hysteronotal shields visible; scapular shields fused with prodorsal shield, trace of fusion visible, weakly sclerotized, incision in lateral margin of prodorsal shield extending to setae *si*; bases of setae *se* separated by 82. Length of hysterosoma from level of setae *c2* to posterior end 290. Setae *c3* lanceolate with acute apex, 20 in length. Posterior margin of opisthosoma rounded, without lobes. Setae *d1* posterior to level of humeral setae *cp*, setae *e1* equidistant from levels of setae *d2* and *e2*. Macrosetae *h2*, *h3* and setae *ps1*,

*ps2*, *f2* setiform; length of setae: *ps1* 4, *ps2* 9, *f2* 6. External copulatory tube as small weakly sclerotized terminal extension. Dorsal measurements: *c2-d2* 122, *d2-e2* 89, *e2-f2* 53, *e1-e2* 44, *h2-h2* 65, *ps1-ps1* 40. Epimerites I, II as in the male. Epigynium 85 x 60; sclerotized folds of oviporus extending to midlevel of epimerites IV. Adanal sclerites absent. Femora I, II with lateral crest, genua I, II without crest.

**Differential diagnosis.** Males of this species resemble those of *P. oconnori* (Figs 8,16) by the shape of opisthosoma, but are much smaller. The males of *P. colapti* are distinguished from that species by smaller size of idiosoma (255-268, *n*=3), thickened and hook-shaped setae *ps2*, and setae *e1* situated distinctly much closer to the level of setae *d2* than to that of *e2* (Fig. 9). The females differ from *P. oconnori* by having the lateral sclerotized crest on femora I, II and by the absence of transverse striation in pygidial part of hysterosoma. In the males of *P. oconnori*, idiosoma length varies from 303 to 310 (*n*=3), setae *ps2* are long setiform, and setae *e1* equidistant from the levels of setae *d2* and *e2*; in the females, the pygidial area of hysterosoma with irregular transverse striation (Fig. 16). By the structure of posterior end of opisthosoma, the females of *P. colapti* resemble *P. simplex* (Fig. 5); however they differ from the latter species by the absence of weakly sclerotized areas in postero-lateral areas of prodorsal shields.

**Etymology.** Specific epithet derived from the generic name of the type host.

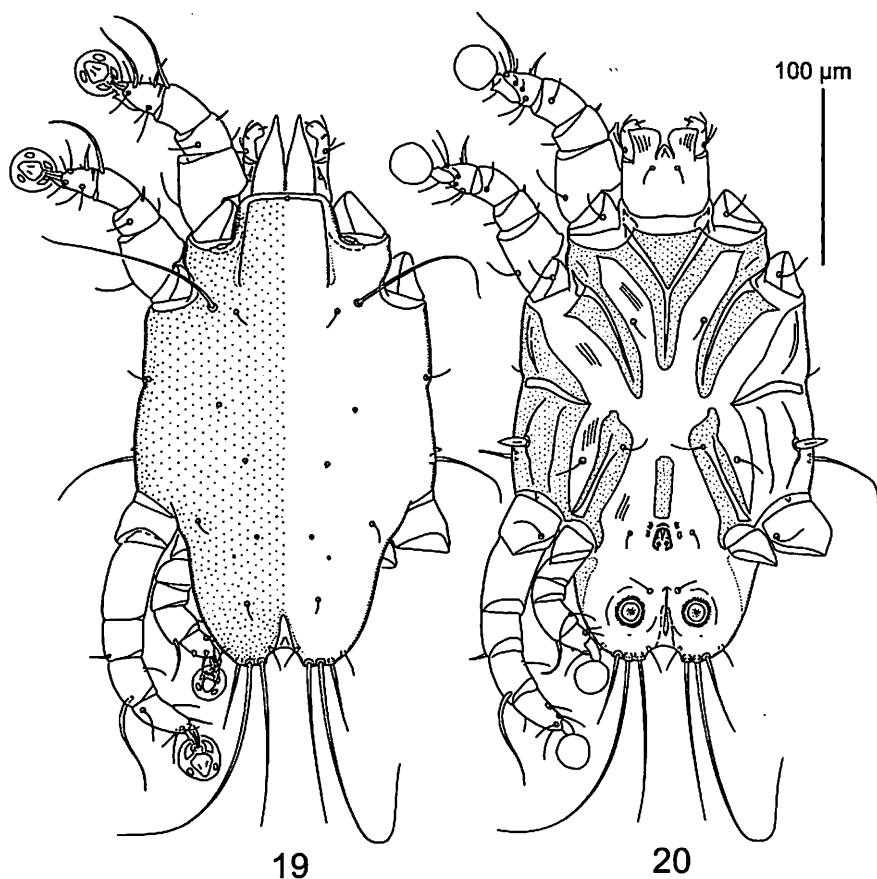
## 6. *Pterotrogus veniliornis* MIRONOV sp. n. (Figs 19-21)

**Type material.** Male holotype, 1 female paratype (UGA 9391, AMNH 324 290) from *Veniliornis cassinii* (MALHERBE, 1862), Venezuela, Amazonas, Mt. Auan-tepui, 28.I.1938, T. GILLIARD; 1 male and 1 female paratypes (UGA 9390, AMNH 270 889), same host, Venezuela, Amazonas, Mt. Duida, 16.XII.1928, OLALLA Brothers. Holotype, 1 female paratype – UMMZ, other paratypes – ZISP.

**Additional material.** 1 male (UGA 7525) from *V. cassinii*, Brazil, Amapa, Serra de Navio, 15.V.1968, coll. unknown; 1 male, 1 female (UGA 9394, AMNH 59423) from *V. kirkii* (MALHERBE, 1845), Trinidad, Princes Town, 28.III.1893, F.M. CHAPMAN.

## Description

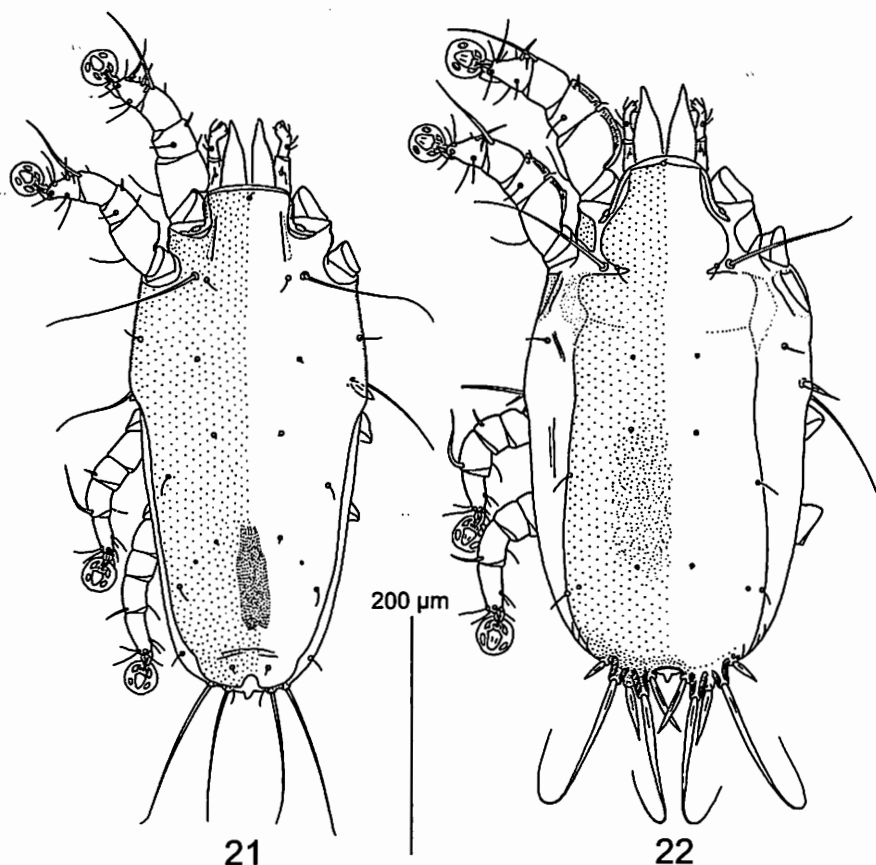
**Male** (holotype). Length of idiosoma 272, greatest width of idiosoma 165 (idiosomal size in paratype 267 x 160). Prodorsal, hysteronotal, scapular and humeral shields fused into complex dorsal shield covering idiosoma, traces of fusion indistinct, surface of dorsum without ornamentation. Anterior part of prodorsal shield with lateral longitudinal ridges; lateral margins of this shield without incisions; bases of setae *se* separated by 80. Length of hysterosoma from level of setae *c2* to lobar apices 156. Setae *c3* lanceolate, with acute apex, 16 in length. Dorsal setae *e1* slightly posterior to the level of setae *d2*; setae *e2* closer to median line than to lateral margins of the body; hysteronotal gland openings *gl* poorly developed. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform; length of setae: *ps1* 14, *ps2* 42, *f2* 9 (Fig. 19). Opisthosoma wide, about half of greatest body width, with short and laterally rounded opisthosomal lobes; terminal cleft small, almost semicircular, 12 in length.



Figs 19-20. *Pterotrogus veniliornis*, male. 19: dorsal view of idiosoma, 20: ventral view of idiosoma.

Dorsal measurements:  $c2-d2$  82,  $d2-e2$  44,  $d2-gl$  22,  $gl-el$  15,  $el-e2$  33,  $e2-h3$  33,  $h2-h2$  37,  $h3-h3$  25,  $ps1-ps1$  16,  $ps2-ps2$  48. Epimerites I, II, and IIIa with well-developed sclerotized areas (Fig. 20); epiandrium as small bow-shaped sclerite; longitudinal pregenital sclerite present; genital shield absent. Setae  $3a$  anterior to  $3b$ . Genital arch  $18 \times 13$ , aedeagus about half length of arch, coxal setae  $4a$  at midlevel of genital arch. Adanal shields absent. Diameter of anal discs 13. Tarsus I longer than wide. Genua and femora I, II without crest. Tarsus III with small apical claw, 27 in length; seta  $r$  very short, about half length of the segment. Legs IV extending by ambulacral discs beyond lobar apices.

*Female* (paratype). Length of idiosoma 428, width of idiosoma 196 (idiosomal size in other paratype  $446 \times 200$ ). Prodorsal, hysteronotal, and



Figs 21-22. Females of the genus *Pterotrogus*, dorsal view of idiosoma. 21: *Pterotrogus veniliornis*, 22: *P. rubricolli*.

scapular shields fused into complex dorsal shield covering idiosoma, traces of fusion indistinct; bases of setae *se* separated by 91. Length of hysterosoma from level of setae *c2* to posterior end 285. Setae *c3* lanceolate, with acute apex, 17 in length. Posterior margin of opisthosoma rounded; median area of opisthosoma with heavily sclerotized longitudinal patch. Setae *d1* posterior to level of humeral setae *cp*, setae *e1* equidistant from levels of setae *d2* and *e2*. Macrosetae *h2*, *h3* and setae *ps1*, *ps2*, *f2* setiform; length of setae: *ps1* 5, *ps2* 31, *f2* 13. External copulatory tube as small cone-like extension. Dorsal measurements: *c2-d2* 128, *d2-e2* 84, *e2-f2* 53, *e1-e2* 44, *h2-h2* 53, *ps1-ps1* 26. Epimerites I, II with wide sclerotized areas as in the male. Epigynum 53 x 64 in width; sclerotized folds of oviporus extending beyond the midlevel of epimerites IV. Adanal sclerites absent. Genua and femora I, II without crest.

**Differential diagnosis.** Males of *P. veniliornis* resemble in general appearance and size those of *P. colapti* and *P. borealis* (Figs 9, 10, 13, 14);

however, the new species clearly differs from those species and all other representatives of the *simplex* group by several unique characters. In both sexes of *P. veniliornis*, the scapular shields are completely incorporated into the complex dorsal shield of idiosoma, and epimerites I, II are surrounded by relatively large sclerotized areas; the males have a longitudinal pregenital sclerite and the females have a heavily sclerotized longitudinal patch in the median part of opisthosoma (Figs 19-21).

**Etymology.** Specific epithet is derived from the generic name of the type host

### Species group *lanceolatus*

**Diagnosis.** In both sexes, setae *ps1*, *ps2* lanceolate; macrosetae *h2*, *h3* with lanceolate enlargement in basal part or setiform, genua and femora I, II with dorsal crest. In males, idiosoma narrowly ovate in general shape, lobes short and enlarged, posterior margin of lobes commonly with short stump- or cone-shaped extensions bearing setae of terminal complex, surface of dorsum without ornamentation, epimerites I, II and IIIa without sclerotized areas, coxal fields III open, setae *f2* lanceolate or setiform. In females, idiosoma ovate as in males, posterior margin commonly with extensions bearing setae of terminal complex, setae *f2* lanceolate.

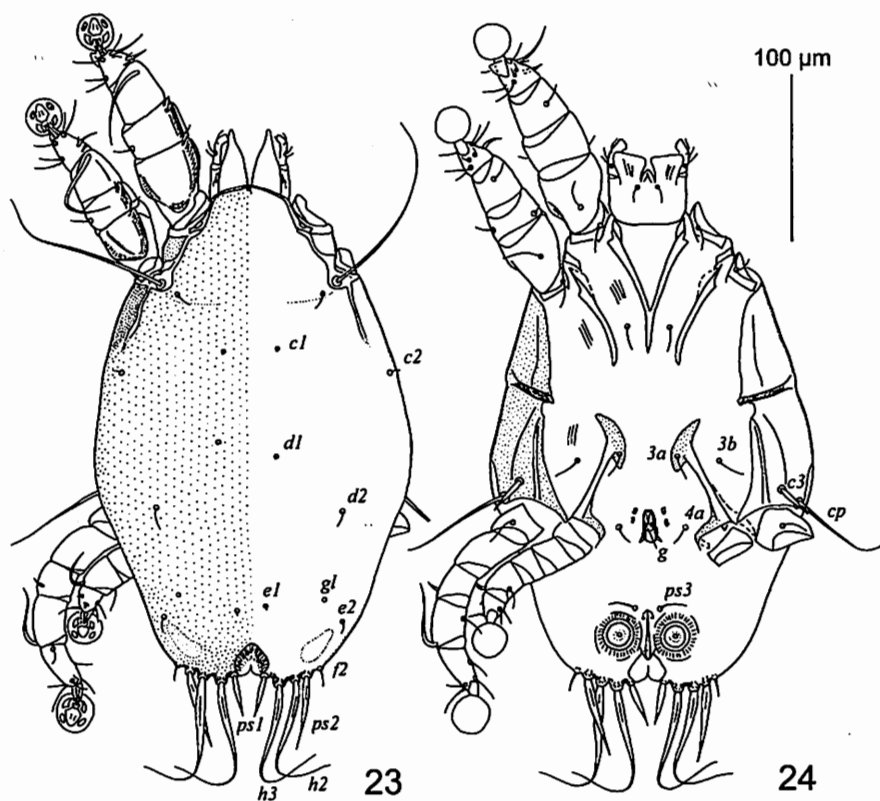
**Remark.** Setae of the terminal complex of setae (*f2*, *ps1*, *ps2*, *h2*, *h3*) having a lanceolate form or lanceolately enlarged in basal part are arranged in a row on the terminal margin of opisthosoma in both sexes of the *lanceolatus* group. It is necessary to point out that in spite of a superficial morphological similarity of these setal complexes in males and females of the *lanceolatus* group (compare Figs 29 and 36), the disposition of homologous setae is not the same. In males, seta *ps2* is between setae *f2* (the outer seta of the row) and *h2*, while in females, seta *ps2* is situated between setae *h2* and *h3*.

### 7. *Pterotrogus leucopogon* MIRONOV sp. n. (Figs 23-24, 27)

**Type material.** Male holotype, 1 male and 2 female paratypes (NU 6395) from *Campephilus leucopogon* (VALENCIENNES, 1826), Argentina, Rio Pilcomayo, 21.IV.1890, J.G. KERR. Holotype, 1 female paratype - UMMZ, other paratypes - ZISP.

#### Description

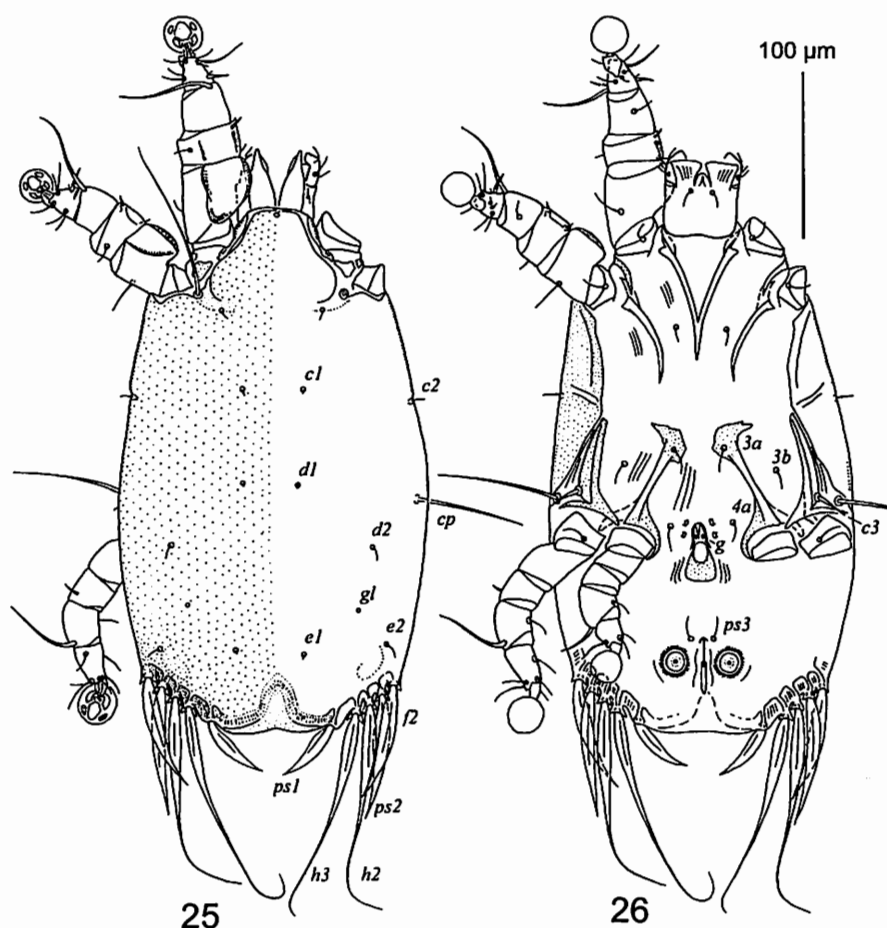
**Male** (holotype). Length of idiosoma 300, greatest width of idiosoma 192 (idiosomal size in paratype 310 x 208). Prodorsal, hysteronotal, scapular and humeral shields fused into complex dorsal shield of idiosoma, traces of fusion indistinct, scapular shields delimited from prodorsal one by narrow groove (Fig. 23); surface of hysteronotum without ornamentation; lateral margins of prodorsal shield with small incisions around bases of setae *se*; bases of setae *se* separated by 104. Length of hysterosoma from level of setae *c2* to lobar apices 183. Setae *c3* narrowly lanceolate, with acute apex, 22 in length. Dorsal setae *e1* slightly anterior to the level of lateral setae *e2*. Setae *ps1*, *ps2* narrowly lanceolate, setae *f2* setiform, macrosetae *h2*, *h3* slightly enlarged in



Figs 23-24. *Pterotrogus leucopogon*, male. 23: dorsal view of idiosoma, 24: ventral view of idiosoma.

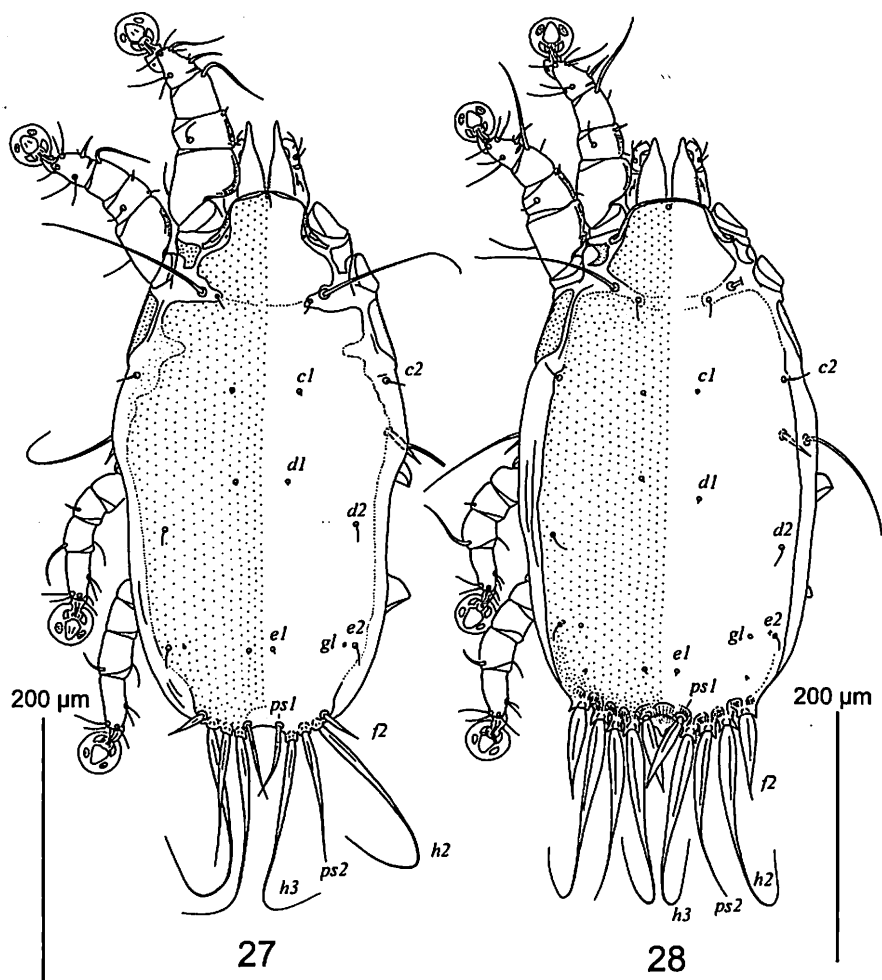
basal part; length of setae: *ps1* 20, *ps2* 38, *f2* 12; greatest width of setae: *ps1* 2, *ps2* 3, *h2* and *h3* 5. Opisthosoma wide, opisthosomal lobes with weak stump-like extensions bearing setae *h2*, *h3*, *ps2*; terminal cleft small, heart-shaped, 25 in length. Dorsal measurements: *c2-d2* 88, *d2-e2* 47, *d2-gl* 32, *gl-e1* 25, *e2-e1* 4-6, *e2-h3* 42, *h2-h2* 54, *h3-h3* 37, *ps1-ps1* 22, *ps2-ps2* 66. Epimerites I, II without sclerotized areas, epimerites IIIa form an oblique T; epandrium absent. Setae *3a* slightly anterior to *3b*. Genital arch 22 x 10, aedeagus about one third of the arch; coxal setae *4a* at midlevel of genital arch. Genital shield present. Adanal shields absent. Diameter of anal discs 13. Tarsus I wider than long. Femora I, II with clear dorsal crest, and weakly developed lateral crest; genua I, II with dorsal crest. Tarsus III with small apical claw, 31 in length; seta *r* very short, about one third of segment length. Legs IV not extending by ambulacral disc to lobar apices.

*Female* (paratype). Length of idiosoma 410, width of idiosoma 232 (idiosomal size in other paratype 424 x 220). Prodorsal and hysteronotal shields fused into complex dorsal shield of idiosoma, lateral area of this shield



Figs 25-26. *Pterotrogus robustus*, male. 25: dorsal view of idiosoma, 26: ventral view of idiosoma.

at level of sejugal region weakly sclerotized, lateral margins of prodorsal shield with angle-like incisions extending to setae *si*; bases of setae *se* separated by 91. Length of hysterosoma from the level of setae *c2* to bases of setae *h3* 287. Setae *c3* narrowly lanceolate, with acute apex, 33 in length. Posterior margin of opisthosoma with weakly expressed opisthosomal lobes, terminal cleft between macrosetae *h3* short trapezoidal, 9 in length. Setae *d1* posterior to level of setae *cp*, setae *e1* and *e2* approximately at the same transverse level. Macrosetae *h2*, *h3* and setae *ps2* slightly thickened in basal part, setae *ps1* blade-like, *f2* narrowly lanceolate; length of setae: *ps1* 50, *ps2* 92-95, *f2* 31, greatest width of setae: *ps1*, *f2* 5, *ps2*, *h2*, *h3* 7. External copulatory tube as small spine on a convex extension between setae *ps1*.



Figs 27-28. Females of the genus *Pterotrogus*, dorsal view of idiosoma. 27: *Pterotrogus leucopogon*, 28: *P. robustus*.

Dorsal measurements:  $c2-d2$  106,  $d2-e2$  93,  $e2-f2$  53,  $h2-h2$  78,  $ps1-ps1$  24. Epimerites I, II as in the male. Epigynum arch-shaped, 69 in length, 71 in width; sclerotized folds of oviporus extending to the level of anterior margins of trochanters IV. Adanal sclerites situated lateral to setae  $ps3$ . Femora I, II and genu I with weakly developed dorsal crests, genu II without crest.

**Differential diagnosis.** Within the *lanceolatus* species group, both sexes of *P. leucopogon* differ from typical species of the group (*P. robustus*, *P. lanceolatus*, and *P. melanoleucos*, see below) in having relatively weakly enlarged setae of terminal complex ( $h2$ ,  $h3$ , and  $ps2$ ), the greatest width of which does not exceed 7, and very short and blunt extension bearing these

setae; males of this species differ from named species of the *lanceolatus* group by having setiform setae *f2*. In both sexes of typical species of the *lanceolatus* group, terminal macrosetae *h2*, *h3* and setae *ps2* are situated on cup-shaped extensions, these setae of terminal complex are more enlarged and their greatest width is 11-13; in males of these species, setae *f2* are lanceolate and as wide as most other setae of the terminal complex.

**Etymology.** Specific epithet is directly accepted from the name of the type host.

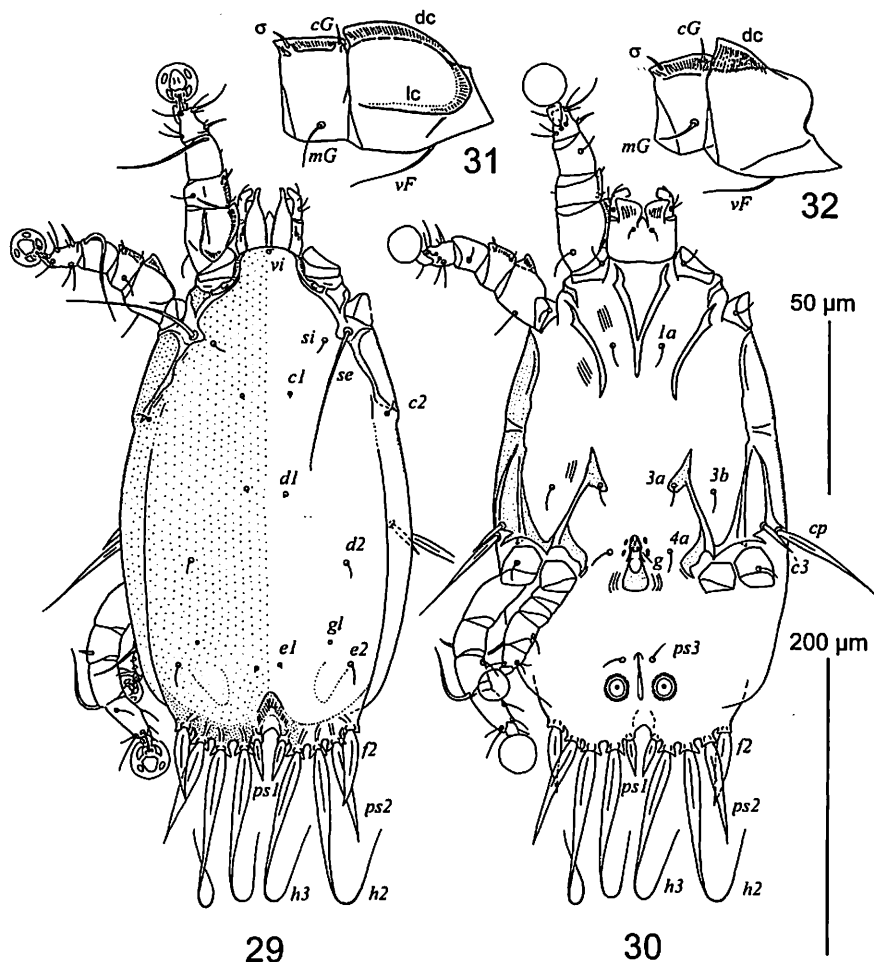
### 8. *Pterotrogus robustus* MIRONOV sp.n. (Figs 25-26, 28)

**Type material.** Male holotype, 1 male and 2 female paratypes (NU 9497, AMNH 314 401) from *Campephilus robustus* (LICHTENSTEIN, 1818), Brazil, Rio Grande de Sul, Between Passo Fundo and Nonoai, 6.II.1929, E. KAEMPFER. Holotype, 1 female paratype - UMMZ, other paratypes - ZISP.

#### Description

**Male (holotype).** Length of idiosoma 312, greatest width of idiosoma 184 (idiosomal size in paratype 294 x 174). Prodorsal, hysteronotal, scapular and humeral shields fused into complex dorsal shield of idiosoma, traces of fusion indistinct, scapular and prodorsal shields delimited by narrow groove (Fig. 25); surface of hysteronotum without ornamentation; lateral margins of prodorsal part with incisions around setae *se*; these setae separated by 86. Length of hysterosoma from level of setae *c2* to lobar apices 196. Setae *c3* spiculiform, 13 in length. Dorsal setae *e1* and *e2* approximately at the same transverse levels. Setae *ps1*, *ps2*, *f2* lanceolate slightly curved, macrosetae *h2*, *h3* with lanceolate enlargement in basal part; length of setae *ps1* 33, *ps2* 62, *f2* 60; greatest width of setae: *f2* 9-10, *ps1* 5 *ps2* 7-8, *h2*, *h3* 7-9. Opisthosomal lobes wide and short, their oblique postero-lateral margins with cup-like extensions carrying bases of setae *h2*, *h3*, *ps2*, *f2*. Terminal cleft short and wide, with heavily sclerotized terminal membrane. Dorsal measurements: *c2-d2* 88, *d2-e2* 69, *d2-gl* 39, *gl-el* 26, *e2-el* 9, *e2-h3* 42, *h2-h2* 110, *h3-h3* 95, *ps1-ps1* 71, *ps2-ps2* 126. Epimerites I, II without sclerotized areas, epimerites IIIa form an L; epiandrium absent. Setae *3a* anterior to *3b*. Genital arch 25 x 8, aedeagus about one third of the arch length, coxal setae *4a* at level of genital arch apex. Genital shield present. Adanal shields absent. Diameter of anal discs 13. Tarsus I longer than wide. Femora I, II with longitudinal dorsal crest and lateral crest; genua I, II with dorsal crest. Tarsus III with rudimentary apical claw, 25 in length; seta *r* short, about one third of the segment length. Legs IV short, ambulacral discs reaching to the level of setae *f2*.

**Female (paratype).** Length of idiosoma 422, width of idiosoma 215 (idiosomal size in other paratype 410 x 218). Trace between fused prodorsal and hysteronotal shields indistinct; scapular shield separated from prodorsal shield by narrow groove, lateral margins of prodorsal shield with small narrow incisions around setae *si* and *se*; bases of setae *se* separated by 88. Length of hysterosoma from the level of setae *c2* to posterior end 272. Setae *c3* spiculiform, 31 in length. Posterior margin of opisthosoma with cup-like



Figs 29-32. *Pterotrogus lanceolatus*, male. 29: dorsal view of idiosoma, 30: ventral view of idiosoma, 31: femur and genu I, 32: femur and genu II. dc – dorsal crest, lc – lateral crest.

extensions carrying setae *h2*, *h3*, *ps2* and with stump-like extension bearing setae *f2*. Setae *d1* posterior to level of setae *cp*; setae *e1* posterior to the level of setae *e2*. Setae *f2*, *ps1*, *ps2* lanceolate, macrosetae *h2*, *h3* with lanceolate enlargement in basal half, with long thread-like apical filament; length of setae: *ps1* 55, *ps2* 122-124, *f2* 66; greatest width of setae *ps1* 9-10, *f2*, *ps2*, *h2*, *h3* 12-13. External copulatory tube as small spine on a convex extension between setae *ps1*. Dorsal measurements: *c2-d2* 133, *d2-e2* 66, *e2-f2* 55, *e2-e1* 54, *h2-h2* 93, *ps1-ps1* 25. Epimerites I, II as in the male. Epigynum arch-shaped, 68 in length, 69 in width; sclerotized folds of oviporus extending to the level of anterior margin of trochanters IV. Adanal sclerites situated lateral

to setae *ps3*. Femora I, II and genua I, II with narrow dorsal crest; the crest of femur II with short tooth.

**Differential diagnosis.** *Pterotrogus robustus* and three species described below (*P. lanceolatus*, *P. melanoleuci*, and *P. guatemalensis*) represent typical species of the *lanceolatus* group. Males of *P. robustus* differ from these species by the position of setae *ps1*, which are the most caudal pair in the terminal complex of setae and are widely separated from each other (about 70); females are distinguished by longer setae *f2* (over 65). In males of three named species, the setae *ps1* are situated on the inner margins of a small terminal cleft, anterior to the level of setae *h3*, and very close to each other (separated by 10-20); in females, setae *f2* are much shorter, 40-46.

**Etymology.** Specific epithet is directly accepted from the name of the type host.

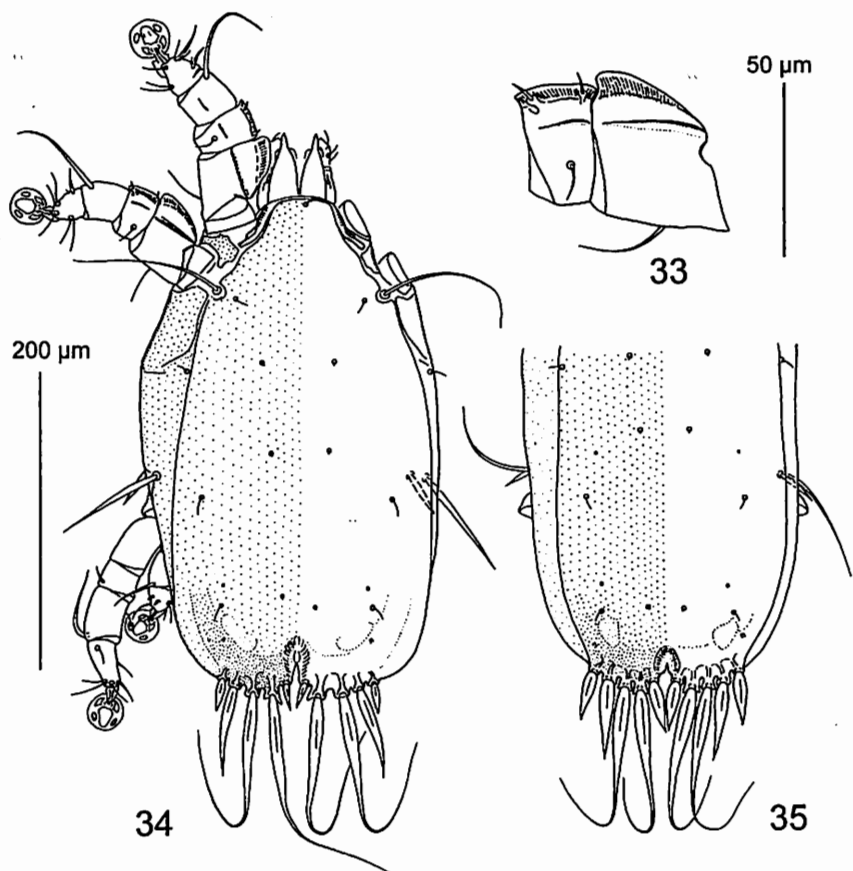
### 9. *Pterotrogus lanceolatus* MIRONOV sp. n. (Figs 29-32, 36)

**Type material.** Male holotype, 1 female paratype (UGA 9466, AMNH 151 527) from *Campephilus guayaquilensis* (LESSON, 1845), Peru, Piura Province, 27.VI.1919, H. WATKINS. Holotype and paratype - UMMZ.

**Additional material.** 3 females (UGA 9465, AMNH 171 235) from *C. guayaquilensis*, Ecuador, Prov. De Loja, Alamon, 24. VIII. 1921, G.K. CHERRIE.

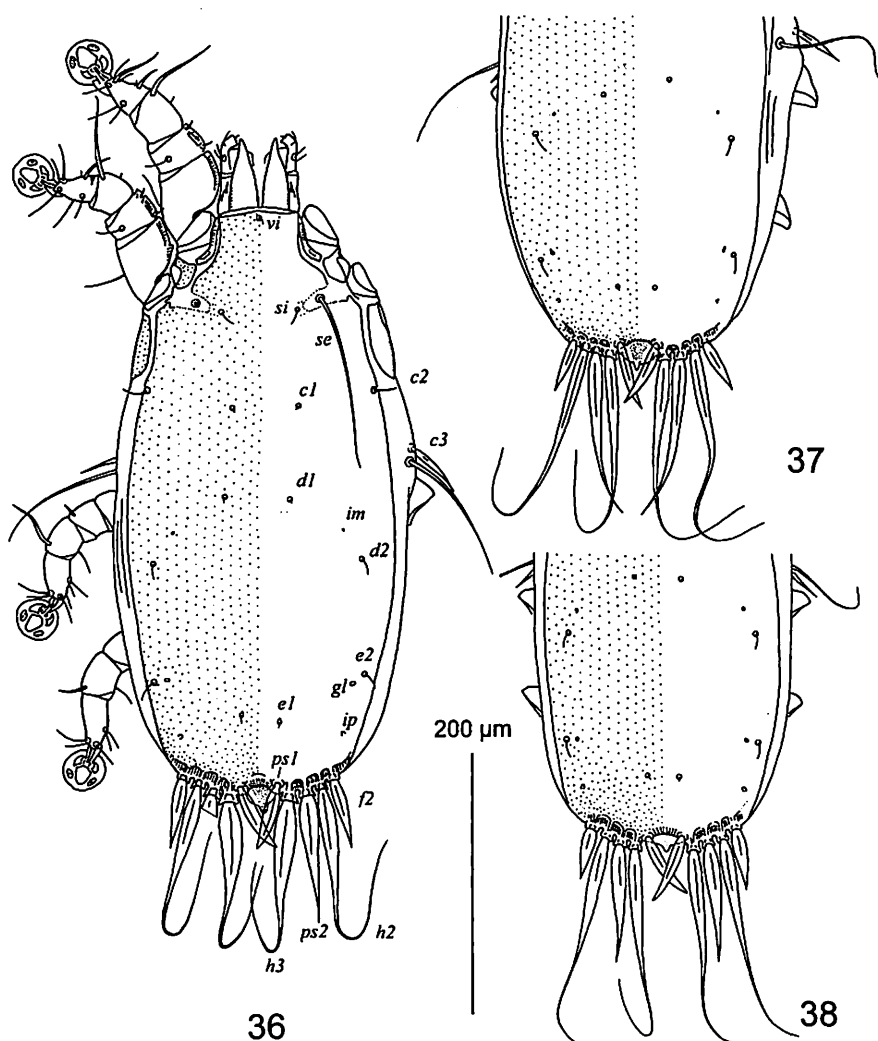
#### Description

**Male** (holotype). Length of idiosoma 340, greatest width of idiosoma 183. Prodorsal, hysteronotal, scapular and humeral shields fused into complex dorsal shield of idiosoma, traces of fusion indistinct, scapular and prodorsal shields delimited by narrow groove (Fig. 29); surface of hysteronotum without ornamentation; lateral margins of prodorsal part with small incisions around setae *se*; bases of setae *se* separated by 98. Length of hysterosoma from level of setae *c2* to lobar apices 218. Setae *c3* narrowly lanceolate, 24 in length. Dorsal setae *e1* and *e2* approximately at the same transverse levels. Setae *ps1*, *ps2*, *f2* lanceolate, macrosetae *h2*, *h3* with lanceolate enlargement in basal part, with filiform apical part; length of setae: *ps1* 23, *ps2* 66, *f2* 44, greatest width of setae: *h2*, *h3*, *ps2*, *f2* 10-13, *ps1* 9-10. Opisthosomal lobes short and wide; posterior margin of each lobe with cup-like extensions carrying setae *h2*, *h3*, *ps2*, and setae *f2*. Terminal cleft ovate, with small extensions bearing setae *ps1*, length of the cleft from anterior end to level of setae *h3* 17. Dorsal measurements: *c2-d2* 95, *d2-e2* 67, *d2-gl* 55, *gl-el* 13-15, *e2-h3* 60, *h2-h2* 62, *h3-h3* 35, *ps1-ps1* 17, *ps2-ps2* 84. Epimerites I, II without sclerotized areas, epimerites IIIa form an oblique T; epiandrium absent. Setae *3a* and *3b*, approximately at the same transverse level. Genital arch 25 x 8, aedeagus about one third of the arch; coxal setae *4a* at midlevel of genital arch. Genital shield present. Adanal shields absent. Diameter of anal discs 13. Tarsus I longer than wide. Femora I, II with well-developed dorsal crest and narrow lateral crest, genua I, II with dorsal crest, the crest of femur II angle-shaped. Tarsus III without apical claw, 31 in length; seta *r* very short, about one third of segment length. Legs IV short, slightly extending by ambulacral discs beyond anal discs.



Figs 33-35: Males of the genus *Pterotrogus*. 33: *Pterotrogus melanoleuci*, femur and genu II, 34: same, dorsal view of idiosoma, 35: *P. guatemalensis*, dorsal view of opisthosoma.

*Female* (paratype). Length of idiosoma 445, width of idiosoma 215. Trace between fused prodorsal and hysteronotal shields indistinct; scapular shield separated from prodorsal shield by narrow groove, lateral margins of prodorsal shield with small incisions around bases of setae *se*; these setae separated by 93. Length of hysterosoma from the level of setae *c2* to bases of setae *h3* 308. Setae *c3* narrowly lanceolate, 39 in length. Posterior margin of opisthosoma with cup-like extensions bearing setae *h2*, *h3*, *ps2*; stump-like extensions carrying setae *f2*. Terminal cleft small, length from anterior end to bases of setae *h3* 17. Setae *d1* posterior to level of setae *cp*, setae *e1* posterior to the level of setae *e2*. Setae *f2*, *ps1*, *ps2* lanceolate; macrosetae *h2*, *h3* with lanceolate enlargement in basal part, with long thread-like apical filament; length of setae: *ps1* 51, *ps2* 86, *f2* 46; greatest width of setae: *ps1*, *f2* 11, *h2*, *h3*, *ps2* 12-13. External copulatory tube as small spine on convex weakly sclerotized extension between setae *ps1*. Dorsal measurements: *c2-d2* 126,



Figs 36-38. Females of the genus *Pterotrogus*. 36: *Pterotrogus lanceolatus*, dorsal view of idiosoma, 37: *P. melanoleuci*, dorsal view of opisthosoma, 38: *P. guatemalensis*, dorsal view of opisthosoma.

*d2-e2* 90, *e2-f2* 78, *e2-e1* 44-53, *h2-h2* 88, *ps1-ps1* 24. Epimerites I, II as in the male. Epigynium 66 x 71; sclerotized folds of oviporus extending to anterior margins of trochanters IV. Adanal sclerites of irregular form situated lateral to setae *ps3*. Femora I, II and genua I, II with narrow dorsal crest; the dorsal crest of femur II with short tooth.

**Differential diagnosis.** *Pterotrogus lanceolatus* is very similar to *P.*

*guatemalensis* (see below), with the most characteristic feature of these species being the angle-shaped dorsal crest of femur II in males (Fig. 32). Males of *P. lanceolatus* differ by distinctly narrower and shorter setae *ps1*, with a length of about half of setae *f2* (Fig. 29, 30), and by longer setae *ps2* (about 65); females differ only by longer idiosoma, which varies from 445-455 ( $n=4$ ). In males of *P. guatemalensis*, setae *ps1* are subequal in size to setae *f2* (Fig. 35), and setae *ps2* shorter (about 46); in single female of that species, the length of idiosoma is 415.

**Etymology.** Specific epithet indicates the lanceolate form of setae of the opisthosoma.

### 10. *Pterotrogus melanoleuci* MIRONOV sp. n. (Figs 33-34, 37)

**Type material.** Male holotype, female paratype (UGA 9462 AMNH 278 277) from *Campephilus melanoleucos* (GMELIN, 1788), Brazil, Amazonas, near Borba, 24.III.1930, OLALLA Brothers. Holotype and paratype - UMMZ.

#### Description

**Male** (holotype). Length of idiosoma 330, greatest width of idiosoma 187. Prodorsal, hysteronotal, scapular and humeral shields fused into complex dorsal shield of idiosoma, traces of fusion indistinct, scapular and prodorsal shields delimited by narrow groove; surface without ornamentation; lateral margins of prodorsal part with small incision around bases of setae *se*; setae *se* separated by 108. Length of hysterosoma from level of setae *c2* to lobar apices 210. Setae *c3* narrowly lanceolate, 24 in length. Dorsal setae *e1* and *e2* approximately at the same transverse levels, hysteronotal gland openings *gl* poorly developed. Setae *ps1*, *ps2*, *f2* lanceolate, macrosetae *h2*, *h3* with lanceolate enlargement in basal part; length of setae: *ps1* 17, *ps2* 53, *f2* 17; greatest width of setae *ps1*, *f2* 3.5-4, *h2*, *h3* and *ps2* 8-9. Opisthosomal lobes short and blunt; posterior margin of each lobe with stump-like extensions bearing setae *ps2*, *f2*, and cup-like extension bearing setae *h2*, *h3* (Fig. 33). Terminal cleft small and narrow, with rectangular ledges bearing setae *ps1*, length of the cleft from anterior end to level of setae *h3* 22. Dorsal measurements: *c2-d2* 88, *d2-e2* 64, *d2-gl* 55, *gl-e1* 9-12, *e2-h3* 60, *h2-h2* 60, *h3-h3* 30, *ps1-ps1* 11, *ps2-ps2* 80. Epimerites I, II without sclerotized areas, epimerites IIIa form an oblique T. Setae *3a* slightly anterior to *3b*. Genital arch 22 x 9, aedeagus about one third of the arch; genital shield present, epiandrium absent; coxal setae *4a* at midlevel of genital apparatus. Adanal shields absent. Diameter of anal discs 14. Tarsus I longer than wide. Femora and genua I, II with dorsal and lateral crests. Tarsus III without apical claw, 28 in length. Legs IV short, slightly extending by ambulacral discs beyond the level of anal discs.

**Female** (paratype). Length of idiosoma 438, width of idiosoma 223. Trace between fused prodorsal and hysteronotal shields indistinct; scapular shield separated from prodorsal shield by narrow groove, lateral margins of prodorsal shield with small incisions around bases of setae *se*; bases of setae *se* separated by 92. Length of hysterosoma from the level of setae *c2* to bases of setae *h3* 294. Setae *c3* narrowly lanceolate, 38 in length. Posterior margin of

opisthosoma rounded, with small terminal cleft between bases of setae *h3*, margins of opisthosoma with stump-like extension bearing setae *h2*, *h3*, *ps2*. Setae *d1* posterior to the level of setae *cp*; setae *e1* posterior to the level of setae *e2*. Setae *f2*, *ps1*, *ps2* lanceolate, macrosetae *h2*, *h3* with lanceolate enlargement in basal part, with long thread-like apical filament; length of setae: *ps1* 45, *ps2* 112, *f2* 40; greatest width of setae: *ps1*, *f2* 6-7, *ps2*, *h2* and *h3* 8-9. External copulatory tube as small spine on a weakly sclerotized convex extension between setae *h3*. Dorsal measurements: *c2-d2* 128, *d2-e2* 88, *e2-f2* 66, *e2-e1* 22, *h2-h2* 82, *ps1-ps1* 26. Epimerites I, II as in the male. Epigynum 75 x 66; sclerotized folds of oviporus extending to anterior margins of trochanters IV. Adanal sclerites of irregular form situated lateral to setae *ps3*. Femora and genua I, II with narrow dorsal crest; the dorsal crest of femur II with small tooth.

**Differential diagnosis.** *Pterotrogus melanoleuci* is similar to *P. lanceolatus* in the form of the setae in the terminal complex. Males of *P. melanoleuci* differ by setae *f2* and *ps1*, which are equal in length and relatively short (17 in length); in contrast, the female's setae differ by having longer setae *ps2* (about 110 in length), which are approximately three times longer than setae *ps1*, *f2*. In the males of *P. lanceolatus*, setae *f2* are 44 in length and approximately twice as long as setae *ps1* (Figs 29, 30); in the females, setae *ps2* are much shorter (about 65) and approximately twice as long as setae *ps1* and *f2*.

**Etymology.** Specific epithet derives from specific name of the type host.

### 11. *Pterotrogus guatemalensis* MIRONOV sp. n. (Figs 35, 38)

**Type material.** Male holotype, 1 male and 1 female paratype (UGA 9461, AMNH 488 504) from *C. guatemalensis* (HARTLAUB, 1844), NW of Colombia, Brava Is., 28.I.1902, J.H. BATTY. Holotype and paratypes - UMMZ.

#### Description

**Male (holotype).** Length of idiosoma 334, greatest width of idiosoma 178. Prodorsal, hysteronotal, scapular and humeral shields fused into complex dorsal shield of idiosoma, traces of fusion indistinct, scapular and prodorsal shields delimited by narrow groove; surface of hysteronotum without ornamentation; lateral margins of prodorsal part with small incisions around setae *se*; bases of setae *se* separated by 100. Length of hysterosoma from level of setae *c2* to lobar apices 220. Setae *c3* narrowly lanceolate, 22 in length. Dorsal setae *e1* and *e2* approximately at the same transverse level. Setae *ps1*, *ps2*, *f2* lanceolate, macrosetae *h2*, *h3* with lanceolate enlargement in basal part (Fig. 35); length of setae: *ps1* 33, *ps2* 46, *f2* 33, greatest width of setae: *h2*, *h3*, *ps2*, 10-11, *ps1*, *f2* 9. Opisthosomal lobes short and wide; posterior margin of each lobe with cup-like extensions carrying setae *h2*, *h3*, *ps2*, and stump-like extension carrying setae *f2*. Terminal cleft ovate, with small extensions bearing setae *ps1*, length of the cleft from anterior end to level of setae *h3* 17. Dorsal measurements: *c2-d2* 93, *d2-e2* 75, *d2-gl* 57, *gl-e1* 17, *e2-h3* 51, *h2-h2* 56, *h3-h3* 33, *ps1-ps1* 15, *ps2-ps2* 73. Epimerites I, II without sclerotized areas, epimerites IIIa form an oblique T. Setae *3a* and *3b* approximately at the

same transverse level. Genital arch  $26 \times 10$ , aedeagus about one third of the arch; coxal setae *4a* at midlevel of genital arch, genital shield present, epiandrium absent. Adanal shields absent. Diameter of anal discs 13. Tarsus I longer than wide. Femora I, II with well-developed dorsal crest and narrow lateral crest, genua I, II with dorsal crest, the dorsal crest of femur II angle-shaped as in *P. lanceolatus* (Fig. 32). Tarsus III without apical claw, 29 in length. Legs IV short, ambulacral discs extending only slightly beyond anal discs.

**Female** (paratype). Length of idiosoma 415, width of idiosoma 196. Trace between fused prodorsal and hysteronotal shields indistinct; scapular shield separated from prodorsal shield by narrow groove, lateral margins of prodorsal shield with small incisions around bases of setae *se*; these setae separated by 86. Length of hysterosoma from the level of setae *c2* to bases of setae *h3* 287. Setae *c3* narrowly lanceolate, 35 in length. Posterior margin of opisthosoma with cup-like extensions bearing setae *h2*, *h3*, *ps2*; stump-like extensions carrying setae *f2*. Terminal cleft small, length from anterior end to bases of setae *h3* 13. Setae *d1* posterior to level of setae *cp*, setae *e1* posterior to the level of setae *e2*. Setae *f2*, *ps1*, *ps2* lanceolate; macrosetae *h2*, *h3* with lanceolate enlargement in basal part, with long thread-like apical filament; length of setae: *ps1* 51, *ps2* 84, *f2* 42; greatest width of setae: *ps1*, *f2* *h2*, *h3*, *ps2* 9-10, *ps2* 11. External copulatory tube as small spine on convex weakly sclerotized extension between setae *ps1*. Dorsal measurements: *c2-d2* 112, *d2-e2* 82, *e2-f2* 66, *e2-e1* 28-31, *h2-h2* 84, *ps1-ps1* 24. Epimerites I, II as in the male. Epigynium arch-shaped,  $69 \times 67$ ; sclerotized folds of oviporus extending to anterior margins of trochanters IV. Adanal sclerites of irregular form situated lateral to setae *ps3*. Femora I, II and genua I, II with narrow dorsal crest; the dorsal crest of femur II with short tooth.

**Differential diagnosis.** This species is very similar to *P. lanceolatus* in size and proportion of setae of the terminal complex. Males of *P. guatemalensis* differ from that species by having larger setae *ps1*, which are equal in size to setae *f2* (Fig. 35), and shorter setae *ps2* (about 46 in length). In the males of *P. lanceolatus*, setae *ps1* are only about half the length of setae *f2* and distinctly narrower (Fig. 36), and setae *ps2* longer, about 65 in length. The single female paratype of *P. guatemalensis* differs only by shorter idiosoma (415); the idiosomal length of *P. lanceolatus* females ranges from 445-455.

**Etymology.** Specific epithet is directly taken from the name of the type host.

## 12. *Pterotrogus rubricollis* MIRONOV sp. n (Fig. 22)

**Type material.** Holotype female, paratype female (UGA 9473, AMNH 276 026) from *Campephilus rubricollis* (BODDAERT, 1783), Venezuela, Amazonas, Rio Casiquiare & Rio Negro, 24.IX.1928, R.S. DECK. Holotype and paratype - UMMZ

### Description

**Female** (holotype). Length of idiosoma 455, width of idiosoma 241 (idiosomal size in paratype  $432 \times 236$ ). Trace between fused prodorsal and

hysteronotal shields indistinct; scapular shield separated and distant from prodorsal shield; lateral margins of prodorsal shield with small angular incisions around setae *se*; bases of setae *se* separated by 108. Length of hysterosoma from the level of setae *c2* to bases of setae *h3* 308. Setae *c3* narrowly lanceolate, 38 in length. Posterior margin of opisthosoma with short extensions as truncated cone bearing macrosetae *h2*, *h3*, with small terminal cleft between bases of setae *h3*. Setae *d1* posterior to the level of setae *cp*; setae *e1* anterior to the level of setae *e2*. Setae *f2*, *ps1*, *ps2* narrowly lanceolate; macrosetae *h2*, *h3* slightly enlarged in basal part; length of setae: *ps1* 49, *ps2* 40, *f2* 22; greatest width of setae *ps1*, *ps2*, *h2*, *h3* 4.5-5, *f2* 3-3.5. External copulatory tube as small spine on a weakly sclerotized convex extension between setae *h3*. Dorsal measurements: *c2-d2* 113, *d2-e2* 88, *e2-f2* 62, *e1-e2* 22-23, *h2-h2* 86, *ps1-ps1* 31. Epimerites I, II without sclerotized areas. Epigynium arch-shaped, 60 x 82; sclerotized folds of oviporus extending to anterior margins of trochanters IV. Adanal sclerites of irregular form situated lateral to setae *ps3*. Femora and genua I, II with narrow dorsal crest; the dorsal crest of femur II with tooth.

Male unknown.

**Differential diagnosis.** This species, known only from the female, is most similar to *P. leucopogon* by having relatively narrow setae *f2*, *ps2* and macrosetae *h2*, *h3*, the greatest width of which does not exceed 5. The new species differs by setae *ps1* and *ps2* being similar in length (48-49 and 40-42, respectively) and cone-like extensions bearing macrosetae *h2*, *h3* (Fig. 22). In females of *P. leucopogon*, setae *ps2* are almost twice as long as setae *ps1* (92-95 versus 50-52), extensions bearing macrosetae *h2*, *h3* are very short, stump-like (Fig. 27).

**Etymology.** Specific epithet is directly accepted from the name of the type host.

### Species group *iron*

**Diagnosis.** In both sexes, setae *h2*, *h3*, *ps1*, *ps2* setiform, femora and genua I, II with dorsal crest. In males, idiosoma greatly widened, anterior end attenuate, posterior end of opisthosoma almost rectangular, opisthosomal lobes very short and wide, surface of hysteronotum without ornamentation, epimerites I, II, IIIa without large sclerotized areas, coxal fields III closed or almost closed, setae *f2* setiform. In females, idiosoma widely ovate, setae *f2* setiform or lanceolate.

### 13. *Pterotrogus iron* MIRONOV sp. n. (Figs 39-42)

**Type material.** Male holotype, 1 male and 1 female paratypes (UGA 9459, AMNH 247 495) from *Campephilus guatemalensis* (HARTLAUB, 1844), W. Panama, Boca del Toro, Almirante, 8.IX.1927, R.R. BENSON. Holotype and paratypes - UMMZ.

### Description

**Male** (holotype). Length of idiosoma 260, greatest width of idiosoma 196 (idiosomal size in paratype 258 x 195). Prodorsal, hysteronotal, scapular and

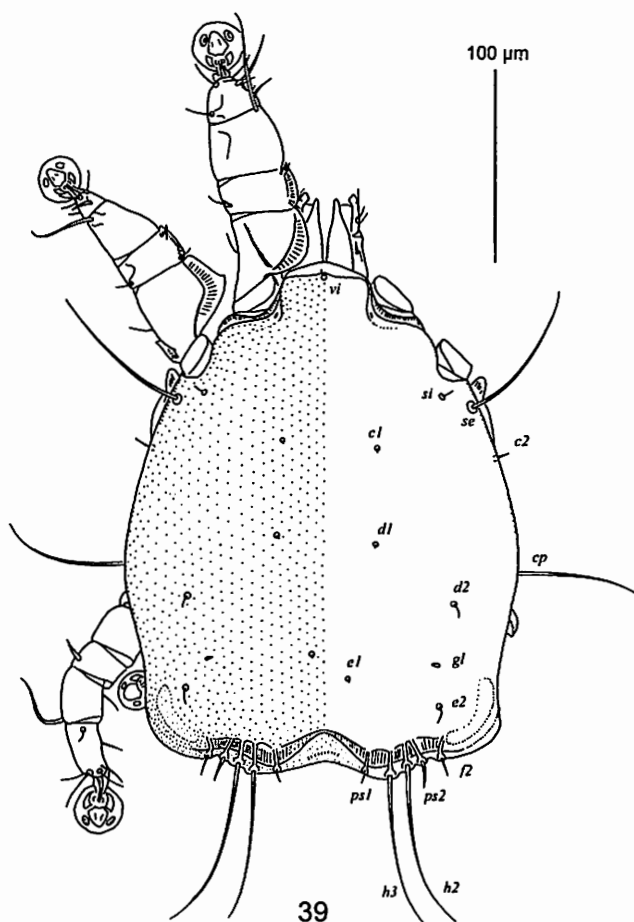


Fig. 39. *Pterotrogus iron*, dorsal view of male.

humeral shields fused into entire dorsal shield of idiosoma, any trace of fusion indistinct; surface of dorsum without ornamentation; lateral margins of prodorsal part without incisions; bases of setae *se* separated by 144. Length of hysterosoma from level of setae *c2* to lobar apices bearing setae *h3* 156. Setae *c3* spiculiform, 11 in length. Dorsal setae *e1* anterior to *e2*, approximately at level of hysteronotal gland openings *gl*. Setae *ps1*, *ps2*, *f2* and macrosetae *h2*, *h3* setiform; length of setae *ps1* 6, *ps2* 13, *f2* 9. Opisthosoma almost as wide as body at the level of humeral setae *cp*; opisthosomal lobes very wide, short, and truncated; terminal cleft shallowly concave, 24 in length, with narrow and heavily sclerotized membrane (Fig. 39). Dorsal measurements: *c2-d2* 71, *d2-e2* 51, *d2-gl* 27, *e2-e1* 15-24, *e2-h3* 33, *h2-h2* 84, *h3-h3* 69, *ps1-ps1* 44,

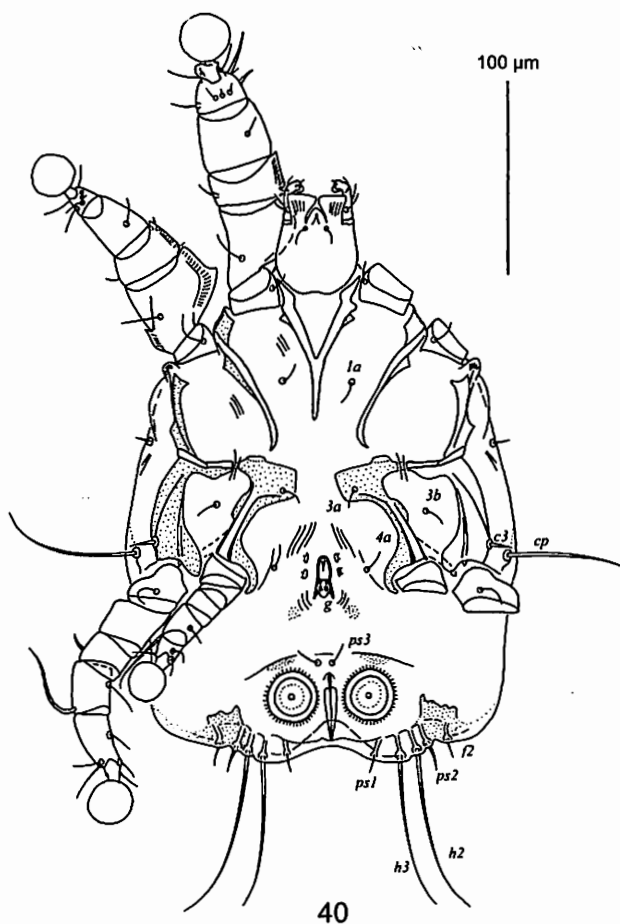
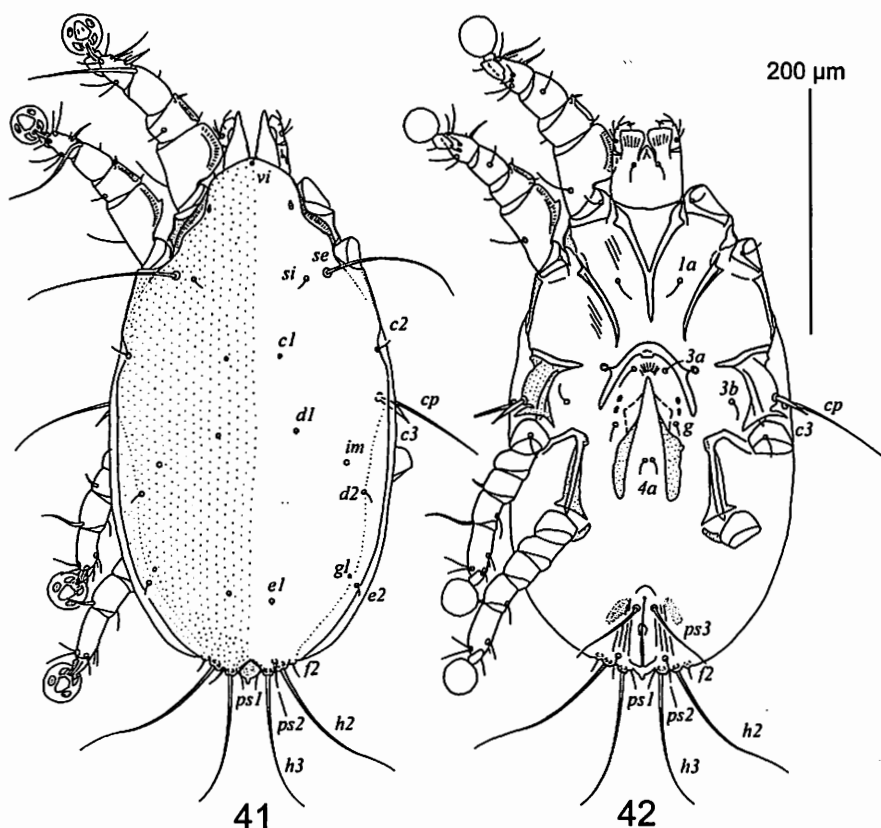


Fig. 40. *Pterotrogus iron*, ventral view of male.

*ps2-ps2* 95. Epimerites I, II without wide sclerotized areas; inner end of epimerites IIIa with large sclerite of irregular form, coxal fields III almost closed, anterior border interrupted by a few striae (Fig. 40). Setae 3a anterior to 3b. Genital arch 20 x 11, aedeagus about one quarter of the arch, genital shield and epiandrium absent; coxal setae 4a slightly anterior to midlevel of the genital arch. Poorly developed adanal shields present; opisthoventral shields anterior to bases of setae *f2*, *ps2* present. Diameter of anal discs 25. Tarsus I wider than long. Femur I with dorsal and lateral crests, femur II with dorsal and basiventral crest, genua I, II with dorsal crest, the dorsal crest of femur II with large tooth. Tarsus III with small apical claw, 29 in length. Legs IV short, extending by ambulacral disc to the midlevel of anal discs.



Figs 41-42. *Pterotrogus iron*, female. 41: dorsal view of idiosoma, 42: ventral view of idiosoma.

*Female* (paratype). Length of idiosoma 420, width of idiosoma 232 (idiosomal size in other paratype 410 x 230). Prodorsal, hysteronotal and scapular shields fused into entire dorsal shield covering almost entire idiosoma, traces of fusion between prodorsal and scapular shields visible, lateral margins of prodorsal shield without incision; bases of setae *se* separated by 118. Length of hysterosoma from the level of setae *c2* to posterior end 263. Setae *c3* narrowly lanceolate, 29 in length. Posterior margin of opisthosoma rounded, with small terminal cleft between setae *h3*. Setae *d1* posterior to level of setae *cp*, setae *e1* posterior to the level of setae *e2*, cupules *im* visible. Setae *f2*, *ps1*, *ps2* and macrosetae *h2*, *h3* setiform; length of setae: *ps1* 13, *ps2* 15, *f2* 11. External copulatory tube as small spine on a convex weakly sclerotized extension between setae *h3*. Dorsal measurements: *c2-d2* 116, *d2-e2* 71, *e2-f2* 66, *e2-e1* 9-15, *h2-h3* 51, *ps1-ps2* 18. Epigynum 57 x 69, with pair of short epimeral extensions; sclerotized folds of oviporus extending beyond midlevel of epimerites IV. Adanal sclerites of irregular form situated lateral to

setae *ps3*. Femora and genua I, II with narrow dorsal crest; the dorsal crest of femur II with one small tooth.

**Differential diagnosis.** Males of *Pterotrogus iron* differ from the second species of the group, *P. quadratus* (see below), by having incompletely closed coxal fields III, anterior margin of which is interrupted by a few longitudinal striae, and the absence of sclerite encompassing bases of setae *ps3*; females are distinguished by setiform setae *f2*. In the males of *P. quadratus*, coxal fields III are completely closed, bases of setae *ps3* are situated on an unpaired small sclerite anterior to anal opening; in the females, setae *f2* are lanceolate.

**Etymology.** Specific epithet indicates the iron-shaped (sub-cuneiform) idiosoma in males.

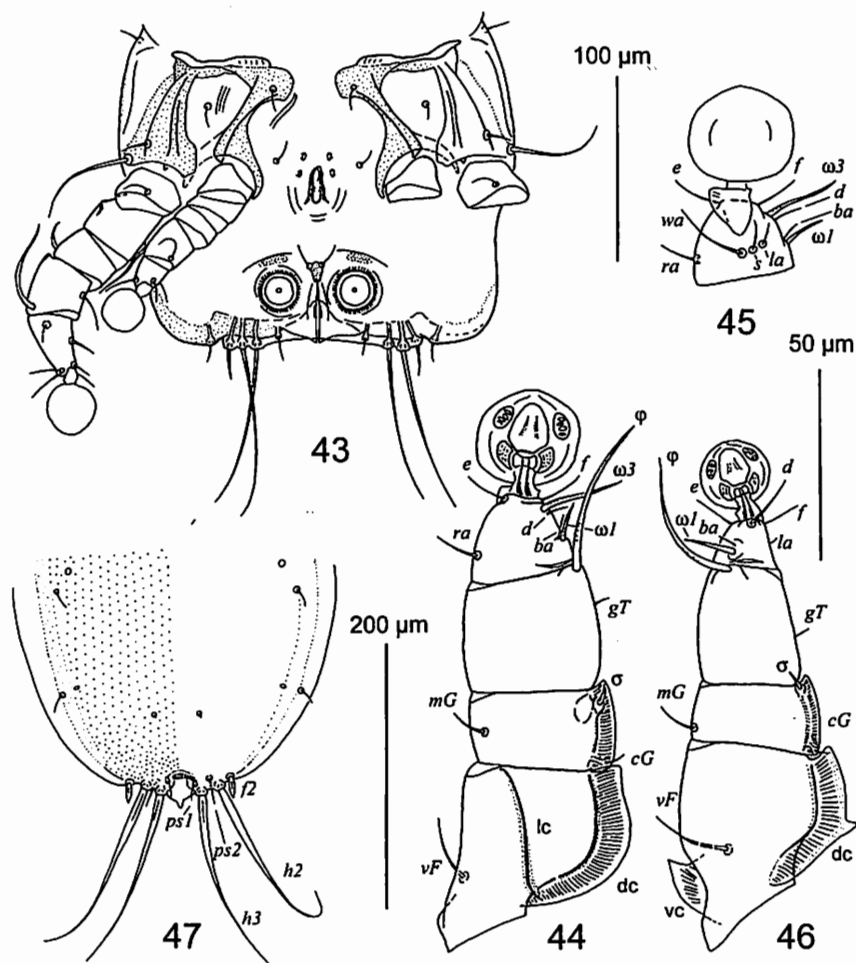
#### 14. *Pterotrogus quadratus* MIRONOV sp. n. (Figs 43-47)

**Type material.** Male holotype, 2 male and 3 female paratypes (UGA 9473, AMNH 276 026) from *Campephilus rubricollis* (BODDAERT, 1783), Venezuela, Amazonas, Rio Casiquiare & Rio Negro, 24.IX.1928, R.S. DECK. Holotype, 1 male and 2 female paratypes – UMMZ, other paratypes – ZISP.

#### Description

**Male** (holotype). Length of idiosoma 263, greatest width of idiosoma 205 (idiosomal size in 2 paratypes 267-270 x 202-208). Prodorsal, hysteronotal, scapular and humeral shields fused into entire dorsal shield of idiosoma, traces of fusion indistinct; surface without ornamentation; lateral margins of prodorsal shield without incisions; bases of setae *se* separated by 155. Length of hysterosoma from the level of setae *c2* to lobar apices bearing setae *h3* 167. Setae *c3* spiculiform, 12 in length. Dorsal setae *e1* anterior to *e2*. Setae *ps1*, *ps2*, *f2* and macrosetae *h2*, *h3* setiform; length of setae *ps1* 7, *ps2* 25, *f2* 14. Opisthosoma as wide as body at the level of humeral setae *cp*, almost rectangular in shape; opisthosomal lobes very wide and short; terminal cleft shallowly concave, 24 in length, with heavily sclerotized interlobar membrane (Fig. 43). Dorsal measurements: *c2-d2* 73 *d2-e2* 47, *d2-gl* 29, *gl-e1* 3-13, *e2-e1* 4-14, *e2-h3* 37, *h2-h2* 84, *h3-h3* 69, *ps1-ps1* 47, *ps2-ps2* 98. Epimerites I, II without wide sclerotized areas; inner end of epimerites IIIa with large sclerite of irregular form, coxal fields III closed. Setae *3a* anterior to *3b*. Genital arch 20 x 10 in width, aedeagus about one third of the arch, genital shield and epiandrium absent; coxal setae *4a* at the level of arch apex. Adanal shields represented by pair of weakly sclerotized transverse sclerites anterior to anal discs and unpaired sclerite bearing setae *ps3*. Weakly sclerotized opisthoventral shields at bases of setae *h2*, *h3* present. Diameter of anal discs 20. Tarsus I wider than long. Femur I with dorsal and lateral crests, femur II with dorsal and basiventral crest, genua I, II with dorsal crest, the dorsal crest of femur II with tooth. Tarsus III with small apical claw, 33 in length. Legs IV short, ambulacral discs reaching only to posterior margin of anal discs.

**Female** (paratype). Length of idiosoma 420, width of idiosoma 245 (idiosomal size in other paratypes 420-428 x 342-258). Prodorsal, hysteronotal and scapular shields fused into entire dorsal shield of idiosoma, traces of



Figs 43-47. *Pterotrogus quadratus*. 43: hysterosoma of male, ventral view, 44: leg I of male, dorsal view, 45: tarsus I of male, ventral view; 46: leg II of male, dorsal view, 47: opisthosoma of female, dorsal view. dc - dorsal crest, lc - lateral crest, vc - basiventral crest.

fusion between prodorsal and scapular shield visible; lateral margins of prodorsal shield without incision; bases of setae *se* separated by 122. Length of hysterosoma from the level of setae *c2* to posterior end 267. Setae *c3* narrowly lanceolate, 27 in length. Posterior margin of opisthosoma rounded, with small terminal cleft between setae *h3*. Setae *d1* posterior to level of setae *cp*, setae *e1* posterior to the level of setae *e2*, cupules *im* visible. Setae *ps1*, *ps2* and macrosetae *h2*, *h3* setiform, setae *f2* lanceolate (Fig. 47); length of setae: *ps1* 13, *ps2* 15, *f2* 11, width of setae *f2* 5. External copulatory tube as small spine on a convex weakly sclerotized extension between setae *h3*. Dorsal

measurements: *c2-d2* 116, *d2-e2* 71, *e2-f2* 66, *e2-e1* 9-15, *h2-h2* 51, *ps1-ps1* 18. Epigynium 57 x 90 in width, with a pair of short lateral extensions; sclerotized folds of oviporus extending beyond midlevel of epimerites IV. Adanal sclerites of irregular form situated lateral to setae *ps3*. Femora and genua I, II with narrow dorsal crest; the dorsal crest of femur II with tooth.

**Differential diagnosis.** The males of *Pterotrogus quadratus* differ from those of the previous species by having coxal fields III completely closed, and a small unpaired sclerite bearing both setae *ps3*; the females differ in having lanceolate setae *f2*. In the males of *P. iron*, coxal fields III have a small interruption in anterior margin, and setae *ps3* are situated on soft integument; in the females, setae *f2* are short setiform.

**Etymology.** Specific epithet points out an almost rectangular form of opisthosoma in males.

### Species group *sinusoidus*

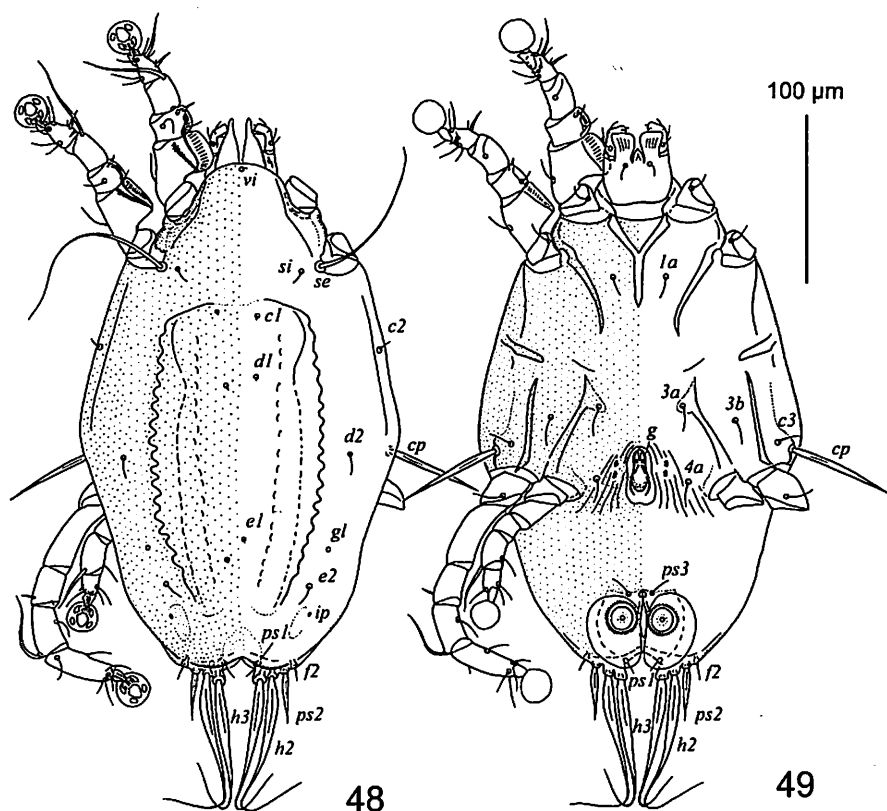
**Diagnosis.** In both sexes, setae *ps2* lanceolate, setae *h2*, *h3* with lanceolate enlargement in basal part, femora and genua I, II with dorsal crests. In males, idiosoma widely ovate, opisthosoma semi-ovate, with small angular lobes, their apices formed by extending bases of setae *h3*, dorsal surface of idiosoma with a pair of longitudinal sinusoidal ridges (Figs 48, 52), most of the ventral surface of idiosoma heavily sclerotized and punctured as typical shields, setae *ps1*, *f2* setiform or spiculiform. In females setae *f2* lanceolate.

### 15. *Pterotrogus sinusoidus* MIRONOV sp. n. (Figs 48-51)

**Type material.** Male holotype, 1 female paratype (UGA 9473, AMNH 276 026) from *Campephilus rubricollis* (BODDAERT, 1783), Venezuela, Amazonas, Rio Casiquiare & Rio Negro, 24.IX.1928, R.S. DECK. Holotype and paratypes – UMMZ.

### Description

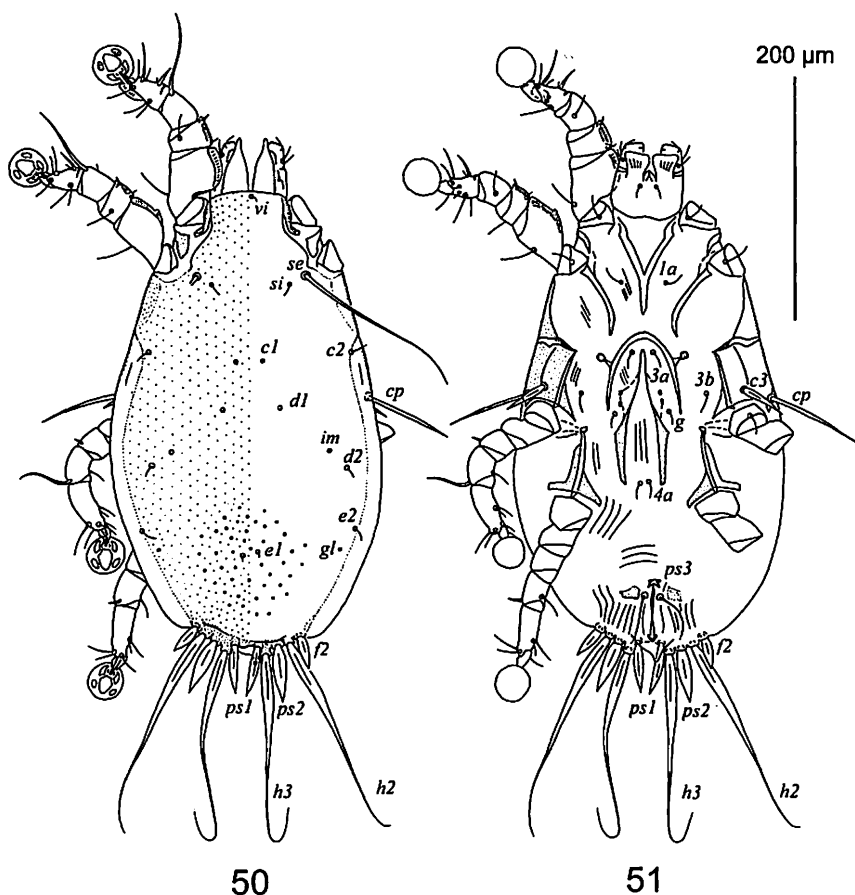
**Male** (holotype). Length of idiosoma 308, greatest width of idiosoma. Prodorsal, hysteronotal, scapular and humeral shields fused into entire dorsal shield of idiosoma, traces of fusion indistinct; dorsal surface with pair of longitudinal sinusoidal sclerotized ridges flanking large rectangular area in the median part of idiosoma (Fig. 48); lateral margins of prodorsal part without incisions; bases of setae *se* separated by 93. Length of hysterosoma from level of setae *c2* to lobar apices 198. Setae *c3* hair-like, 10 in length. Dorsal setae *e1* anterior to *e2*, approximately at the level of hysteronotal gland openings. Setae *ps2* narrowly lanceolate, macrosetae *h2*, *h3* with lanceolate basal enlargement, setae *ps1*, *f2* setiform; length of setae *ps1* 7, *ps2* 20, *f2* 13; greatest width of setae *h2*, *h3* 5.5, *ps2* 2.5. Opisthosomal lobes as two small angle-like extensions, apex bearing setae *h3*. Terminal cleft small, parallel-sided, anterior end convex, blunt-angular; length of cleft 13, width 20. Dorsal measurements: *c2-d2* 64, *d2-e2* 78, *d2-gl* 55, *e1-e2* 11-20, *e2-h3* 56, *h2-h2* 38, *h3-h3* 24, *ps1-ps1* 20, *ps2-ps2* 51. Entire ventral surface of idiosoma as heavily sclerotized as the dorsum and forming entire ventral shield, soft tegument remains only



Figs 48-49. *Pterotrogus sinusoides*, male. 48: dorsal view of idiosoma, 49: ventral view of idiosoma.

around trochanters, gnathosoma, genital apparatus and anal area; epiandrium absent. Setae *3a* slightly anterior to *3b*. Genital arch  $33 \times 11$ , aedeagus about one third of the arch, epiandrium and genital shield absent; coxal setae *4a* at basal level of genital arch. Adanal shields absent. Diameter of anal discs 15. Tarsus I longer than wide. Femora I, II with dorsal and lateral crests, genua I, II with dorsal crest. Tarsus III with small apical claw, 37 in length. Legs IV extending slightly beyond the level of anal discs.

*Female* (paratype). Length of idiosoma 380, width of idiosoma 201. Prodorsal, hysteronotal and scapular shields fused into entire dorsal shield of idiosoma, traces of fusion between prodorsal and scapular shields visible; opisthosomal part of dorsum with sparsely situated small pits; lateral margins of prodorsal shield without incision around scapular setae; bases of setae *se* separated by 89. Length of hysterosoma from the level of setae *c2* to posterior end 245. Setae *c3* lanceolate, 33 in length. Posterior margin of opisthosoma rounded. Setae *d1* slightly posterior to level of setae *cp*, setae *e1* posterior to



Figs 50-51. *Pterotrogus sinusoides*, female. 50: dorsal view of idiosoma, 51: ventral view of idiosoma.

level of setae *e2*, cupules *im* visible. Setae *f2*, *ps1*, *ps2* lanceolate; macrosetae *h2*, *h3* enlarged in basal part, filiform in apical part; length of setae: *ps1* 45, *ps2* 45, *f2* 23. External copulatory tube as small spine on weakly sclerotized convex extension between setae *h3*. Dorsal measurements: *c2-d2* 98, *d2-e2* 51, *e2-f2* 89, *e2-el* 14-18, *h2-h2* 67, *ps1-ps1* 18. Epimerites I, II without sclerotized areas. Epigynum 58 x 60, with a pair of short lateral extensions; sclerotized folds of oviporus extending beyond midlevel of epimerites IV. Adanal sclerites of irregular form situated lateral to setae *ps3*. Femora I, II and genua I, II with dorsal crest, the crest of femur II with small tooth.

**Differential diagnosis.** Males of *Pterotrogus sinusoides* differ from the second representative of the *sinusoides* group, *P. macrosinusoides* (see

below), by relatively narrow sinusoid ridges (width about 5) and narrower terminal cleft (about 20) (Figs 48, 49). As in the *sinusoidus* species group, females are known only for *P. sinusoidus*, they may be compared only with representatives of other groups of *Pterotrogus*. In general appearance, the females of *P. sinusoidus* resemble those of the *lanceolatus* group by having setae *f2*, *ps1*, *ps2* of lanceolate form. Within *lanceolatus* group it is most similar to *P. lanceolatus* and differs by having scapular shields fused to the prodorsal shield, small pits on opisthosoma part of the dorsum and short setiform setae *ps2* (Figs 50, 51). In females of *P. lanceolatus*, scapular shields are separated from prodorsal shield, the dorsum is monotonously punctured, and setae *ps2* are long and lanceolate (Fig. 36).

**Etymology.** Specific epithet indicates the sinusoid dorsal ridges in males.

#### 16. *Pterotrogus macrosinusoidus* MIRONOV sp. n (Figs 52-55)

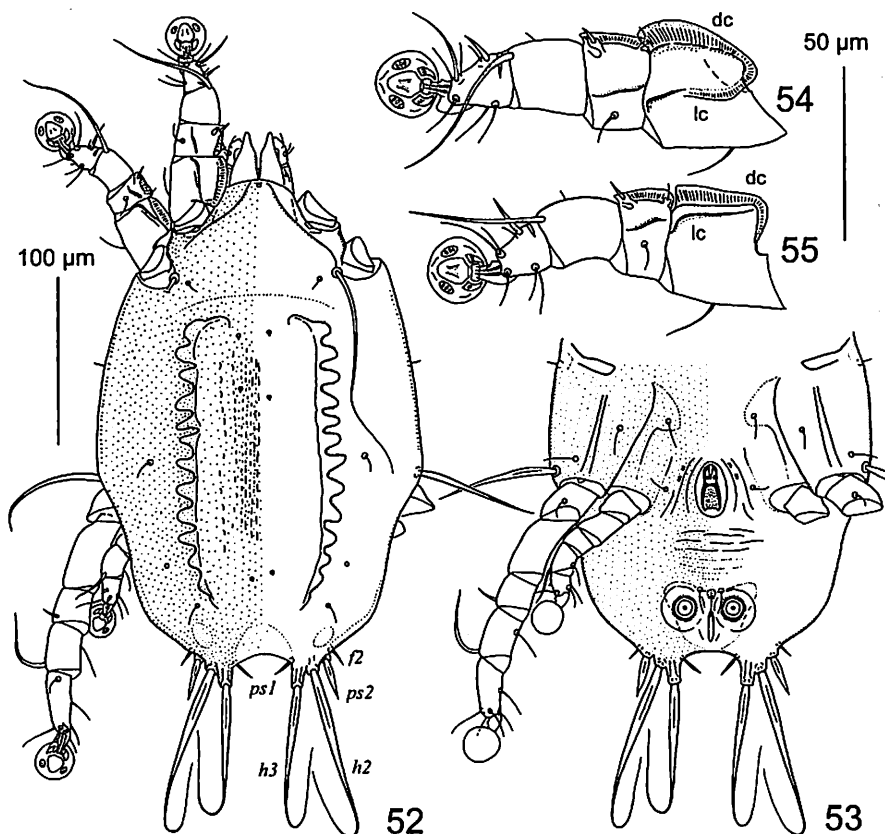
**Type material.** Male holotype, 2 male paratypes (UGA 9459, AMNH 247 495) from *Campephilus guatemalensis* (HARTLAUB, 1844), W. Panama, Boca del Toro, Almirante, 8.IX.1927, R.R. BENSON. Holotype and 1 paratype - UMMZ, 1 paratype - ZISP.

#### Description

**Male (holotype).** Length of idiosoma 303, greatest width of idiosoma 192. Prodorsal, hysteronotal, scapular and humeral shields fused into entire dorsal shield of idiosoma; surface with pair of longitudinal sinusoidal sclerotized ridges 10-12 in width (Fig. 52); lateral margins of prodorsal part without incision around scapular setae; bases of setae *se* separated by 93. Length of hysterosoma from level of setae *c2* to lobar apices 192. Setae *c3* hair-like, 35 in length. Dorsal setae *e1* anterior to *e2*. Setae *ps2* lanceolate, macrosetae *h2*, *h3* with enlarged basal part, setae *ps1*, *f2* setiform; length of setae: *ps1* 13, *ps2* 22, *f2* 9. Opisthosomal lobes small angular, apex of each lobe formed by extension bearing seta *h3*; terminal cleft parallel-sided, anterior margin shallowly concave, length of the cleft 20, width 35. Dorsal measurements: *c2-d2* 55, *d2-e2* 88, *d2-gl* 65, *gl-el* 6-9, *e2-e1* 13-17, *e2-h3* 51, *h2-h2* 58, *h3-h3* 45, *ps1-ps1* 33, *ps2-ps2* 73. Entire ventral surface of idiosoma as heavily sclerotized as dorsal idiosomal shield, soft tegument remains only around trochanters, gnathosoma, genital apparatus and anal slit (Fig. 53); epandrium absent. Setae *3a* slightly anterior to *3b*, situated on inner ends of epimerites IIIa. Genital arch 29 x 10, aedeagus about one third of the arch; coxal setae *4a* at midlevel of genital arch. Adanal shields absent. Diameter of anal discs 13. Tarsus I longer than wide. Femora I, II and genua I, II with dorsal and lateral crests (Figs 54, 54). Tarsus III with small apical claw, 33 in length; seta *r* very short, about one third of the segment length. Legs IV extending slightly beyond the level of anal discs.

Female unknown.

**Differential diagnosis.** The males of *P. macrosinusoidus* differ from the previous species, *P. sinusoidus*, by having wider sinusoid ridges (10-12 in width), and wider terminal cleft, about 35 (Figs 52, 53). In *P. sinusoidus*, the



Figs. 52-55. *Pterotrogus macrosinuosoides*, male. 52: dorsal view of idiosoma, 53, ventral view of hysterosoma, 54: femur and genu I, 55: femur and genu II. dc – dorsal crest, lc – lateral crest.

widths of sinusoid-like ridges are only 4-5, and terminal cleft is 20 in width (Fig. 48, 49).

**Etymology.** Specific epithet stresses large amplitude of sinusoid dorsal ridges in males.

### Phylogeny of *Pterotrogus*

The branch-and-bound search produced a single shortest tree (Fig. 56) having a length of 62 steps. Standard indices excluding uninformative characters are  $CI=0.8667$ ,  $RI=0.9521$ ,  $RC=0.8292$ . The analysis supported monophyly of the genus *Pterotrogus* and three species groups (*iron*, *lanceolatus*, *sinuosoides*), while the *simplex* group appeared paraphyletic.



Among the analysed taxa of pteronyssids restricted to woodpeckers, the genera *Pterotrogus* and *Zygepigynia* GAUD & CORPUZ-RAROS, 1985 represent two sister clades clearly distinct from the morphologically diverse genus *Neopteronyssus*, which is widely distributed on the Old World Picidae, and *Stenopteronyssus*, which occurs on the tribe Colaptini in the New World. In the cladogram, the evolutionary branch of *Pterotrogus* and *Zygepigynia* is characterised by the shortened solenidion  $\sigma I$  on genu I in both sexes (character 39), the hysteronotal shield covering most of the hysterosoma in females (characters 14), and relatively short hypertrophied legs III in males (character 44). The main apomorphies of *Pterotrogus* that differentiate it from *Zygepigynia* are a complete fusion of prodorsal and hysteronotal shields into a single dorsal shield in both sexes (character 3), and very long extensions of oviporal folds in females (character 19).

The basal part of the *Pterotrogus* cluster forms a comb with one unresolved node and bears four lineages of morphologically primitive species referred to the paraphyletic *simplex* group, and the upper part of this comb produces a well-supported cluster with three subclusters corresponding to the derived species groups *iron*, *lanceolatus*, and *sinusoidus*. A low number of apomorphies in lineages of the *simplex* group and unresolved relationships between some of them shows the primitiveness of species comprising this group. This primary divergence of the *simplex* group was probably related to cospeciation with woodpecker genera, which were diversifying in the New World, or even before their invasion to this area (see below discussion of host associations). The first morphological changes on the way to derived species groups were the moving of openings *gl* and setae *el* to the more posterior position in males (node 36, characters 20, 21) and then setae *el* in females (node 35, character, 30), modifications obviously related to changes of opisthosomal form. The cluster uniting derived species groups (node 34) is supported by five apomorphies as follows: development of dorsal crests on femora I, II in both sexes (characters 38, 39), greatly widened idiosoma (character 4) and shortened legs IV (character 40) in males; tooth on dorsal crest of femora II (character 48) in females.

The *iron* group, which by the structure of idiosomal setae remains more similar to the *simplex* group, is mainly characterised by apomorphies in males: opisthosoma widened and truncated posteriorly, closed coxal fields III, tooth on dorsal crest of femur II, and basiventral crest on femur II (characters 5, 3, 10, 40, 41, respectively). Females of this group are characterised by a widened opisthosoma (character 13).

The branch bearing both *lanceolatus* and *sinusoidus* groups (node 32) is characterised by apomorphies expressed in the transformation of some setae of the terminal complex from setiform to lanceolate form (characters 26, 32, 33, and 34). Nevertheless, subsequent evolution of the two groups was quite different. In the *lanceolatus* group, the main trends of evolution were a modification of all setae of the terminal complex into the lanceolate form and enlargement of the basal extensions supporting these setae. The branch bearing the whole *lanceolatus* group (node 30) is characterised by the

formation of opisthosoma with extended bases of terminal setae and development of lanceolate form in setae *ps1* in males (characters 5.1 and 22). The most primitive species of this group, *Pterotrogus leucopogon*, retains setiform setae *f2* in males and has no cup-like setal bases on posterior margin of opisthosoma (Fig. 23). The cluster bearing most derived species of the *lanceolatus* group (node 29) is supported by the following features in males: development of the genital shield (character 13), lanceolate form of setae *f2* (character 24), cup-like bases of setae *h2* and *h3* (characters 27 and 28), elongation of setae *f2* relative to setae *ps1* (character 29), and loss of apical claw on tarsus III (character 45).

The cluster of the *sinusoidus* group is characterised by the following apomorphies in males: semi-ovate opisthosoma with small lobes (character 5.2), development of unique sinusoid-like dorsal ridges (character 9.1), total ventral sclerotisation of idiosoma (character 11.2), setiform setae *cp3* (character 22) and thickened rod-like setae *cp* (character 23). It is worthy to note that development of setiform setae *c3* in males appears as homoplasy, but it is obviously an independent process in males of the *sinusoidus* group and *P. borealis* (*simplex* group), because in the latter species these setae are modified in both males and females (characters 22, 31), while in the *sinusoidus* group, the females retain lanceolate setae *c3* (Fig. 51).

Thus, the evolution of the genus *Pterotrogus* had two stages of divergence in the course of its evolution; the first was a divergence of primitive species recently comprising the *simplex* group, and the second was a divergence of one progressive lineage into three lineages of derived species groups.

### Host parasite associations

Based on the host associations of *Pterotrogus* species (Table 3) and on phylogenetic relationships within the genus (Fig. 56), and also taking into consideration data on host associations of pteronyssids with Picidae from other areas (ČERNÝ & SHUMILO, 1973; FACCINI & ATYEO, 1981; GAUD, 1989, 1990a, b, 1991; MIRONOV, 1989, 2003), it is possible to propose a preliminary hypothesis on evolution and cospeciation with hosts. Construction of a hypothesis is severely impaired by incomplete data on phylogenetic relationships even between genera of Picidae. Investigations based on morphological characters (SIMPSON & CRACRAFT, 1981; SWIERCZEWSKI & RAIKOV, 1981; SHORT, 1982; DEL HOYO *et al.*, 2002) give relatively clear and comprehensive concepts of generic relationships within Picidae, while studies based on molecular methods (DEFILIPPS & MOORE, 2000; PRICHITKO & MOORE, 2000; WEIBEL & MOORE, 2002a, b; WEBB & MOORE, 2005) produce a number of concepts that disagree both with each other and with traditional concepts. Moreover the molecular based investigations are quite incomplete regarding species and genera included into analyses. Therefore I follow here the conception of SWIERCZEWSKI & RAIKOV (1981) and DEL HOYO *et al.* (2002), as they are the most complete and comprehensive.

Table 3. Host associations and geographical locality of *Pterotrogus* species

Mite species and species groups	Host species	Location	Reference
<b><i>simplex</i> group</b>			
<i>P. borealis</i>	<i>Picoides borealis</i>	USA: Mississippi, Missouri, Texas, Virginia	Present study
<i>P. colapti</i>	<i>Colaptes punctigula guttatus</i>	Brazil	Present study <sup>1</sup>
<i>P. oconnori</i>	<i>Dryocopus pileatus</i>	USA: Kentucky, Louisiana, Texas	Present study
<i>P. principalis</i>	<i>Campephilus principalis</i>	USA	MIRONOV <i>et al.</i> , 2005
<i>P. simplex</i>	<i>Melanerpes erythrocephalus</i>	Canada; USA: Michigan	HALLER, 1882; FACCINI & ATYEO, 1981
<i>P. veniliornis</i>	<i>Veniliornis cassini</i>	Brazil, Venezuela	Present study
"	<i>V. kirkii</i>	Trinidad	Present study
<b><i>lanceolatus</i> group</b>			
<i>P. guatemalensis</i>	<i>Campephilus guatemalensis</i>	Colombia	Present study
<i>P. lanceolatus</i>	<i>C. guyaquilensis</i>	Peru	Present study
<i>P. leucopogon</i>	<i>C. leucopogon</i>	Argentina	Present study
<i>P. melanoleuci</i>	<i>C. melanoleucos</i>	Brazil	Present study
<i>P. robustus</i>	<i>C. robustus</i>	Brazil	Present study
<i>P. rubricolli</i>	<i>C. rubricollis</i>	Venezuela	Present study
<b><i>iron</i> group</b>			
<i>P. iron</i>	<i>C. guatemalensis</i>	Panama	Present study
<i>P. quadratus</i>	<i>C. rubricollis</i>	Venezuela	Present study
<b><i>sinusoidus</i> group</b>			
<i>P. macrosinusoidus</i>	<i>C. guatemalensis</i>	Panama	Present study
<i>P. sinusoidus</i>	<i>C. rubricollis</i>	Venezuela	Present study

Considering host associations of *Pterotrogus* species (Table 3), all genera of New World woodpeckers, except *Campephilus*, bear only representatives of the *simplex* group, the most primitive group of the genus. Within the *simplex* group, each species is restricted to one woodpecker genus, or perhaps to one host species only. Three derived species groups (*iron*, *lanceolatus*, and *sinusoidus*) are associated exclusively with the genus *Campephilus*. It is especially interesting that two species of this genus (*Campephilus guatemalensis*, *C. rubricollis*) bear representatives from each derived species group. A similar case is known for the woodpecker *Chrysocolaptes lucidus* (SCOPOLI, 1786) in Philippines, which bears four closely related *Zygepignia* species (GAUD & CORPUZ-RAROS, 1985). The *lanceolatus* group is most widely distributed, its species being found on six of seven *Campephilus* species inhabited by *Pterotrogus*. Within the genus *Campephilus*, only the Ivory-billed Woodpecker, *C. principalis*, shows an exception in host associations and bears a representative of *simplex* group, as for other

woodpecker genera from the New World. Taking into consideration quite different morphological appearance of derived species groups, that apparently means that they are adapted to different locations in plumage (unfortunately unknown to us), it is possible to suggest that most species of the genus *Campephilus*, at least those, who bear mites of the *lanceolatus* group, could also harbour representatives of the *iron* and *sinusoidus* groups.

According to my hypothesis, the genus *Pterotrogus* was probably formed on the common ancestor of the New World genera *Dryocopus*, *Campephilus* (Campephilini), *Colaptes*, *Veniliornis* (Colaptini) and *Melanerpes* (Melanerpini) or even earlier, before the genus *Picoides* (Campetherini) split from the lineage. In the course of primary cospeciation with these diverging genera of woodpeckers, the genus *Pterotrogus* has diversified into species specific to each host genus. The mite lineage associated with *Campephilus* has probably undergone a splitting onto three lineages and intensive specialisation. Only *C. principalis*, probably because of earlier deviation, has retained a representative of the *simplex* group, *P. principalis*. Subsequent cospeciation of these three *Pterotrogus* lineages with Central and South American species of *Campephilus* has led to the formation of three derived species groups.

Two cases of host associations need a special discussion. There is some doubt that *P. oconnori* was inherited by *Dryocopus pileatus* from its ancestor, rather it may be on this host as a result of host shifting. The genera *Dryocopus* and *Campephilus* are very closely related (SWIERCZEWSKI & RAIKOV, 1981; SHORT, 1982) and it is reasonable to expect closely related mite species on them. At the same time, species of *Dryocopus* widely distributed in the Old World, *D. martius* (LINNAEUS, 1758) and *D. javensis* (HORSFIELD, 1821), do not bear any species of *Pterotrogus* or closely related genera but are occupied only by mites of a phylogenetically distant genus *Neopteronysus* (MIRONOV, 1989, 2003). The woodpecker genus *Chrysocolaptes*, which is also suggested to be close to *Campephilus* and *Dryocopus* (SWIERCZEWSKI & RAIKOV, 1981), has mites of the genus *Zygepigynia*, a genus phylogenetically closer to *Pterotrogus* than is *Neopteronysus*; this supports the cospeciation hypothesis. However, this would make it necessary to explain how lineages of *Dryocopus* from the Old World and New World by some unknown reasons retained representatives of different generic groupings of pteronyssids associated with woodpeckers (*Pterotrogus*-*Zygepigynia* versus *Neopteronysus*).

The second questionable case concerns *Picoides borealis*, and could similarly concern *Veniliornis* species, if the latter genus is actually related to *Picoides* and also belongs to the tribe Campetherini (WEIBEL & MOORE, 2002a, b) rather than the Colaptini (SHORT, 1982; DEL HOYO *et al.*, 2002). It is possible to admit that *Pterotrogus* species has appeared on these hosts in the result of shifting from other woodpecker genera of the New World, for instance *Melanerpes erythrocephalus* and *D. pileatus*. According to WEIBEL & MOORE (2002a, b), the lineage including closely related woodpecker genera *Picoides* and *Veniliornis* is much distant from that of large-sized *Campephilus*, *Colaptes*, *Dryocoptes* and *Melanerpes*, while species of the *simplex* group inhabiting woodpeckers of all these genera are closely related.

At the same time, there are no any records that other well-explored species of the genus *Picoides* (*Pic. trydactylus*, *Pic. pubescens* LINNAEUS, 1766, *Pic. villosus* LINNAEUS, 1766) and the closest genus in the Old World, *Dendrocopos* KOCH, 1816, bear any *Pterotrogus* species. Rather, these woodpeckers commonly have representatives of the genera *Neopteronysus* and *Pteronyssus* (ČERNÝ & SCHUMILO, 1973; FACCINI & ATYEO, 1981; MIRONOV, 1989, 2002, 2003). In suggesting that *Picoides borealis* and *Veniliornis* species have inherited respective *Pterotrogus* species from the ancestors it is necessary to admit that representatives of this genus have gone extinct on all other species of *Picoides* and closely related Old World genera (*Campethera* GRAY, 1841, *Dendrocopos* and *Dendropicos* MALHERBE, 1849).

I expect that subsequent extensive explorations of the mite fauna of New and Old World woodpeckers would reveal many more pteronyssids, which will lead to better understanding of the phylogenetic relationships within this mite group and their evolution on these hosts.

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