A review of the feather mite genus *Pteronyssoides* HULL, 1931 (Astigmata: Pteronyssidae) from African and European passerines (Aves: Passeriformes) with analysis of mite phylogeny and host associations

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Abstract

A systematic review of the feather mite genus *Pteronyssoides* ROBIN, 1877 is given, including an improved diagnosis of the genus and subgenera, description of 14 new species from African passerines, cladistic analysis of the genus and a brief discussion of associations with passeriform hosts. New species are described as follows: *Pteronyssoides emberizae* sp.n. from *Emberiza flaviventris* (Emberizidae), *P. eupasseris* sp. n. from *Passer griseus* (Ploceidae), *P. euplecti* sp. n. from *Euplectes hordaceus* (Ploceidae), *P. faini* sp. n. from *Lonchura bicolor poensis* (Estrildidae), *P. foudiae* sp. n. from *Foudia madagascariensis* (Ploceidae), *P. microscutatus* from *Euplectes axillaris* (Ploceidae), *P. ovoscutatus* sp. n. from *Cyanomitra verticalis* (Nectariniidae), *P. oxylabis* from *Oxylabes madagascariensis* (Timaliidae), *P. plocei* sp. n; from *Ploceus superciliaris* (Ploceidae), *P. pytiliae* sp. n. from *Pytilia melba belli* (Estrildidae), *P. queleae* sp. n. from *Quelea quelea* (Ploceidae), *P. serini* sp. n. from *Serinus sulphuratus* (Fringillidae), *P. triangularis* sp. n. from *Parus caeruleus* (Paridae), and *P. viduinus* sp. n. from *Vidua macroura* (Viduidae).

Maximum parsimony analysis based on 45 morphological characters confirmed current taxonomic subdivision of the genus into two subgenera, *Pteronyssoides* s. str. and *Holonyssoides* MIRONOV, 1993, and revealed three species groups within the nominal subgenus (*nectariniae*, *ovoscutatus*, and *parinus*). Two contrasting morphological tendencies are displayed by the subgenera. The main tendency in *Holonyssoides* is strengthening of dorsal shields in both sexes, while three different lineages of *Pteronyssoides* s. str. show a trend to reduced hysteronotal shield in females.

Based on the phylogenetic relationships between mite species and their currently known distribution among passerines, and taking into consideration phylogenetic relationships between higher passerine taxa, it is hypothesized that the genus *Pteronyssoides* originated on the ancestors the parvorder Passerida. Owing to subsequent cospeciation, its representatives are widely dispersed on two major passeridan lineages (Passeroidea and Sylvoidea); due to host-switching events in the course of evolution, these mites also colonized tits (Paridae) within Passerida and two phylogenetically distant lineages (Dicruridae and Paradisaeidae) belonging to the core Corvoidea (parvorder Corvida).

Key words: Pteronyssidae, *Pteronyssoides*, systematics, phylogeny, host associations, cospeciation.

Introduction

The feather mite family Pteronyssidae (Astigmata: Analgoidea) currently includes about 150 species in 22 genera (FACCINI & ATYEO, 1981; GAUD & ATYEO, 1996; MIRONOV, 1989, 2000, 2001, 2003). As permanent ectoparasites of birds, pteronyssids are mainly associated with Passeriformes and Piciformes, and a few species are known from Coraciiformes. These mites are typical representatives of the feather mite morphotype adapted to inhabit vanes of large feathers, the flight feathers and the large upper covert feathers of wings (MIRONOV, 1999).

Among six pteronyssid genera restricted to passerines (FACCINI & ATYEO, 1981; MIRONOV, 2001), the genus *Pteronyssoides* HULL, 1931 (Astigmata: Pteronyssidae) is a relatively species-rich taxon that includes 14 species associated with various families of higher passerines. Representatives of the genus are medium- and small-sized pteronyssids (260-400 µm in length), most commonly located on the ventral surfaces of large covert feathers. The most noticeable morphological peculiarity of this genus among other pteronyssids is a great variability of the hysteronotal sclerite complex in females. Due to this feature, identification of species, in contrast to most feather mite taxa, is much easier for the females than for the males.

The genus *Pteronyssoides* was originally established based on their free epimerites I, a feature that is relatively rare in Pteronyssidae where the most common state is the fusion of epimerites (HULL, 1931; GAUD & MOUCHET, 1959, GAUD & TILL, 1961). In the generic revision of pteronyssids (FACCINI & ATYEO, 1981), its diagnosis was enlarged and specified and one species was removed to the genus *Metapteronyssus* GAUD, 1981; however, *Pteronyssoides* continued to encompass mites with very diverse appearances. Further, two species groups, *obscurus* and *truncatus*, were arranged in separate genera, *Scutulanyssus* MIRONOV, 1985 and *Sturnotrogus* MIRONOV, 1989, respectively (MIRONOV, 1985, 1989). Finally, based on general structure of the dorsal shields, two subgenera, *Pteronyssoides* s. str. and *Holonyssoides* MIRONOV, 1993, were established within the genus (MIRONOV, 1993).

Representatives of the genus *Pteronyssoides* are known only from higher passerines (Oscines) of the Old World: most species were described from Africa (GAUD, 1952, 1957; GAUD & MOUCHET, 1959; GAUD & TILL, 1961; MIRONOV & KOPIJ, 2000; MIRONOV, 2001), and a few species are known from the Palaearctic (MIRONOV, 1985, 1989) and South-East Asia (SUGIMOTO, 1941; GAUD & PETITOT, 1948; MIRONOV, 1993). Nevertheless, species diversity of this genus remains quite poorly explored, because many avian species of the vast host-group Passeriformes have never been examined.

In the course of our study of feather mites associated with African passerines we have found 14 new species among materials obtained from various sources, and have re-examined all *Pteronyssoides* species formerly described from this area. In the present paper, we give an improved diagnosis of the genus and subgenera, a key and systematic review of all known species, descriptions of new species from African passerines, and a phylogenetic analysis of this genus based on morphological characters. We also briefly discuss known host associations of the genus and provide a preliminary hypothesis of its evolution on passerines.

Material and methods

Specimens

The material used in the present study was received from four main sources: Musée royal de l'Afrique central (Tervuren, Belgium), Institut royal des Sciences naturelles de Belgique (Brussels, Belgium), University of Georgia (Athens, USA), and Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia). Some type specimens and important comparative materials were loaned from the Muséum national d'Histoire naturelle (Paris, France) and A. Mickiewicz University (Poznan, Poland).

An emended diagnosis of the genus and descriptions of new species are given in the standard formats used for pteronyssid taxa (FACCINI & ATYEO, 1981; MIRONOV, 1992, 2001). The general morphological terms, and leg and idiosomal chaetotaxy follow GAUD & ATYEO (1996). Regarding the terms used for hysteronotal shield fragments in females, we generally follow the scheme proposed by MIRONOV (1992) that was elaborated for the genus *Pteroherpus* GAUD, 1981; however, because the pair of sclerites in the posterior part of the opisthosoma in most *Pteronyssoides* species is entire and extends to the posterior margin of the body, we refer to all these sclerites as the opisthosomal sclerites ('op', Fig. 3a), and where these sclerites are split we refer to the anterior piece as the main fragment of the opisthosomal sclerite (mf), and to the posterior piece as the pygidial fragment (pf).

All measurements in the descriptions are given in micrometres (µm). A full set of measurements is given only for the holotype (male) and one paratype (female); the range of idiosomal size (length, width) is displayed for the rest of the paratype specimens.

Measuring technique for particular structures:

(i) distance between different pairs of setae is the shortest distance between the transverse levels formed by setae of respective pairs.
(ii) prodorsal shield length is measured along midline, and width is greatest width at posterior margin.
(iii) hysterosoma is measured from the level of sejugal furrow to bases of setae *h3*.
(iv) hysteronotal shield length in males is the greatest length from the anterior margin to bases of setae *h3*; width is measured at anterior margin.
(v) distance between prodorsal and humeral shield and the length of transventral sclerite in males are measured along midline.

As FACCINI & ATYEO (1981) and MIRONOV (1989) provided exhaustive synonymies for all formerly known *Pteronyssoides* species we do not give synonymies in the present review. Specimen depositories and reference accession numbers are given using the following abbreviations: AMNH – American Museum of Natural History, New York, USA; AMU – A. Mickiewicz University, Poznan, Poland; BMOC or MZUM – Museum of Zoology, University of Michigan, Ann Arbour, USA; IRSNB – uncatalogued collection of Prof. A. FAIN, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; NMB – National Museum of Bloemfontein, Free State, South Africa; NU – Nebraska University, Lincoln, USA; SAIMR – South African Institute of Medical Research, Johannesburg, South Africa; TRT – Collection of E. TROUESSART in Muséum national d'Histoire naturelle, Paris, France, UGA – University of Georgia, Athens, USA; USNM – National Museum of Natural History, Washington DC, USA; YSU – Youngstown State University, Youngstown, Ohio, USA; ZISP – Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia. Where the collection number consists of two sections, the first section refers to the collection number of the mite specimens and its depository, if another depository is not specifically pointed out; the second is a collection number of the respective host specimen. Location data are given in an original form, as in slide specimens. Systematics and scientific names of birds follow DICKINSON (2003), and passerine phylogeny used in the discussion of host associations follows recent conceptions based on molecular studies (ERICSON *et al.*, 2002; ERICSON & JOHANSON, 2003; BARKER *et al.*, 2004; BERESFORD *et al.*, 2005).

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 autoapomorphic characters are 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). In the present case, included apomorphies may potentially represent characteristics for species groups, which could be recognised in future investigations of diversity.

Avenzoaria calidridis OUDEMANS, 1904 (Avenzoariidae) from *Calidris alpina* (LINNAEUS, 1758), a representative of an analgoid family that retains many plesiomorphic features (DABERT & MIRONOV, 1999), was used as a distant outgroup. Representatives of two closely related pteronyssid genera, *Scutulanyssus dasyrhitidis* (GAUD & ATYEO, 1981) from *Psalidoprocne fuliginosa* SHELLEY, 1887, and *Sturnotrogus subtruncatus* (TROUESSART, 1885) from *Gracula religiosa* LINNAEUS 1758, were used as potential close outgroups to test monophyly of the genus *Pteronyssoides*. Two species, *Pteronyssoides lonchurae* (SUGIMOTO, 1941) and *P. pari* (LINNAEUS, 1758), which were poorly described and for which materials were not available for study, and *P. pycnonoti* MIRONOV, 1993 known only from females are not included.

In total, 30 taxa and 45 characters, 2 of which represent autapomorphies in the ingroup, were included in the analysis (Tables 1, 2). Constructing 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 were 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 and bound algorithm was used for the maximum parsimony analysis and reconstruction of phylogeny. For *a posteriori* optimization of character states, we 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). Drawings and editing of tree were accomplished with Winclada, version 1.0 (NIXON, 1999).

Taxonomy

Pteronyssidae OUDEMANS, 1941
Pteronyssoides HULL, 1931

TYPE SPECIES: *Pteronyssus striatus* ROBIN, 1877.
DIAGNOSIS: *Both sexes*: Epimerites I free (tips connected by thin sclerite in *P. latior*). Unpaired seta *vi* present. Prodorsal shield pear-shaped or trapezoidal, extending beyond row of scapular setae, not encompassing setae *c1* (Figs. 1a, 3a, 24a, e); scapular setae *se, si* on the shield, or *se* in lateral incision. Setae *c2* hair-like, commonly short, length less than half the distance between setae *se*. Setae *c3* long hair-like, lanceolate, or lanceolately enlarged in basal part (form of these setae may vary between different sexes of the same species). Setae *dp2* of palpae hair-like, simple. Setae *ba* of tarsi I-II hair-like, short. Genual solenidion $\sigma 1$ longer than tarsal solenidion *1* on legs I. Genual solenidion $\sigma 2$ present or absent. Tarsus III with 5 setae. Ventral membrane of tarsus I variable in size, in most species about half the length of the segment, in some species greatly reduced (Figs. 2a, b, 5d, 13c, 29d, e). Surface of coxal fields I, II covered with striated tegument.
Male: Opisthosomal lobes commonly short and bluntly rounded (elongated in *P. latior*) (Figs. 1a, 27a, 28a). Posterior margin of opisthosomal lobes with slightly extended bases of setae *h2, h3* and without terminal membrane (or with narrow membrane as in *P. oxylabis*). Terminal cleft usually small, V- or U-shaped. Supranal concavity ovate, short, open posterior into terminal cleft. Setae *c2* commonly in antero-median angle of humeral shields or mesal to it. Setae *ps1* anterior to the level of setae *h3*. Hysteronotal shield without heavily sclerotized ridges. Coxal fields III open. Transventral sclerite and epiandrium present. Epiandrium usually horseshoe-shaped and always fused with posterior margin of transventral sclerite; branches of epiandrium usually encompass genital apparatus (Figs. 1b, 21a, c, 25a, b, 27b). Anal discs circular, large, with finely striated membrane. Adanal shield in most species present, usually represented by median longitudinal sclerite; lateral extensions or additional lateral fragments present or absent (Figs. 2g, 4c, f, 20c, 21d, 27d). Adanal membranes present. Setae *h3* long setiform. Tarsus III elongated, slightly curved, commonly with bidentate apex (Fig. 2d), rarely with acute apex (Figs. 5e, 28c). Setae *r* in most species longer than tarsus III. Tarsus IV with small dorsobasal spine, shorter or subequal in length to tibia IV; setae *d, e* modified into barrel-shaped suckers (Figs. 2e, 4h, 13h, 27f).
Female: Idiosoma moderately elongated, without opisthosomal lobes. Set of hysteronotal shields variable, represented by two main types: (I) large hysteronotal shield covering almost entire dorsal surface of hysterosoma, except lateral areas (subgenus *Holonyssoides*) (Figs. 30a-c); (II) variable complex of sclerites in posterior half of hysterosoma commonly consisting of unpaired central sclerite and a pair of opisthosomal sclerites (subgenus *Pteronyssoides* s. str., *ovoscutatus* group) (Figs. 3a, 7a-c); rarely any fragments of hysteronotal shield absent (*P. striatus*) (Fig. 26a). Hysteronotal gland openings *gl* on striated teguments, rarely on lateral sclerites (*P. oxylabis, P. promeropis*) (Figs. 22d, 30a). Epigynium bow-shaped or semicircular, not touching epimerites IIIa; sclerotized folds of oviporus short (Fig. 3b). External copulatory tube absent.

HOSTS: Passeriformes: Dicruridae, Estrildidae, Fringillidae, Motacillidae, Nectariniidae, Paradisaeidae, Paridae, Passeridae, Ploceidae, Promeropidae, Pycnonotidae, Timaliidae, and Viduidae.

SPECIES INCLUDED: see Table 3.

Key to *Pteronyssoides* species

(*Pteronyssoides lonchurae* and *P. pari* are not included)

Females

1. Prodorsal shield with acute or rectangular posterior angles and with posterior margin straight or slightly concave. Hysteronotal shield represented by large shield covering almost entire hysterosoma and extending by anterior end to level of sejugal region or

Table 1 — Characters used in the phylogenetic analysis.

No	Characters and coding
1	Prodorsal and scapular shields: widely separated (0), close to each other (1).
2	Posterior angles of prodorsal shield: rounded or bluntly cut (0), rectangular or acute (1).
3	Proportion of prodorsal shield: approximately as long as wide (0), about two times longer than wide (1).
4	Sclerotized patches in prodorsal shield: absent (0), present (1).
5	Ventral membrane: absent (0), present, well, developed (1), greatly reduced (2).
6	Solenidion $\sigma 2$ of genu I: present (0), absent (1).
7.	Anterior part of hysteronotal shield in female: well developed (0), shied absent in anterior one third of hysterosoma or greatly narrowed (1).
8.	Opisthosomal sclerite in female: not split developed or from main body of hysteronotal shield (0), split from main body at least partly (1).
9.	General structure opisthosomal sclerite in females: one-pieced (0), paired (1).
10.	Structure of paired opisthosomal sclerite in female: entire, extending to setae *h2, h3* (0), split into main opisthosomal and pygidial fragments (1), split into fragments, but pygidial fragments fused each other (2), almost completely reduced (3).
11.	Form of anterior end of opisthosomal sclerites in female: blunt or rounded (0), acute (1).
12.	Central sclerite in female: not split from the main body of hysteronotal shield (0), formed as separate sclerite (1), lost (2).
13.	General structure of central sclerite in female: longitudinal plate connected with shields covering opisthosoma (0), ovate (1), longitudinal plate with acute posterior angles (2), lambda-shaped (3).
14.	Position of ovate central sclerite in female: anterior end not extending to level of trochanters IV (0), extending to level of trochanters IV (1).
15	Structure of generally ovate central sclerite in female: small ovate (0), large ovate (1), rudimentary (2), heart-shaped (3).
16.	Lateral shields in female: not separated from main body hysteronotal shield (0), separated, well developed (1), greatly reduced, rudimentary (2), lost (3).
17.	Structure of lateral shields in female: longitudinal sclerites posterior to openings *gl* (0), long sclerites, about half-length of hysterosoma (1), small, ovate (2).
18.	Position of openings *gl* in female: on shield (0), on striated tegument (1).
19.	Humeral shield dorsal to *cp* in female: developed (0), not developed (1).
20.	Longitudinal median lacuna on opisthosoma in female: absent (0), present (1).
21.	Position of setae *e1* in female: on shield (0), on striated tegument (1).
22.	Position of setae *e1* regarding ovate central sclerite in female: at midlevel of central sclerite (0), at level of posterior end of central sclerite (1).
23.	Position of setae *e2* in female: on opisthosomal sclerites (0), off opisthosomal sclerites (1).
24.	Position of setae *ps1* in female: terminal or near posterior margin of opisthosoma (0), approximately at level of setae *h2* (1).
25.	Ratio of idiosoma length /width in male: idiosoma elongated, ratio 1.6-2 (0), shortened, ratio 1.3-1.4 (1).
26.	Distance between prodorsal and hysteronotal shields in male: about 3/4 of prodorsal shield length or less (0), equal to prodorsal shield length (1).
27.*	Sclerites between prodorsal and hysteronotal shields in male: absent (0), pair of small transverse sclerites present (1).
28.*	Transventral sclerite in male: absent (0), present (1).
29.	Adanal apodemes in male: narrow (0), wide (1).
30.	Adanal shield in male: absent (0), present (1).
31.	Lateral parts of adanal shield in male: present (0), absent (1).
32.	Position of setae *c2* in male: on margin of humeral shield (0), on striated tegument (1).
33.	Position of setae *f2* position in male: dorsal, near margin (0), submarginal or ventral (1).
34.	Lobar apices bearing setae *h3* in male: not expressed (0), well developed (1).
35.*	Position of setae *h2* in male: on most lobar margin (0), dorsal, slightly distant from margin (1).
36.	Relative distance between cupules *ih* and setae *ps3* in male: cupules *ih* more distant from midline than setae *ps3* (0), cupules *ih* closer to midline than *ps3* (1).
37.	Sclerotized band between cupules *ih* and setae *ps2* in male: absent (0), present (1).
38.*	Legs III in males: not hypertrophied (0), hypertrophied (1).

No	Characters and coding
39.	Apex of tarsus III in male: apical extension poorly developed (0), large claw-like or spine-like apex (1), bidentate apex (2).
40.	Membrane on inner margin of tarsus III in male: absent (0), present (1).
41.	Relative length of setae *w* and *s* of tarsus III in male: seta *w* longer than *s* (0), seta *s* longer than *w* (1).
42.	Position of seta *w* in tarsus III in male: in basal one quarter of segment (0), at midlevel or at level of basal one third of segment (1).
43.	Length of seta *r* of tarsus III in male: longer than tarsus (0), shorter than tarsus (1).
44.	Form of outer margin of tarsus III in male: moderately convex (0), with blunt angle (1), with rectangular ledge (2).
45.	Dorsobasal spine on tarsus IV in male: absent (0), present (1).

* Parsimony uninformative characters.

Table 2 — Data matrix of characters states for *Pteronyssoides* and outgroup taxa. Character states are scored as 0 to 3, inapplicable states as "-"

	1	1111111112	2222222223	3333333334	44444
	1234567890	1234567890	1234567890	1234567890	12345
Avenzoaria calidridis	0000000000	-0---0-000	0-00000000	-000000000	00-00
Scutulanyssus dasyrhitidis	0000100000	-0---00000	0-00000101	0000000110	00000
Sturnotrogus subtruncatus	0000110000	-0---10000	0-00000101	0000000110	00000
Pteronyssoides (P.) striatus	0000111113	-2---3-100	1-10000101	0010000120	00001
P.(P.) lambda	0000111112	0130-3-100	1-00000101	0010000120	00021
P.(P.) emberizae	0000111111	011003-100	1000010101	1011000121	00001
P.(P.) eupasseris	0000111111	011003-100	1000000101	1011100121	00001
P.(P.) euplecti	0000111110	111003-100	1000000101	1010010121	00001
P.(P.) faini	0010211110	111113-110	1100000101	1100000110	00001
P.(P.) foudiae	0000111110	111113-100	1100000101	1010000121	00001
P.(P.) microscutatus	0000111110	111023-100	1000000101	1010010121	00001
P.(P.) motacillae	0000111110	011003-100	1000000101	1010000120	00001
P.(P.) ovoscutatus	0000111110	111003-110	1000000101	1010011121	00001
P.(P.) passeris	0000111110	011133-100	1001000101	1011010121	00001
P.(P.) plocei	0000111110	111003-100	1000010101	1010010121	00001
P.(P.) pytiliae	0000111110	111113-100	1000000101	1010000120	00001
P.(P.) queleae	0010211110	111113-100	1100000101	1110000111	00001
P.(P.) serini	0000111111	011003-100	1000000101	1011000121	00001
P.(P.) viduinus	0000111110	111003-110	1000000101	1010011121	00001
P.(P.) garioui	0000101100	02---3-100	0-10100100	-000000120	11011
P.(P.) nectariniae	0000101110	02---3-100	0-10100100	-000000120	11111
P.(P.) promeropis	0000101100	000--10000	0-10000101	1000000120	11111
P.(P.) parinus	0000111110	02---22100	1-10000101	0000000120	00001
P.(P.) piscinotus	0000111110	012--22100	1-10001101	0000000120	00001
P.(P.) triangularis	0000111110	012--22100	1-10000101	0000000120	00001
P.(Holonyssoides) desmiphorus	1101200000	-0---3-101	0-00100111	1000000120	00001
P.(H.) holoplax	1101200000	-0---3-101	0-00100111	1000000120	00001
P.(H.) latior	1100100000	-0---3-100	0-01000100	-001000120	00001
P.(H.) oxylabis	1100110100	-0---11000	0-01000101	0000000120	00001
P.(H.) timaliae	1101210000	-0---3-101	0-00000111	1000000120	00001

humeral setae *cp*; this shield may be split by narrow transverse band of soft tegument into anterior and posterior fragments (Figs. 26b-d, 30a-c). (subgenus *Holonyssoides*) 22

– Prodorsal shield with rounded posterior angles and with convex posterior margin. Hysteronotal shield represented by variable complex of separate sclerites situated posterior to trochanters III, commonly the set of sclerites includes an unpaired central sclerite and a pair of opisthosomal sclerites (Figs. 3a, 7a-d, 19a-c, 22a-d); or hysteronotal shield absent (Fig. 26a). (subgenus *Pteronyssoides* s. str.) 2

2. Hysteronotal shield absent, entire dorsal surface of hysterosoma covered with striated tegument (Fig. 26a) . . . . *P.(P.) striatus* (Robin, 1877)

– Complex of sclerites or entire shield in posterior half of hysterosoma present 3

3. Set of hysteronotal sclerites consists of a pair of lateral sclerites with openings *gl* on their anterior ends and unpaired shield covering posterior part of

opisthosoma and reaching by its narrow anterior end to the level of setae *d1* (Fig. 22d) . . . . *P.(P.) promeropis* MIRONOV & KOPIJ, 2000
– Lateral sclerites absent or rudimentary, hysteronotum with complex of 2-6 sclerites 4
4. Central sclerite absent (Figs. 19c, e, 22a). 5
– Central sclerite present (Figs. 7a-d, 19b, 22b, c). . 7
5. Posterior third of opisthosoma covered with single shield having narrow median incision on anterior margin; adanal shield present (Figs. 19c, d) . . . . *P.(P.) garioui* GAUD & MOUCHET, 1959
– Pair of opisthosomal sclerites present; adanal shield absent. 6
6. Opisthosomal sclerites with setae *e1* on anterior ends. Rudiments of lateral shields absent (Fig. 19e) . . . . *P. nectariniae* MIRONOV, 2001
– Opisthosomal sclerites not extending to setae *e1*. Rudiments of lateral shields present (Fig. 22a). . . . . *P.(P.) parinus* (KOCH, 1841)
7. Central sclerite lambda-shaped, with two posterior branches; the most posterior end of opisthosoma covered with unpaired pygidial sclerite (Fig. 19b) . . . . *P.(P.) lambda* GAUD & MOUCHET, 1959
– Another structure of hysteronotal sclerites 8
8. Central sclerite with a pair of acute posterior angles. Rudimentary lateral sclerites present (Figs. 22b, c) 9
– Central sclerite ovate. Lateral sclerites absent (Figs. 7a-d, 11a-d, 15a-d) 10
9. Central sclerite fishtail-shaped (Fig. 22b). . . . . *P.(P.) piscinotus* MIRONOV, 1989
– Central sclerite triangular (Fig. 22c) . . . . *(P.) triangularis* sp. n.
10. Openings *gl* at level of trochanters III, closely to setae *d2*; setae *e2* on anterior ends of opisthosomal sclerites (Fig. 7c) . . . . *P.(P.) faini* sp.n.
– Openings *gl* posterior to trochanters IV; setae *e2* on lateral margin of opisthosomal sclerites 11
11. Central sclerite rudimentary, not wider than 15; opisthosomal sclerites with several erratically disposed longitudinal striae, margins of these sclerites blurred (setae *e2* may be off these shields) (Fig. 11a) . . . . *P.(P.) microscutatus* sp. n.
– Central sclerite well developed, ovate or circular, at least 20 in width; opisthosomal sclerites monotonously punctured, entire or separated by transverse striated band into well-defined opisthosomal and pygidial fragments (Figs. 3a, 11b-d, 15a-d) 12
12. Central sclerite with narrowed anterior end extending to the midlevel between trochanters III and IV; setae *e1* posterior to central sclerite. (Fig. 15c). . . . . *P.(P.) queleae* sp. n.
– Central sclerite ovate or egg-shaped, its anterior end not extending beyond the level of trochanter IV; setae *e1* lateral to central sclerite. 13
13. Opisthosomal sclerites separated by transverse band of striated tegument into main body of opisthosomal sclerite (mf) and small pygidial fragments (pf) (Figs. 3a, 15d) 14
– Opisthosomal sclerites entire, extending to bases of setae *h2, h3* (Figs. 11b-d) 16
14. Anterior end of central sclerite not extending beyond level of openings *gl*. Length of idiosoma over 410 (417-448); setae *e1* distinctly posterior to level of openings *gl*, by 15 or more (Figs. 3a-b) . . . . *P.(P.) emberizae* sp. n.
– Anterior end of central sclerite extending beyond the level of openings *gl*. Length of idiosoma less than 410; setae *e1* approximately at level of openings *gl* 15
15. Main pieces of opisthosomal sclerites extend to midlevel of central sclerite; distance from anterior end of opisthosomal sclerites to setae *h3* about 95 (Fig. 7a) . . . . *P.(P.) eupasseris* sp. n.
– Main pieces of opisthosomal sclerites extend to level of posterior end of central sclerite; distance from anterior end of opisthosomal sclerites to setae *h3* about 80 (Fig. 15d). . . . . *P.(P.) serini* sp. n.
16. Anterior end of opisthosomal sclerites acute and extending approximately to midlevel of central sclerite (Figs. 11a, c, 15a) 19
– Anterior end of opisthosomal sclerites blunt and extending only to the level of posterior end of central sclerite (Figs. 11b, d) 17
17. Central sclerite relatively small, 20-25 in width; openings *gl* far anterior to central sclerite (Fig. 11b) . . . . *P.(P.) motacillae* MIRONOV, 1985
– Central sclerite large, over 45 in width, openings *gl* at the level of central sclerite. 18
18. Central sclerite heart-shaped, with blunt anterior end, commonly wider than long. Prodorsal shield without lateral incisions (Fig. 11d). . . . . *P.(P.) passeris* (GAUD, 1952)
– Central sclerite egg-shaped, anterior end of this sclerite narrower than posterior end (Fig. 7d). . . . . *P.(P.) foudiae* sp. n.
19. Central sclerite 2.3-2.5 times longer than wide. Posterior margin of opisthosoma with sclerotized copulatory extension (Fig. 15b) . . . . *P.(P.) pytiliae* sp. n.
– Central sclerite not more than 2 times longer than wide. Posterior margin of opisthosoma without copulatory extension. . . . . 20.
20. Anterior end of central sclerite does not extend beyond the level of openings *gl* (Fig. 7b) . . . . *P.(P.) euplecti* sp. n.
– Anterior end of central sclerite slightly extends beyond the level of openings *gl*. 21
21. Humeral shields developed dorsal to bases of setae *cp* (Fig. 15a). . . . . *P.(P.) plocei* sp. n.
– Humeral shields not developed dorsal to bases of setae *cp* 22
22. Central sclerite almost circular (Fig. 19a). . . . . *P.(P.) viduinus* sp.n.
– Central sclerite ovate, 1.3-1.5 times longer than wide (Fig. 11c) . . . . *P.(P.) ovoscutatus* sp.n.
23. Prodorsal and scapular shields widely separated; prodorsal shield as wide as half of idiosoma width.

Hysteronotal shield split into anterior and posterior fragments by transverse band of soft cuticle at level of setae *e1*. Lateral sclerites present (Fig. 30a) . . . . *P. (H.) oxylabis* sp. n.

– Prodorsal and hysteronotal shields separated by narrow groove of soft tegument; greatest width of prodorsal shields about 2/3 of idiosoma width. Hysteronotal shield entire. Lateral sclerites absent (Figs. 26b-d, 30b, c) 24

24. Lateral margins of hysteronotal shield with rounded incision at level of openings *gl*; posterior end of opisthosoma without longitudinal median lacuna; posterior ends of epimerites I connected (Figs. 30c, d) . . . . *P.(H.) latior* TROUESSART, 1887

– Lateral margins of hysteronotal shield without incisions; posterior end of opisthosoma with longitudinal median lacuna; posterior ends of epimerites I free (Figs. 26b-d). 25

25. Prodorsal shield 1.2-1.3 times wider than long. Bases of setae *h3* bidentate. Ratio of idiosoma length/width 1.8-1.9 (Fig. 30b) . . . . *P.(H.) timaliae* MIRONOV, 1993

– Prodorsal shield 1.5-2 times wider than long. Bases of setae *h3* with blunt apices. Ratio of idiosoma length/width 1.5-1.6 26

26. Posterior pairs of small bracket-shaped patches on prodorsal shield situated anterior to its posterior margin; length of idiosoma 345-380 (Fig. 26b). . . . . *P. (H.) desmiphorus* (GAUD, 1952)

– Posterior pair of bracket-shaped sclerotized patches situated on the margin of prodorsal shield, anterior pair of these patches may be indistinct; length of idiosoma 300-335 27

27. Anterior end of hysteronotal shield wider than distance between setae *se*; ratio of idiosoma length/width about 1.6 (Fig. 26c). . . . . *P. (H.) holoplax* GAUD & MOUCHET, 1959

– Width of anterior end of hysteronotal shield less than distance between setae *se*; ratio of idiosoma length/width about 1.5 (Fig. 26d). . . . . *P. pycnonoti* MIRONOV, 1993.

Males

1. Prodorsal shield with acute or rectangular posterior angles; scapular shields large, separated from prodorsal shield by one groove or by relatively narrow band of striated tegument with 3-4 striae (Figs. 24a, e, 27a, 28a). (subgenus *Holonyssoides*) 23

– Prodorsal shield with rounded or bluntly cut posterior angles, scapular shields clearly separated from prodorsal shields by large area of soft tegument with numerous striae (Figs. 1a, 4a, e, 17a, f). (subgenus *Pteronyssoides* s. str.) 2

2. Prodorsal shields two times longer than wide; ventral membrane of tarsus I greatly reduced; tarsus III with acute apex (Figs. 5a, d, e, 13a, c, d). 3

– Prodorsal shield equal or slightly shorter than wide; ventral membrane of tarsus I about 1/3-1/2 of segment length; tarsus III with bidentate apex (Figs. 1a, 2a, b, d) 4

3. Anterior margin of hysteronotal shield strongly convex, semicircular; openings *gl* almost at level of setae *d2* (Figs. 5a-e) . . . . *P.(P.) faini* sp.n.

– Anterior margin of hysteronotal shield straight or slightly concave; openings *gl* posterior to level of setae *d2* (Figs. 13a-d) . . . . *P.(P.) queleae* sp. n

4. Solenidion $\sigma 2$ of genu I present; seta *w* of tarsus III shorter or equal in length to seta *s*, clearly lanceolate in form (Figs. 17d, e, h) 5

– Solenidion $\sigma 2$ of genu I absent; seta *w* of tarsus III longer than seta *s*, spiculiform, setiform or slightly enlarged in apical part (Figs. 2d, 4d, g) 7

5. Adanal shield present. Anterior angles of hysteronotal shield with narrow extensions curved forward. Idiosoma 1.5-1.6 times longer than wide (Figs. 23a-d) . . . . *P.(P.) promeropis* MIRONOV & KOPIJ, 2000

– Adanal shield absent. Anterior angles of hysteronotal shields without narrow extensions. Idiosoma 1.2-1.3 times longer than wide (Figs. 17a, f, 18c, d). 6

6. Setae *c2* thickened and longer than prodorsal shield; seta *w* approximately at midlevel of tarsus III (Figs. 17a-e, 18c). . . . . *P.(P.) garioui* GAUD & MOUCHET, 1959

– Setae *c2* hair-like, short, less than half-length of prodorsal shield; seta *w* at level of proximal one third of tarsus III (Figs. 17f-h, 18 d) . . . . *P.(P.) nectariniae* MIRONOV, 2001

7. Outer margin of tarsus III with rectangular ledge. Anterior angles of hysteronotal shield acute, extending laterally (Figs. 16d-f, 18b). . . . . *P.(P.) lambda* GAUD & MOUCHET, 1959

– Outer margin of tarsus III slightly bowed. Anterior angles of hysteronotal shield rectangular or rounded 8

8. Posterior margin of prodorsal shield with a pair of narrow obliquely directed incisions. (Fig. 8d). . . . . *P.(P.) motacillae* MIRONOV, 1985

– Posterior margin of prodorsal shield without incisions 9

9. Setae *c2* longer or subequal to prodorsal shield length. 10

– Setae *c2* not longer than half-length of prodorsal shield 13

10. Lateral margin of opisthosoma with heavily sclerotized ledge at level of setae *e2*. Setae *c2* 1.5-1.7 times longer than prodorsal shield. Setae *c3* not thickened. Adanal shield consist of three separate pieces (Figs. 21d, 23e, 25b) . . . . . *P.(P.) striatus* (ROBIN, 1877)

– Lateral margin of opisthosoma without sclerotized ledge at level of setae *e2*. Setae *c2* subequal to prodorsal shield length; setae *c3* greatly thickened. Adanal shield entire, T-shaped or cross-shaped (Figs. 20a, c, 21a, c) 11

11. Two small additional sclerites between prodorsal and hysteronotal shields present; inner margin of oisthoventral sclerite bearing adanal membrane concave (Figs. 20e, 21c). . *P.(P.) piscinotus* MIRONOV, 1985

– Sclerites between prodorsal and hysteronotal shields absent; margin of oisthoventral sclerite bearing adanal membrane straight 12

12. Length of setae *f2* (32-40), about half of opisthosoma width at level of setae *ps2* (Figs. 20a-c, 21a) . . . . *P.(P.) parinus* (KOCH, 1841)

– Length of setae *f2* (55-65), approximately equal to opisthosoma width (Fig. 20f). . . . . *P.(P.) triangularis* sp. n.

13. Membrane of tarsus III absent or poorly developed (Figs. 9f, 12f) 14

– Inner margin of tarsus III between setae *w* and *s* with a well-developed membrane (Figs. 2d, 4d, g, 8c) 15

14. Setae *ps1* subequal to prodorsal shield length. Posterior margin of prodorsal shield straight. Idiosoma wide, ratio of length/width 1.2-1.4 (Figs. 9d, 10d) . . . . *P.(P.) passeris* (GAUD, 1952)

– Setae *ps1* less than one third of prodorsal shield length. Posterior margin of prodorsal shield clearly convex. Idiosoma elongated, ratio of length/width 1.6-1.7 (Figs. 12d, e, 14b) . . . . *P.(P.) pytiliae* sp. n

15. Opisthosomal lobes with short apical extensions bearing setae *h3* (Fig. 1a, b, 4a, 13e) 16

– Posterior margin of opisthosomal lobes bluntly rounded, with slightly extended bases of setae *h2, h3* (Figs. 12 a, b, 16 a, b) 18

16. Setae *h2* situated dorsally, slightly distant from postero-lateral margins of opisthosomal lobes (Figs. 4a-c) . . . . *P.(P.) eupasseris* sp. n

– Setae *h2* situated on the most margins of opisthosomal lobes 17

17. Anterior margin of hysteronotal shield concave. Terminal cleft with narrow membrane in anterior part. Setae *c3* slightly thickened in basal part (Figs. 1a, b, 2f, g). . . . . *P.(P.) emberizae* sp. n.

– Anterior margin of hysteronotal shield straight. Terminal cleft without membrane. Setae *c3* not thickened (Figs. 13e, f, 14d) . . . *P.(P.) serini* sp. n.

18. Distance between prodorsal and hysteronotal shields approximately equal to prodorsal shield length. Lateral margins of prodorsal shield without incisions (Figs. 12a) . . . . *P.(P.) plocei* sp. n.

– Distance between prodorsal and hysteronotal shields not longer than 3/4 of prodorsal shield length; lateral margins of prodorsal shield with incisions around or posterior to setae *se* (Figs. 4e, 5f, 8a). 19

19. Distance *gl:e1* 1.5-2 times longer than distance *d2:gl* (Fig. 4e, 8a) 20

– Distances *gl:e1* and *d2:gl* approximately equal (Figs. 5f, 9a). 21

20. Ratio of idiosoma length/width 1.45-1.55. Adanal shield commonly with 1-2 two pairs of short lateral extensions of irregular form (Figs. 4e, f) . . . . *P.(P.) euplecti* sp. n.

– Idiosoma more elongated, ratio of length/width 1.60-1.75. Adanal shields without noticeable lateral extensions (Figs. 8a, b). . . *P.(P.) microscutatus* sp. n.

21. Cupules *ih* situated more widely apart than setae *ps3*; area between bases setae *ps2* and cupules *ih* without sclerotized band; seta *w* of tarsus III with rounded apex (Figs. 5f-h). . . . . *P. foudiae* sp.n.

– Cupules *ih* closer to midline than setae *ps3*; narrow sclerotized band between base of setae *ps2* and cupules *ih* present; seta *w* of tarsus III thick spiculiform (Fig. 9a-c) 22

22. Distance *e2:h3* 45-50, distance between setae *e2* 90-95. Adanal shield commonly extending to level of posterior margin of trochanters IV (Figs. 9a, b, 10c) . . . . *P. ovoscutatus* sp. n.

– Distance *e2:h3* 35-40, distance between setae *e2* 75-80. Adanal shield not extending to trochanters IV (Figs. 16a, b, 18a). . . . . *P. viduinus* sp. n.

23. Prodorsal shield with almost rectangular posterior angles, not extending laterally; setae *c1* on anterior margin of hysteronotal shield; adanal shield large cross-shaped (Figs. 27a-d, 29b) . . . . *P. (H.) oxylabis* sp. n.

– Prodorsal shield with acute posterior angles greatly extending laterally; setae *c1* on striated tegument between prodorsal and hysteronotal shields; adanal shield as longitudinal plate or absent (Figs. 24a, c, e, 28a, d, 29a) 24

24. Opisthosomal lobes elongated with setae *h3* on lobar apices; posterior ends of epimerites I commonly connected; adanal apodemes absent; inner margin of tarsus III with tooth-like extension, apex of segment enlarged (Figs. 28a-c, 29a). Length of idiosoma 380-420. . . *P.(H.) latior* (TROUESSART, 1887)

– Opisthosomal lobes short and bluntly rounded; posterior tips of epimerites I free; opisthosoma with wide adanal apodemes; inner margin of tarsus III without tooth, apex of the segment narrow, bidentate (Figs. 24a, c, e,f). Length of idiosoma less than 350 25

25. Setae *e1* equidistant from the levels of openings *gl* and setae *e2*; prodorsal shield 1.2-1.3 times wider than long (Figs. 28d, e). . . . . *P. (H.) timaliae* MIRONOV, 1993

– Setae *e1* much closer to the level of openings *gl*, distance *gl:e1* about one third of distance *gl:e2*; prodorsal shield 1.5-1.7 times wider than long (Figs. 24a, e) 26

26. Length of idiosoma 245-265; one pair of sclerotized bracket-shaped patches present and situated on the posterior margin of prodorsal shield (Fig. 24e). . . . . *P. (H.) holoplax* GAUD & MOUCHET, 1959

– Length of idiosoma 280-320; two pairs of sclerotized bracket-shaped patches present, both situated anterior to margin of prodorsal shield (Fig. 24a). . . . . *P. (H.) desmiphorus* (GAUD, 1952)

Pteronyssoides (s. str.) HULL, 1934

TYPE SPECIES: *Pteronyssus striatus* ROBIN, 1877.
DIAGNOSIS: *Both sexes*: Prodorsal shield with rounded posterior angles; scapular shields narrow with acute inner

angle, separated from prodorsal shield by relatively large space of striated tegument with numerous fine striae. *Females*: Anterior half of hysteronotum without any fragments of hysteronotal shield (except for *P. lambda*); posterior half of hysteronotum with complex of several sclerites (commonly with unpaired central sclerite and pair of opisthosomal sclerites extending to the bases of setae *h2, h3*), or with entire shield (*P. garioui*), or without shields (*P. striatus*) (Figs. 3a, 7a-d, 19a-c, e, 22a-d, 26a). The subgenus includes 24 species, 22 of which are arranged into 3 species groups (*ovoscutatus, nectariniae,* and *parinus*) (Table 3).

Group *ovoscutatus*

DIAGNOSIS: *Both sexes*: Prodorsal shield with slightly convex posterior margin and rounded posterior angles. Solenidion $\sigma 2$ of genu I absent. *Males*: Setae *f2* situated ventrally or submarginally, lateral or anterolateral to setae *ps2* (except for *P. faini* having setae *f2* in marginal position) (Figs. 2g, 4c, f, 5c, g); tarsus III with convex outer margin, seta *w* of tarsus III setiform or spiculiform, longer than setae *s* and situated in basal quarter of the segment (Figs. 2d, 4d, g). *Females*: Arrangement of hysteronotal shield: pair of opisthosomal sclerites (entire or split into properly opisthosomal and pygidial fragments), and unpaired central sclerite of generally ovate form (Figs. 3a, 7a-d).

The group includes 15 species.

Pteronyssoides (Pteronyssoides) emberizae sp. n.
(Figs. 1a, b, 2a-g, 3a-d)

TYPE MATERIAL: Male holotype, 1 male and 6 female paratypes (IRSNB) ex *Emberiza flaviventris* STEPHENS, 1915 (Emberizidae), Rwanda, Akanyaru, 29.X.1955, A.FAIN. Holotype, 5 female paratypes – MRAC, 1 male, 1 female paratypes – ZISP.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 372 x 277 (in 1 paratype 388 x 286). Length of hysterosoma 257. Prodorsal shield: posterior angles rounded, lateral margins without incisions, posterior margin slightly convex, length along median line 96, width at posterior margin 103, setae *se* separated by 84 (Fig. 1a). Setae *c2* thin hair-like, situated in anteromedian angle of humeral shields; setae *c3*, long, thickened in basal part, about 125 in length, greatest width 4. Hysteronotal shield: anterior margin slightly concave, anterior angles slightly acute, length 190, width 118. Distance between prodorsal and hysteronotal shields along midline about 85. Opisthosomal lobes with short angular apices formed by extended bases of setae *h3* (Figs. 2f, g) Setae *f2* situated submarginally, anterolateral to *ps2*. Terminal cleft wide V-shaped, with narrow membrane in anterior part, 11 long, length of cleft including supranal concavity 46. Dorsal measurements: *c2:d2* 88, *d2:e2* 92, *d2:gl* 25, *gl:el* 26, *e2:h3* 60, *e2:e2* 100, *h3:h3* 57. Transventral sclerite 11 in length along median line. Tips of epiandrium extending to midlevel of genital apparatus; genital arch 21 x 22; aedeagus about half as long as genital arch. Setae *4a* at midlevel of genital apparatus. Adanal shield as short longitudinal bar, not extending to level of trochanters IV (Fig. 2g). Adanal membranes short, extending to level of *ps3*. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 101, *ps3:ps3* 50, *ih:ih* 65, *g:g* 10. Ventral membrane of tarsus I about one third of segment (Fig. 2a, b). Tarsus III 90 long, with bidentate apex, with membrane on inner margin; setae *w* thick setiform, 37 in length; setae *s* narrowly lanceolate 20 in length; setae *r* about 2 times longer than segment (Fig. 2d). Tarsus IV shorter than tibia IV; modified seta *d* at midlevel of the segment (Fig. 2e).

Female (paratype): Idiosoma length x width 445 x 286 (in 5 other paratypes 417-448 x 277-286). Length of hysterosoma 310. Prodorsal shield as in the male, 115 x 124, setae *se* separated by 106. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* long setiform, slightly thickened in basal quarter, about 108 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites split into main opisthosomal and pygidial fragments, and terminal sclerite (Fig. 3a). Central sclerite ovate, 46 x 31 (in other paratypes 38-44 x 28-37), its anterior end not extending to level of openings *gl*. Main fragments of opisthosomal sclerites as large polygonal plates, their anterior ends extending to midlevel of central sclerite; pygidial fragments as small sclerotized areas at bases of setae *h2, h3*. Distance from anterior end of opisthosomal sclerite to setae *h3* 90-95. Terminal sclerite with bow-shaped supranal concavity. Posterior margin of opisthosoma between setae *h3* slightly convex. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *c1, d1* greatly reduced and poorly visible; setae *e1* posterior to openings *gl*, approximately at midlevel of central sclerite; setae *e2* on lateral margins of opisthosomal sclerites. Setae *ps1* situated terminally, at level of *h3*. Dorsal measurements: *c2:d2* 152, *d2:e2* 84, *d2:gl* 28, *gl:e1* 28-31, *e2:h3* 69-72, *h3:h3* 128. Epigynium bow-like, 38 x 109 (Fig. 3b).

DIFFERENTIAL DIAGNOSIS: *Pteronyssoides emberizae* is closest to *P. serini* and *P. eupasseris* (see below) by having clear lobar apices in males and opisthosomal shield split into main and pygidial fragments in females. The males of *P. emberizae* differ from these species by thickened setae *c3* and concave anterior margin of prodorsal shield (Figs. 1a, b); the females are distinguished by central sclerite not extending to the level of hysteronotal gland openings *gl* (Fig. 3a). In males of *P. serini* and *P. eupasseris*, setae *c3* are not thickened, and anterior margin of hysteronotal shield is straight (Figs. 4a, 13e); in the females, the anterior end of central sclerite slightly extends beyond the level of openings *gl* (Figs. 7a, 15d)

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssoides (Pteronyssoides) eupasseris sp. n.
(Figs. 4a-d, 6a, 7a)

TYPE MATERIAL: Male holotype, 2 male and 2 female paratypes (MRAC 180 282) ex *Passer griseus* VIEILLOT, 1817 (Passeridae), Central African Republic, Bougouni, X.1950, coll. unknown, 2 male and 2 female paratypes (MRAC 180 281), same data. Holotype, paratypes – MRAC.
Additional material: 1 male, 2 females (MRAC 180 282-a) ex *Passer griseus*, Central African Republic, Bozoum, XI.1950, coll. unknown; 4 males, 1 female (MRAC 180 280), same host, Central African Republic, Bossangoa, VII.1951, coll. unknown.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 360 x 245 (in 2 paratypes 350-365 x 205-230). Length of hysterosoma 246. Prodorsal shield: posterior angles rounded, lateral margins without incisions, posterior margin slightly convex, size 102 x 116, setae *se* separated by 97. Setae *c2* hair-like, short, situated in anteromedian angles of humeral shield; setae *c3* setiform, long, about 115 in length. Hysteronotal shield: anterior margin almost straight, anterior angles rectangular, size 202 x 128. Distance between prodorsal and hysteronotal shields about 55. Opisthosomal lobes with short angular apices formed by extending bases of setae *h3*; bases of setae *h3* with poorly expressed bidentation; setae *h2* slightly moved anterior from lobar margin (Fig. 4b). Setae *f2* situated ventrally, anterolateral to setae *ps2*. Terminal cleft V-shaped, with narrow membrane, 27 long, length including supranal concavity 48. Dorsal measurements: *c2:d2* 83, *d2:e2* 89, *d2:gl* 30, *gl:el* 53, *e2:h3* 62, *e2:e2* 83, *h3:h3* 46. Transventral sclerite 13 in length; tips of epiandrium extending to base of genital apparatus; genital arch 23 x 19; aedeagus about half as long as genital arch. Setae *4a* at midlevel of genital apparatus. Adanal shield as longitudinal bar with lateral extensions of irregular form; anterior end extending to trochanters IV (Fig. 4c). Adanal membranes short. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 81, *ps3:ps3* 46; *ih:ih* 58, *g:g* 14. Ventral membrane of tarsus I about half as long as the segment. Tarsus III 71 in length, with bidentate apex, with narrow membrane on inner margin; setae *w* spiculiform with acute apex, 34 in length; setae *s* narrowly lanceolate, 17 in length; setae *r* about twice as long as the segment (Fig. 4d). Tarsus IV slightly shorter than tibia IV; modified seta *d* closer to apex of the segment.
Female (paratype): Idiosoma length x width 400 x 240 (in 3 other paratypes 360-395 x 200-230). Length of hysterosoma 270. Prodorsal shield as in the male, 124 x 128, setae *se* separated by 108. Setae *c2* short hair-like; setae *c3* setiform, about 75 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites split into main and pygidial fragments, and terminal sclerite (Fig. 7a). Central sclerite ovate, 51 x 33 (in other 3 paratypes 33-45 x 30-35), its anterior end extending beyond openings *gl*. Main fragment of opisthosomal sclerites extending to posterior half of central sclerite and not extending to openings *gl*; distance from anterior ends of opisthosomal sclerites to setae *h3* 95. Posterior margin of opisthosoma between setae *h3* almost straight. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *c1, d1, e1* greatly reduced; setae *e1* at level of openings *gl*, approximately at midlevel of central sclerite; setae *e2* on lateral margins of opisthosomal sclerites. Setae *ps1* situated terminally at level of *h3*. Dorsal measurements: *c2:d2* 95, *d2:e2* 104, *d2:gl* 40, *e2:h3* 55, *h3:h3* 97. Epigynium bow-like, 26 x 96.

DIFFERENTIAL DIAGNOSIS: This species is most similar to *P. serini* (see below) (Figs. 13e-f, 15d) by having opisthosoma lobes with extending apices in males and opisthosomal sclerites split into fragments in females. The males of *P. eupasseris* differ from that species by having setae *h2* moved from the lobar margin to dorsal surface; females are distinguished by having longer opisthosomal shields (about 95) extending to midlevel of central sclerite. In the males of *P. serini*, the setae *h2* occupy the marginal position on the lobes; in the females, the length of opisthosomal shields is about 80.

ETYMOLOGY: Combination of *eu* (true, Latin) and generic name of the type host to stress that this species rather than *P. passeris* (see below) is actually associated with the Passeridae.

Pteronyssoides (Pteronyssoides) euplecti sp. n.
(Figs. 4e-h, 6b, 7b)

TYPE MATERIAL: Male holotype, 4 female paratypes (YSU 2064 AMNH 268 596, 2 slides) ex *Euplectes hordeaceus* LINNAEUS, 1758 (Ploceidae), W. Africa, Gulf of Guinea, Sao Tome Island, 26.II.1929, J.G. CORREIA; 1 male paratype (YSU 2065 AMNH 268 596), same data, except date 25.II.1929. Holotype, 4 female paratypes – MZUM, 1 male paratype – ZISP.
Additional material: 4 males, 5 females (MRAC 180 289 – 180 292) ex *Euplectes hordeaceus*, Ghana, Lovi Camp, Mole Reserve, 26.VIII.1968, coll. unknown; 1 male, 1 female (MRAC 180 288) ex *E. h. hordaceus*, Cameroon, XI.1955, coll. unknown; 1 female (MRAC 180 299 SAIMR FMT-83-3-61) ex *E. ardens* (BODDAERT, 1783), South Africa, Transvaal, Haenerstburg, 26.XI.1961, coll. unknown; 4 males (IRSNB), same host, Rwanda, Akanyaru, 18.I.1956, A. FAIN.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 320 x 214 (in 1 paratype 346 x 236). Length of hysterosoma 211. Prodorsal shield: with rounded posterior angles, with deep incisions posterior to setae *se*, posterior margin almost straight, size 84 x 93, setae *se* separated by 77. Setae *c2* thin hair-like, situated on anteromedian angle of humeral shield; setae *c3* long, with thickened basal part, about 105 in length. Hysteronotal shield: anterior margin straight, anterior angles rectangular, size 177 x 96. Distance between prodorsal and hysteronotal shields about 55. Opisthosomal lobes bluntly rounded, with clearly extended bases of setae *h2, h3*; bases of setae *h3* bidentate. Setae *f2* situated ventrally anterior to *ps2*. Terminal cleft wide V-shaped, with narrow membrane, 16 long, length of cleft including supranal concavity 38. Dorsal measurements: *c2:d2* 68, *d2:e2* 79, *d2:gl* 12-13, *gl:e1* 28, *e2:h3* 46, *e2:e2* 90, *h3:h3* 40. Transventral sclerite 9 in length; tips of epiandrium almost extending beyond base of genital apparatus; genital apparatus 22 in length, 18 in width, aedeagus directed backward, about half as long as genital arch. Setae *4a* at base of genital apparatus. Adanal shield as longitudinal bar extending to trochanters IV, with lateral extensions of irregular shape (Figs. 4f, 6b). Adanal membranes short. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 75, *ps3:ps3* 43, *ih:ih* 36, *g:g* 5. Ventral membrane of tarsus I about half-length of segment. Tarsus III 73 in length, with bidentate apex, with narrow membrane on inner margin; setae *w* spiculiform, 28 in length; setae *s* narrowly lanceolate, 16 in length; setae *r* slightly longer than segment (Fig. 4g). Tarsus IV as long as tibia IV, modified seta *d* closer to base of the segment (Fig. 4h).

Female (paratype): Idiosoma length x width 362 x 224 (in other 3 paratype 358-362 x 196-202). Length of hysterosoma 261. Prodorsal shield as in the male, 103 x 105, setae *se* separated by 88. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* setiform, about 65 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites, terminal sclerite (Fig. 7b). Central sclerite ovate, 46 x 25 (in other paratypes 44-52 x 19- 22); its anterior end at level of openings *gl*. Opisthosomal sclerites large, slightly extending by acute anterior ends beyond midlevel of central sclerite; length of opisthosomal sclerites from anterior end to setae *h3* 106-111. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *e1* at level of anterior half of central sclerite; setae *e2* on lateral margin of opisthosomal sclerites. Setae *ps1* situated dorsally, slightly anterior to setae *h3*. Dorsal measurements: *c2:d2* 94, *d2:e2* 74, *d2:gl* 22, *gl:e1* 7-11, *e2:h3* 70, *h3:h3* 96. Epigynium bow-like, 28 x 81.

DIFFERENTIAL DIAGNOSIS: The males of *P. euplecti* are very similar to *P. microscutatus* (Figs. 8a, 10a) by the shape of opisthosoma and position of openings *gl* closer to setae *d2* than to *e1*, while the females (Fig. 7b) are more similar to *P. plocei* (Fig. 15a) than to *P. microscutatus* by having the central sclerite of ovate form; in females of the latter species, the central sclerite is rudimentary, rod-shaped (Fig. 11a). The males of *P. euplecti* differ by having a relatively wider idiosoma with ratio of length/width 1.45-1.55 (n=5, all non-deformed specimens from the type host were measured) versus 1.6-1.75 in *P. microscutatus* (n=4). The females of *P. euplecti* are clearly distinguished from those of *P. plocei* by the more posterior position of the central sclerite, the anterior end of which does not extend beyond the level of openings *gl*.

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssus (Pteronyssoides) faini sp. n.
(Figs. 5a-e, 6c, 7c)

TYPE MATERIAL: Male holotype, 2 male and 3 female paratypes (YSU 2180 AMNH 298 102) ex *Lonchura bicolor poensis* (FRASER, 1843) (Estrildidae), Spanish Guinea, Fernando Po Island, Santa Isabel, 12.IV.1929, J.G. CORREIA. Holotype, 1 male and 2 female paratypes – MZUM, other paratypes – ZISP.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 318 x 186 (in 2 paratypes 311-322 x 180-198). Length of hysterosoma 206. Prodorsal shield: with rounded posterior angles, with lateral incisions around setae *se*, posterior margin slightly convex, size 74 x 70, setae *se* separated by 60. Setae *c2* hair-like, short, situated on striated tegument; setae *c3* hair-like, thin, about 60 in length. Hysteronotal shield with widely rounded anterior end (Fig. 5a), greatest length 180, width of anterior part at level of setae *d2* 90. Distance between prodorsal and hysteronotal shields about 56. Opisthosomal lobes rounded, without membrane, bases of setae *h2, h3* not extended. Setae *d2* very close to openings *gl*; setae *f2* situated situated marginally, lateral to setae *ps2* (Fig. 5b) Terminal cleft as a wide V, 16 long, with narrow membrane; length of the cleft including supranal concavity 34. Dorsal measurements: *c2:d2* 50, *d2:e2* 90, *d2:gl* 2-3, *gl:e1* 66, *e2:h3* 50, *e2:e2* 75, *h3:h3* 66. Transventral sclerite thin, 5 in length; tips of epiandrium short, not extending to genital apparatus; genital arch 25 x 12 in width, aedeagus almost equal in length to genital arch. Setae *4a* at midlevel of genital arch. Adanal shield as short longitudinal bar, not extending to level of trochanters IV (Fig. 5c). Adanal membranes short. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 67, *ps3:ps3* 40, *ih:ih* 60, *g:g* 8. Ventral membrane on tarsus I reduced (Fig. 5d). Tarsus III 46 in length, with acute apex, without membrane; setae *w* setiform, 16 in length; setae *s* thin spiculiform, 11 in length; setae *r* slightly longer than segment (Fig. 5e). Tarsus IV subequal in length to tibia IV; modified seta *d* at midlevel of the segment.

Female (paratype): Idiosoma length x width 372 x 202 (in 2 other paratype 363-380 x 94-205). Length of hysterosoma 255. Prodorsal shield as in the male, length 82, width 65, setae *se* separated by 56. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* setiform, about 35 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites extending to bases of setae *h2, h3*, and terminal sclerite (Fig. 7c). Central sclerite large ovate, with attenuate anterior end, 78 x 40 (in other paratypes 80-84 x 38-43); anterior end of the sclerite extending to the level of posterior margins of trochanters III. Opisthosomal sclerites relatively short and narrow, scarcely extending by anterior ends to level of posterior end of central sclerite, length of opisthosomal sclerites 80-84. Posterior margin of opisthosoma with pair of convex extensions, setae *ps1* dorsal, anterior to level of bases of setae *h2*. Setae *d1, d2, e1* and openings *gl* on striated tegument; openings *gl* at level of trochanters

III, close to level of setae *d2*; setae *e1* at level of posterior third of central sclerite; setae *e2* in anterior ends of opisthosomal sclerites. Dorsal measurements: *c2:d2* 59, *d2:e2* 106, *d2:gl* 0-4, *gl:e1* 67, *e2:h3* 80, *ps1:h3* 22, *h3:h3* 75. Epigynium semicircular, 37 x 71.

DIFFERENTIAL DIAGNOSIS: This species is closely related to *P. lonchurae* described from *Lonchura malacca formosana* (SWINHOE, 1865) in Taiwan (SUGIMOTO, 1941) by having a relatively large central sclerite of ovate form in females and deeply concave anterior margin of transventral sclerite in males. Females of *P. faini* differ from that species by a longer central sclerite, which extends to the midlevel between trochanters III and IV; the males differ by a rounded anterior margin of hysteronotal shield. According to the drawings of *P. lonchurae* in the original description (SUGIMOTO, 1941), central sclerite in females scarcely extends to the level of trochanters IV; in the male, the hysteronotal shield has a more or less straight anterior margin.

ETYMOLOGY: The species is named in honour of the great acarologist Prof. A. FAIN (Institut Royal des Scieneces Naturelles de Belgique, Brussels, Belgium).

Pteronyssoides(Pteronyssoides) foudiae sp. n. (Figs. 5f-h, 6d, 7d)

TYPE MATERIAL: Male holotype, 8 male and 7 female paratypes (MRAC 180 248) ex *Foudia madagascariensis* LINNAEUS, 1766 (Ploceidae), Madagascar, Briekaville, X.1951, coll. unknown. Holotype, paratype – MRAC, paratypes – ZISP.
Additional material: 2 males, 1 female (NU 9450 USNM 128 688) ex *Foudia eminentissima aldabrana* RIDGWAY, 1893, Seychelles, Aldabra Island, 10.X.1892, W.L. ABBOT.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 310 x 212 (in 8 paratypes 305-320 x 195-225). Length of hysterosoma 205. Prodorsal shield: with rounded posterior angles, with poorly developed incisions posterior to setae *se*, posterior margin convex, size 87 x 86, setae *se* separated by 73. Setae *c2* thin setiform, situated on anteromedian angle of humeral shield; setae *c3* long, hair-like, about 80 in length. Hysteronotal shield: anterior margin almost straight, size 172 x 104. Distance between prodorsal and hysteronotal shields about 50. Opisthosomal lobes rounded, with clearly extending bases of setae *h2, h3*; bases of setae *h3* bidentate. Setae *h3* slightly enlarged in basal part. Setae *f2* ventral, anterior to setae *ps2*. Terminal cleft as wide V, with narrow membrane, 14 long, length of cleft including supranal concavity 35. Dorsal measurements: *d2:e2* 67, *d2:e2* 86, *d2:gl* 20, *gl:e1* 25, *e2:h3* 47, *e2:e2* 83, *h3:h3* 31. Transventral sclerite 6 in length; tips of epiandrium extending to base of genital apparatus; genital apparatus 25 x 17, aedeagus about half-length of genital arch. Setae *4a* at level of genital apparatus base. Adanal shield as longitudinal bar, not extending to trochanters IV (Figs. 5g, 6d). Adanal membranes short. Diameter of anal discs 17. Ventral measurements: *ps2:ps2* 56, *ps3:ps3* 36, *ih:ih* 41, *g:g* 6. Ventral membrane on tarsus I poorly developed, about one quarter of segment length. Tarsus III 64 in length, with narrowed bidentate apex, with narrow membrane on inner margin; setae *w* lanceolate, rounded apically, 17 in length,; setae *s* narrowly lanceolate, 16 in length; setae *r* slightly longer than segment (Fig. 5h). Tarsus IV subequal in length to tibia IV; modified seta *d* at midlevel of the segment.
Female (paratype): Idiosoma length x width 350 x 197 (in 6 other paratypes 350-360 x 195-210). Length of hysterosoma 232. Prodorsal shield as in the male, 100 x 102, setae *se* separated by 86. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* hair-like, about 70 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites, and terminal sclerite (Fig. 7d). Central sclerite large, widely ovate, 80 x 46 (in other paratypes 72-83 x 44-51); anterior end extending beyond trochanters IV. Opisthosomal sclerites large, extending by anterior ends to the level of posterior end of central sclerite, length of opisthosomal sclerites 87. Setae *ps1* dorsal, slightly anterior to the level of setae *h3*. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *e1* at level of posterior third of central sclerite; openings *gl* at midlevel of central sclerite; setae *e2* on lateral margin of opisthosomal sclerites. Distances between setae and openings: *c2:d2* 88, *d2:e2* 77, *d2:gl* 19, *gl:e1* 12-17, *e2:h3* 58, *ps1:h3* 10, *h3:h3* 103. Epigynium bow-like, 28 x 73.

DIFFERENTIAL DIAGNOSIS: The males of *P. foudiae* are similar to *P. euplecti* by the shape of opisthosoma and structure of tarsus III, but smaller in general size; they differ from that species by having cupules *ih* separated more widely than setae *ps3*. The females of *P. foudiae* clearly differ from *P. euplecti* (Fig. 7b) by having much larger central sclerite (72-83 x 44-51, n=7) extending by anterior end to the level between trochanters III and IV (Fig. 7d). In males of *P. euplecti,* cupules *ih* are closer to midline than setae *ps3* (Fig. 6b); in females, central sclerite is smaller (44-52 x 19- 22, n=10, specimens from the type hosts).

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssoides (Pteronyssoides) lonchurae (SUGIMOTO, 1941)

The original description of this species from *Lonchura malacca formosana* (Estrildidae) in Taiwan (SUGIMOTO, 1941) is quite schematic and incomplete. Based on the drawing of the female it is possible only to conclude that *Pteronyssoides lonchurae* without doubts belongs to the *ovoscutatus* group. Any materials of this species from the type host were not available for our study.

Pteronyssoides (Pteronyssoides) microscutatus sp. n.
(Figs. 8a-c, 10a, 11a)

TYPE MATERIAL: Male holotype and 1 male paratype (MRAC 180 297) ex *Euplectes axillaris* (SMITH A., 1838) (Ploceidae), Swaziland, Malkerns, 30.XII.1967, coll. unknown; 2 male and 4 female paratypes (MRAC 180 294 – 180 296), same data.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 358 x 227 (in 3 paratype 330-350 x 195-225). Length of hysterosoma 240. Prodorsal shield: with rounded posterior angles, with deep incisions posterior to setae *se*, posterior margin almost straight, size 96 x 95, setae *se* separated by 81. Setae *c2* thin hair-like, situated on anteromedian angle of humeral shield; setae *c3* long, with thickened basal part, about 85 in length. Hysteronotal shield: anterior margin straight, anterior angles rectangular, size 187 x 104. Distance between prodorsal and hysteronotal shields about 75. Opisthosomal lobes bluntly rounded, with clearly extended bases of setae *h2, h3*; bases of setae *h3* bidentate. Setae *f2* situated ventrally, anterior to *ps2*. Terminal cleft wide V-shaped, with narrow membrane, 16 long, length of cleft including supranal concavity 43. Dorsal measurements: *c2:d2* 83, *d2:e2* 88, *d2:gl* 7-8, *gl:el* 15-17, *e2:h3* 50, *e2:e2* 86, *h3:h3* 36. Transventral sclerite 10 in length; tips of epiandrium almost extending beyond base of genital apparatus; genital apparatus 21 x 10, aedeagus about half-length of genital arch. Setae *4a* at base of genital apparatus. Adanal shield as longitudinal bar, not extending to trochanters IV (Fig. 8b). Adanal membranes short. Diameter of anal discs 17. Ventral measurement: *ps2:ps2* 67, *ps3:ps3* 38, *ih:ih* 27, *g:g* 11. Ventral membrane of tarsus I about half as long as segment. Tarsus III 62 in length, with bidentate apex, with narrow membrane on inner margin; setae *w* thick knife-like, 28 in length; setae *s* narrowly lanceolate, 16 in length; setae *r* slightly longer than segment (Fig. 8c). Tarsus IV slightly shorter than tibia IV; modified seta *d* closer to base of the segment.
Female (paratype); Idiosoma length x width 383 x 222 (in other 3 paratype 375-390 x 220-235). Length of hysterosoma 257. Prodorsal shield as in the male, 106 x 108, setae *se* separated by 96. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* setiform, about 55 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites, terminal sclerite (Fig. 11a). Central sclerite, very small, short rod-shaped 20 x 8 (in other paratypes 20-32 x 8-15); its anterior end at level of openings *gl*. Anterior ends of opisthosomal sclerites not extending to central sclerite, their borders poorly expressed, surface with a few erratically disposed longitudinal striae; length of opisthosomal sclerites from anterior end to setae *h3* 80.

Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *e1* at level of anterior half of central sclerite; setae *e2* near lateral margin of opisthosomal sclerites (in some specimens off these sclerites). Setae *ps1* situated dorsally, slightly anterior to setae *h3*. Dorsal measurements: *c2:d2* 106, *d2:e2* 86, *d2:gl* 22, *gl:el* 7-80, *e2:h3* 60, *h3:h3* 90. Epigynium bow-shaped, 33 x 88.

DIFFERENTIAL DIAGNOSIS: The males of this species are very similar to *P. euplecti* by the shape of dorsal shields and opisthosoma, while the females clearly differ from those of all other species of the *ovoscutatus* group. The males of *P. microscutatus* differ from that species by relatively more elongated idiosoma with ratio of length to width 1.45-1.55 (Figs. 8a, b) versus 1.6-1.75 in *P. euplecti* (Fig. 4e); the females are clearly distinguished from all species of the *ovoscutatus* group by the small rod-shaped central sclerite and opisthosomal shields with blurred borders and irregular longitudinal striae (Fig. 11a). In the females of most similar species of the *ovoscutatus* group (*P. euplecti, P. ovoscutatus, P. plocei,* and *P. foudiae*), the central sclerite is ovate, over 20 in width, and opisthosomal shields have disctinct borders (Figs. 7b, 11c).

ETYMOLOGY: The specific epithet points out the very small central sclerite in females.

Pteronyssoides (Pteronyssoides) motacillae MIRONOV, 1985 (Figs. 8d-f, 10b, 11b)

MATERIAL EXAMINED: Male holotype, 3 male and 4 female paratypes (ZISP 968) ex *Motacilla flava* LINNAEUS, 1758 (Motacillidae), Russia, Kaliningrad Province, Rybachy, 11.IX.1982, S. MIRONOV.

This species is known from three species of wagtails, *M. flava* (type host), *M. alba leucopsis* GOULD, 1838, and *M. citreola* PALLAS, 1776 in Europe and Asia (MIRONOV, 1985).

Pteronyssoides (Pteronyssoides) ovoscutatus sp. n.
(Figs. 9a-c, 10c, 11c)

TYPE MATERIAL: Male holotype, 2 male and 7 female paratypes (MRAC 147 203, 10 slides) ex *Cyanomitra verticalis* (LATHAM, 1790) (Nectariniidae), Cameroon, Galim, 17.VIII.1971, F. PUYLAERT. Holotype, 1 male and 5 female paratypes – MRAC, 1 male and 2 female paratypes – ZISP.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 340 x 233 (in 2 paratypes 322-335 x 220-224). Length of hysterosoma 230. Prodorsal shield: with rounded posterior angles, with lateral incisions around setae *se*, posterior margin slightly convex, size 98 x 93, setae *se* separated by 81. Setae *c2* setiform, short (less half the length of distance between *se*), situated in anteromedian angle of humeral shield; setae *c3* long, thickened basally, about 95 in length, 4 in width at base. Hysteronotal shield: anterior margin straight, anterior angles rectangular, size 190 x 112. Distance between prodorsal and hysteronotal shields about 50. Opisthosomal lobes with bluntly rounded posterior margin, with clearly extending bases of setae *h2, h3*; bases of setae *h3* bidentate. Setae *f2* situated ventrally, anterolateral to *ps2*. Terminal cleft wide V-shaped, with narrow membrane, 19 long, length of cleft including supranal concavity 40. Dorsal measurements: *c2:d2* 68, *d2:e2 96*, *d2:gl* 25, *gl:e1* 22-23, *e3:h3* 50, *e2:e2* 92, *h3:h3* 40. Transventral sclerite 12 in length; tips of epiandrium extending to base of genital apparatus; genital arch 25 x 15, aedeagus about half-length of genital arch. Setae *4a* at midlevel of genital apparatus. Adanal shield as longitudinal bar, arrowhead-shaped on anterior end (Figs. 9b, 10c). Adanal membranes short. Posterior part of opisthosomal lobes with narrow sclerotized band between bases of seta *ps2* and respective cupula *ih*. Diameter of anal discs 19. Ventral measurements: *ps2:ps2* 83, *ps3:ps3* 45, *ih:ih* 30, *g:g* 7. Ventral membrane about 2/3 length of tarsus I. Tarsus III 68 in length, with bidentate apex, with narrow membrane on inner margin; setae *w* spiculiform, 27 in length; setae *s* narrowly lanceolate, 19 in length; setae *r* slightly longer than segment (Fig. 9c). Tarsus IV long as tibia IV; modified seta *d* closer to base of the segment.

Female (paratype): Idiosoma length x width 363 x 212 (in 6 other paratypes 355-382 x 192-205). Length of hysterosoma 255. Prodorsal shield as in the male, 100 x 109, setae *se* separated by 93. Setae *c2* hair-like, short, situated on striated tegument. Setae *c3* setiform, about 65 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites, terminal sclerite (Fig. 11c). Central sclerite ovate, 52 x 34 (in other paratypes 44-50 x 28- 31), anterior end slightly extending beyond the level of openings *gl*. Opisthosomal sclerites large, anterior ends attenuate, not extending to midlevel of openings *gl*, length of opisthosomal sclerite 95. Posterior margin between setae *h3* slightly convex; setae *ps1* dorsal, slightly anterior to *h3*. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *e1* slightly anterior to midlevel of central sclerite; setae *e2* on lateral margin of opisthosomal sclerites. Distances between setae and openings: *c2:d2* 105, *d2:e2* 72, *d2:gl* 22, *gl:e1* 10-11, *e2:h3* 60, *h3:h3* 93. Epigynium bow-like, 28 x 78h.

DIFFERENTIAL DIAGNOSIS: Among the typical representatives of the *ovoscutatus* group, this species is most similar to *P. viduinus* (Figs. 16a, 19a) by the shape of opisthosomal lobes and having the transverse sclerotized bands between cupules *ih* and setae *ps2* in males and small-sized central sclerite in females. The males of *P. ovoscutatus* differ from that species by the longer and wider posterior part of opisthosoma, *e2:h3* 45-50, *e2:e2* 90-95 (n=3), versus 35-40 and 75-82 (n=17) in *P. viduinus*. The females of *P. ovoscutatus* differ only by the ovate form of central sclerite with length/width ratio about 1.5; in *P. viduinus*, the central sclerite is almost circular, length to width ratio 1-1.2 (Fig. 19a).

ETYMOLOGY: Combination of *ovum* (egg, Latin) and *scutum* (shield, Latin) to point out the form of the central sclerite in females.

REMARK: Taking into consideration the general host specificity of the *ovoscutatus* group to Estrildidae and Ploceidae (see discussion of host associations) and other feather mite taxa detected on the slide series from *Cyanomitra verticalis*, we strongly suggest that the association of *P. ovoscutatus* with this host is probably the result of contamination. The slide series (MRAC 147 203, 94 slides) from this host specimen contains five more feather mite species of four genera: *Anisodiscus* GAUD & MOUCHET, 1957, *Hadrophyllodes* ATYEO, 1971, *Montesauria* OUDEMANS, 1905 (Proctophyllodidae), one species of each, and two species of *Trouessartia* CANESTRINI, 1899 (Trouessartiidae). Representatives of the two former genera are typical for Nectariniidae, while mites of the *heterocaula* species group (*Montesauria*), and the *estrildae* and *geometrica* species groups (*Trouessartia*) are restricted to Estrildidae (ATYEO, 1977; SANTANA, 1976; MIRONOV & FAIN, 2003).

Pteronyssoides (Pteronyssoides) passeris (GAUD, 1952) (Figs. 9d-f, 10d, 11d)

MATERIAL EXAMINED: Male holotype (MRAC 180 250) ex *Dicrurus f. forficatus* LINNAEUS, 1766 (Dicruridae), Madagascar, Mabonoro, X. 1951; 1 male, 2 females (MRAC 180 251), same host, Madagascar, Tenerive, VIII.1962, coll. unknown; 1 male, 1 female (UGA 9274 AMNH 413 706), same host, Madagascar, Tulear Prov., Manombo, 3.X.1929, A.L. RAND & R. ARCHBOLD; 1 male (MRAC 180 256) ex *D. atripennis* SWAINSON, 1837, Cameroon, IX.1955, coll. unknown; 11 males, 8 females (MRAC 180 252 - 180 255) ex *D. adsimilis* BECHSTEIN, 1794, Zululand, St. Lucia, X.1965, F. ZUMPT; 1 male (MRAC 180 257), same host, South Africa, Cape Province, I.1954, coll. unknown.

Pteronyssoides passeris was formerly known only from the type host, *D. forficatus*, in Madagascar (GAUD, 1952; GAUD & TILL, 1961). The present study shows that it is distributed on various species of drongos (Corvida: Dicruridae) in central and southern Africa. By unknown reasons, this species was given a misleading specific epithet ''*passeris*'', although its hosts do not belong to the family Passeridae and even to the parvorder Passerida.

Pteronyssoides (Pteronyssoides) plocei sp. n. (Figs. 12a-c, 14a, 15a)

TYPE MATERIAL: Male holotype, 2 male and 3 female paratypes (IRSNB) ex *Ploceus superciliosus* (SHELLEY, 1873) (Ploceidae), Rwanda, Akanyaru, 28.X.1955, A. FAIN. Holotype, paratypes – MRAC.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 345 x 223 (in 1 paratypes 348 x 227). Length of hysterosoma 212. Prodorsal shield: with rounded posterior angles, lateral margins without incision, posterior margin almost straight, size 94 x 85, setae *se* separated by 75.

Setae *c2* thin hair-like situated in anteromedian angle of humeral shields; setae *c3* long, hair-like, about 85 in length. Hysteronotal shield: anterior margin straight, anterior angles almost rectangular, size 162 x 90. Distance between prodorsal and hysteronotal shields along median line about 80. Opisthosomal lobes rounded, with poorly extended bidentate bases of setae *h3*. Setae *f2* situated ventrally, anterolateral to setae *ps2*. Terminal cleft V-shaped, with narrow membrane, 13 long, length of cleft including supranal concavity 32. Dorsal measurements: *c2:d2* 82, *d2:e2* 85, *d2:gl* 22, *gl:e1* 22, *e2:h3* 38, *e2:e2* 88, *h3:h3* 20. Transventral sclerite 6 in length; tips of epiandrium slightly extending beyond base of genital apparatus; genital arch 19 x 17; aedeagus about half as long as genital arch. Setae *4a* at level of genital apparatus base. Adanal shield as longitudinal bar, not extending to level of trochanters IV (Fig. 12b). Adanal membranes short. Diameter of anal discs 15. Ventral measurements: *ps2:ps2* 60, *ps3:ps3* 41, *ih:ih* 29, *g:g* 5. Ventral membrane of tarsus I about half as long as segment. Tarsus III 60 long, with bidentate apex and with narrow membrane on inner margin; setae *w* and *s* thick spiculiform, 26 and19 in length, respectively; setae *r* slightly longer than segment (Fig. 12c). Tarsus IV subequal to tibia IV; modified seta *d* closer to base of the segment.

Female (paratype): Idiosoma length x width 385 x 230 (in 2 other paratype 365-400 x 215-235). Length of hysterosoma 280. Prodorsal shield: with rounded posterior angles, lateral margins with short and narrow incision posterior to setae *se*, posterior margin convex, length along median line 112, greatest width 109, setae *se* separated by 90. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* setiform, about 60 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites, terminal sclerite (Fig. 15a). Central sclerite ovate, 50 x 31 (in other 2 paratypes 50-51 x 38-30), anterior end extending beyond level of openings *gl*. Opisthosomal sclerites large, extending by anterior ends to midlevel of central sclerite; length of opisthosomal sclerite from anterior end to setae *h3* 104. Posterior margin of opisthosoma between setae *h3* slightly convex. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *e1* approximately at midlevel of central sclerite; setae *e2* on lateral margin of opisthosomal sclerites. Setae *ps1* situated dorsally, slightly anterior to setae *h3*. Distances between setae and openings: *c2:d2* 118, *d2:e2* 81, *d2:gl* 25-28, *gl:e1* 6-14, *e2:h3* 64, *h3:h3* 93. Epigynium bow-like, 25 x 81.

DIFFERENTIAL DIAGNOSIS: This species is most similar to *P. euplecti* by having a relatively large space of striated tegument between prodorsal and hysteronotal shields in males, and in the form of central and opisthosomal sclerites in females. In the males of *P. plocei*, length of prodorsal shield is approximately equal to the space between prodorsal and hysteronotal shields, and incisions on lateral margins of this shield are absent (Fig. 12a); in the females, the anterior end of central sclerite is extended beyond the level of openings *gl* (Fig. 15a). In the males of *P. euplecti*, the distance between shields is about 3/4 of prodorsal shield length and the lateral margin of the shield has incisions (Fig. 4e); in the females, the central sclerite in not extended beyond openings *gl* (Fig. 7b).

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssoides (Pteronyssoides) pytiliae sp. n.
(Figs. 12d-f, 14b, 15b)

TYPE MATERIAL: Male holotype, 1 male paratype (UGA 3077 USNM 487 835) ex *Pytilia melba belli* OGILVIE-GRANT, 1907 (Estrildidae), Mozambique, Tete District, 14 mi ESE Chicoa, 18.VIII.1964, A.L. MOORE; 3 female paratypes (UGA 3075 USNM 211 914), same host, Uganda, SE Ruwenzori, 6.V.1906, E. DENT. Holotype, 3 female paratypes – MZUM, 1 male paratype – ZISP.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 357 x 224 (idiosomal size in 1 paratype 340 x 205). Length of hysterosoma 230. Prodorsal shield: posterior angles rounded, lateral margins with narrow incision posterior to setae *se*, posterior margin slightly convex, size 102 x 96, setae *se* separated by 84. Setae *c2* hair-like, short, situated in anteromedian angle of humeral shields; setae *c3*, hair-like, about 80 in length. Hysteronotal shield: anterior margin straight, anterior angles almost rectangular, size 187 x 108. Distance between prodorsal and hysteronotal shields about 55. Opisthosomal lobes rounded, with extended bases of setae *h2, h3;* bases of setae *h3* bidentate. Setae *f2* ventral, anterolateral to setae *ps2*. Terminal cleft widely V-shaped, with narrow membrane, length 11, length of cleft including supranal concavity 35. Dorsal measurements: *c2:d2* 68, *d2:e2* 93, *d2:gl* 22, *gl:e1* 31, *e2:h3* 48, *e2:e2* 80, *h3:h3* 36. Transventral sclerite 9 in length; tips of epiandrium slightly extending beyond base of genital apparatus; genital arch 22 x 17; aedeagus about half as long as genital arch. Setae *4a* at level of base of genital apparatus. Adanal shield as longitudinal bar with lateral extensions of irregular form, not extending to level of trochanters IV (Fig. 12e). Adanal membranes short. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 54, *ps3:ps3* 30, *ih:ih* 35, *g:g* 7. Ventral membrane of tarsus I about half as long as segment. Tarsus III 50 long, with narrow bidentate apex, without membrane on inner margin; setae *w* spiculiform, 25 in length; setae *s* narrowly lanceolate 12 in length; setae *r* slightly longer than segment (Fig. 12f). Tarsus IV shorter than tibia IV; modified seta *d* at midlevel of the segment.

Female (paratype): Idiosoma length x width 371 x 212 (in 2 other paratypes 364-377 x 210-215). Length of hysterosoma 252. Prodorsal shield as in the male, 105 x 107, setae *se* separated by 84. Setae *c2* short hair-like, situated on striated tegument. Setae *c3* setiform, about 68 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites, terminal sclerite

(Fig. 15b). Central sclerite narrowly ovate, 63 x 28 (in other 2 paratypes 51-62 x 25-27), its anterior half extending beyond level of openings *gl*. Opisthosomal sclerites large, extending by anterior ends to midlevel of central sclerite; length of opisthosomal sclerite from anterior end to setae h3 95-104. Posterior margin of opisthosoma between setae *h3* slightly convex, with well-sclerotized copulatory extension. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *e1* anterior to level of openings *gl*; setae *e2* on opisthosomal sclerites, distant from its outer margin. Setae *ps1* situated dorsally, slightly anterior to *h3*. Dorsal measurements: *c2:d2* 87, *d2:e2* 90, *d2:gl* 47, *gl:e1* 15-17, *e2:h3* 57, *h3:h3* 84. Epigynium bow-like, 28 x 78.

DIFFERENTIAL DIAGNOSIS: This species is very similar to *P. euplecti, P. plocei* and *P. microscutatus* by the shape and size of opisthosoma and relatively large distance between prodorsal and hysteronotal shield in males, and by having an ovate central sclerite situated slightly anterior to opisthosomal sclerites in females. The males of *P. pytiliae* differ from these species by the absence of a membrane on inner margin of tarsus III (Fig. 12f); the females are distinguished by noticeably elongated central sclerite, which is 2-2.5 times longer than wide, and sclerotized copulatory extension on posterior margin of opisthosoma (Fig. 15b). In females of the three similar species, the central sclerite is only 1.2-1.5 times longer than wide and the copulatory extension is not expressed.

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssoides (Pteronyssoides) queleae sp. n.
(Figs. 13a-d, 14c, 15c)

TYPE MATERIAL: Male holotype, 1 male and 3 female paratypes (MRAC 180 246), 2 male, 4 female paratypes (MRAC 180 245, 180 247) ex *Quelea quelea* (LINNAEUS, 1758) (Ploceidae), South Rhodesia, Kariba, II.1964, coll. unknown. Holotype, 2 male and 2 female paratypes – MRAC; 1 male and 2 female paratypes – ZISP.
Additional material: 5 males, 5 females (MRAC 180 242 - 180 244) ex *Q. quelea*, Senegal, VIII.1955, coll. unknown; 2 males, 3 females (MRAC 180 23439, 180 440), same host, Cameroon, Waza, 1960, coll. unknown; 4 males, 1 female (MRAC 180 241), same host, Morocco, Dakar, V. 1955, coll. unknown; 2 males, 1 female (MRAC 180 259, 3 slides), same host, Senegal, 1.VIII.1955, P. MOREL.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 315 x 171 (in 3 paratypes 300-325 x 170-185). Length of hysterosoma 189. Prodorsal shield: posterior angles rounded, lateral margins with incisions around setae *se*, posterior margin slightly convex, size 88 x 65, setae *se* separated by 56. Setae *c2* hair-like, short, situated on striated tegument; setae *c3* setiform, about 45 in length. Hysteronotal shield: anterior margin almost straight, anterior angles rectangular, size 159 x 65. Distance between prodorsal and hysteronotal shields about 65. Opisthosomal lobes with bluntly rounded posterior margins, with slightly extended bases of setae *h2, h3*. Setae *f2* ventral, anterolateral to setae *ps2*. Terminal cleft wide V-shaped, with narrow membrane, 6 long, length including supranal concavity 22. Dorsal measurements: *c2:d2* 62, *d2:e2* 76, *d2:gl* 22, *gl:e1* 16, *e2:h3* 38, *e2:e2* 51, *h3:h3* 30. Transventral sclerite 9 in length; tips of epiandrium extending base of genital apparatus; genital arch 16 in length, 11 in width; aedeagus about half as long as genital arch. Setae *4a* at level of base of genital apparatus. Adanal shield as short longitudinal bar, not extending to level of trochanters IV (Fig. 13b). Adanal membranes short. Diameter of anal discs 11. Ventral measurements: *ps2:ps2* 48, *ps3:ps3* 16, *ih:ih* 33, *g:g* 5. Ventral membrane of tarsus I reduced (Fig. 13c). Tarsus III 46 in length, with obliquely cut apex, with short membrane on inner margin; setae *w* spiculiform, 19 in length; setae *s* narrowly lanceolate 10 in length; setae *r* slightly longer than segment (Fig. 13d). Tarsus IV subequal in length to tibia IV; modified seta *d* at midlevel of the segment.
Female (paratype): Idiosoma length x width 360 x 177 (in 3 other paratypes 370-375 x 185-210). Length of hysterosoma 245. Prodorsal shield as in the male, 95 x 75, setae *se* separated by 59. Setae *c2* short hair-like; setae *c3* setiform, about 44 in length. Arrangement of hysteronotal shields: central sclerite and pair of opisthosomal sclerites extending to bases of setae *h2, h3* (Fig. 15c). Central sclerite large pear-shaped, 72 x 40 (in other paratypes 72-78 x 38-43), its anterior end at midlevel between trochanters III and IV. Opisthosomal sclerites not extending to level of posterior end of central sclerite; their length from anterior end to setae *h3* 64. Posterior margin of opisthosoma between setae *h3* slightly convex. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *c1, d1, e1* greatly reduced and barely distinct; setae *e1* slightly posterior to central sclerite; openings *gl* at midlevel of central sclerite; setae *e2* on lateral margins of opisthosomal sclerites. Setae *ps1* situated dorsally, slightly anterior to *h3*. Dorsal measurements: *c2:d2* 87, *d2:e2* 94, *d2:gl* 22, *gl:e1* 32, *e2:h3* 72, *h3:h3* 46. Epigynium bow-like, 28 x 69.

DIFFERENTIAL DIAGNOSIS: This species is most similar to *P. faini* in having a narrow prodorsal shield in both sexes and a large ovate central sclerite in females. Both sexes of *P. queleae* differ from that species by having openings *gl* situated posterior to setae *d2*; males differ by having a narrow idiosoma that is two times longer than wide (Fig. 13a); the females are distinguished by setae *e1* being disposed posterior to central sclerite (Fig. 15c). In both sexes of *P. faini* openings *gl* are very close to setae *d2*; in the males, the idiosoma is 1.7-1.8 times longer than wide (Fig. 5a); in the females, setae *e1* at level of posterior third of central sclerite (Fig. 7c).

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssoides (Pteronyssoides) serini sp. n.
(Figs. 13e-h, 14d, 15d)

TYPE MATERIAL: Male holotype, 1 female paratype (MRAC 180 285) ex *Serinus sulphuratus* (LINNAEUS, 1766) (Fringillidae), South Africa, Cape Province, East London, X.1966, coll. unknown. Holotype and paratype – MRAC.

Additional material: 1 male (MRAC 180 298) ex *Serinus mozambicus* (STATIUS MULLER, 1776) South Africa, Kruger National Park, Skukuza Camp, 9.II.1962, coll. unknown; 2 females (MRAC 180 293 SAIMR FMT-13-5-62), same host, South Africa, Swaziland, Malkerns, 30.XII.1967, coll. unknown.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 375 x 260. Length of hysterosoma 237. Prodorsal shield: posterior angles rounded, lateral margins without incisions, posterior margin convex, size 113 x 120, setae *se* separated by 105. Setae *c2* hair-like, short, situated in anteromedian angles of humeral shield; setae *c3* setiform, long, about 125 in length. Hysteronotal shield: anterior margin almost straight, anterior angles rectangular, size 199 x 143. Distance between prodorsal and hysteronotal shields about 60. Opisthosomal lobes with rounded lateral ledge with seta *h2* and slightly extended apex bearing seta *h3*. Setae *f2* submarginal, lateral to setae *ps2*. Terminal cleft V-shaped, without membrane, 28 long, length including supranal concavity 48; setae *ps1* closer to *h3* than to anterior end of the cleft. Dorsal measurements: *c2:d2* 76, *d2:e2* 97, *d2:gl* 32, *gl:e1* 31, *e2:h3* 55, *e2:e2* 92, *h3:h3* 46. Transventral sclerite 13 in length; tips of not epiandrium extending to base of genital apparatus; genital arch 24 x 17; aedeagus about half as long as genital arch. Setae *4a* at midlevel of genital apparatus. Adanal shield as longitudinal bar with short lateral extensions in posterior part, extending to trochanters IV (Fig. 14d). Adanal membranes short. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 83, *ps3:ps3* 44, *ih:ih* 57, *g:g* 8. Ventral membrane of tarsus I about half as long as segment. Tarsus III 79 long, with bidentate apex, with sclerotized membrane on inner margin; setae *w* spiculiform, 36 in length; setae *s* narrowly lanceolate, 18 in length; setae *r* about twice as long as segment (Fig. 13g). Tarsus IV shorter than tibia IV; modified seta *d* closer to apex of the segment (Fig. 13h).

Female (paratype): Idiosoma length x width 400 x 240. Length of hysterosoma 288. Prodorsal shield as in the male, 120 x 130, setae *se* separated by 113. Setae *c2* hair-like, short, situated on striated tegument; setae *c3* setiform, about 108 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites separated into main opisthosomal and pygidial fragments, and terminal sclerite (Fig. 15d). Central sclerite ovate, 51 x 25, anterior end extending to level of openings *gl*. Main fragments of opisthosomal sclerites as polygonal plates, anterior ends at level of posterior end of central sclerite, distance from their anterior end to setae *h3* 80. Posterior margin of opisthosoma between setae *h3* almost straight. Setae *d1, d2, e1,* and openings *gl* on striated tegument; setae *c1, d1, e1* greatly reduced; setae *e1* slightly posterior to openings *gl*, approximately at level of anterior half of central sclerite; setae *e2* on lateral margins of opisthosomal sclerites. Setae *ps1* situated terminally. Dorsal measurements: *c2:d2* 128, *d2:e2* 96, *d2:gl* 37, *gl:e1* 9-10, *e2:h3* 64, *h3:h3* 97. Epigynium bow-like, 24 x 97.

DIFFERENTIAL DIAGNOSIS: This species is most similar to *P. eupasseris* by having the extending lobar apices in males and arrangement of hysteronotal shields in females. The males of *P. serini* differ from that species by the position of setae *h2* on the most margins of opisthosomal lobes (Figs. 13e, f); the females are distinguished by short opisthosomal sclerites, which do not extend to midlevel of central sclerite (Fig. 15d). In the males of *P. eupasseris*, setae *h3* are moved anterior from the lobar margin (Figs. 4a, b); in the females, the opisthosomal shields commonly extend to the midlevel of the central sclerite (Fig. 7a).

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

REMARK: Female specimens from *Serinus mozambicus* are noticeably smaller in size (375 and 380, n=2) than the female from the type host; however, the limited number of specimens does not allow estimating whether this is intraspecific variability or the specimens from different *Serinus* species represent separate species.

Pteronyssoides (Pteronyssoides) viduinus sp. n.
(Figs. 16a-c, 18a, 19a)

TYPE MATERIAL: Male holotype (MRAC 147 346), ex *Vidua macroura* (PALLAS, 1764) (Viduidae), Cameroon, no date, J. MOUCHET; 17 male and 17 female paratypes (MRAC 180 274 – 180 279), same host, Cameroon, XI.1955, coll. unknown. Holotype and all paratypes – MRAC.

DESCRIPTION: *Male (holotype)*: Idiosoma length x width 315 x 210 (in 17 paratypes 305-325 x 195-225). Length of hysterosoma 202. Prodorsal shield: posterior angles rounded, lateral margins with incisions posterior to setae *se*, posterior margin slightly convex, size 94 x 87, setae *se* separated by 73. Setae *c2* hair-like, short, situated in anteromedian angles of humeral shield; setae *c3* setiform, slightly enlarged in basal part, about 100 in length. Hysteronotal shield: anterior margin almost straight, anterior angles rectangular, size 160 x 100. Distance between prodorsal and hysteronotal shields about 65. Opisthosomal lobes with bluntly rounded posterior margins, with extended bases of setae *h2, h3*; bases of setae *h3* bidentate. Setae *f2* ventral, anterolateral to setae *ps2*. Terminal cleft V-shaped, with narrow membrane, 11 long, length including supranal concavity 30. Dorsal measurements: *c2:d2* 68, *d2:e2* 81, *d2:gl* 21, *gl:e1* 20, *e2:h3* 38, *e2:e2* 78, *h3:h3* 31. Transventral sclerite 12 in length; tips of epiandrium extending to base of genital apparatus; genital arch 21 x 17; aedeagus about half-length of genital arch. Setae *4a* at midlevel of genital apparatus. Adanal shield as longitudinal bar not extending to trochanters IV (Fig. 16b). Adanal membranes short. Posterior part of opisthosomal lobes with triangular sclerite extending from bases of seta *ps2* to respective cupula *ih*. Diameter of anal discs 16. Ventral measurements: *ps2:ps2* 59, *ps3:ps3* 34, *ih:ih* 30, *g:g* 7. Ventral membrane of tarsus I about half-length of segments. Tarsus III 60 in length, with bidentate apex, with membrane on inner margin; setae *w* narrowly lanceolate, 21 in length; setae *s* narrowly lanceolate 14 in length; setae *f* slightly thickened; setae *r* slightly longer than the segment (Fig. 16c). Tarsus IV shorter than tibia IV; modified seta *d* at midlevel of the segment.

Female (paratype): Idiosoma length x width 365 x 205 (in 16 paratypes 365-380 x 195-225). Length of hysterosoma 250. Prodorsal shield as in the male, 105 x 102, setae *se* separated by 86. Setae *c2* hair-like, short situated on striated tegument; setae *c3* setiform, about 65 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites extending to bases of setae *h2, h3*, and terminal sclerite (Fig. 19a). Central sclerite shortly ovate or circular, 46 x 38 (in paratypes 49-52 x 41-48), anterior end extending to level of openings *gl*. Anterior ends of opisthosomal shields at level of posterior half of central sclerite; length of opisthosomal sclerites 82-86. Posterior margin of opisthosoma between setae *h3* slightly convex. Setae *d1, d2, e1*, and openings *gl* on striated tegument; setae *c1, d1, e1* greatly reduced; setae *e1* posterior to level of openings *gl*, approximately at midlevel of central sclerite; setae *e2* on lateral margins of opisthosomal sclerites. Setae *ps1* situated dorsally, at level of setae *h3*. Dorsal measurements: *c2:d2* 100, *d2:e2* 73, *d2:gl* 22, *gl:e1* 16-17, *e2:h3* 57, *h3:h3* 102. Epigynium bow-like, 34 x 70.

DIFFERENTIAL DIAGNOSIS: This species is very similar to *P. ovoscutatus* by the shape of opisthosoma in males and arrangement of hysteronotal sclerites in females. The males of *P. viduinus* are generally smaller and differ from that species by shorter terminal part of opisthosoma (*e2:h3* 35-40, *e2:e2* 75-80, n=15) (Figs. 16a); females are distinguished by the central sclerite, which is almost circular in shape (Fig. 19a). In the males of *P. ovoscutatus*, these measurements of opisthosoma are 45-50 and 90-95, respectively (n=3); in females, the central sclerite is distinctly ovate, 1.3-1.5 times longer than wide (Fig. 11c).

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Group *nectariniae*

DIAGNOSIS: *Both sexes*: Prodorsal shield with straight or slightly concave posterior margin and blunt posterior angles. Solenidion $\sigma 2$ of genu I present. *Males*: Setae *f2* situated dorsally, near the margin of opisthosoma; outer margin of tarsus III with more-or-less expressed blunt angle, seta *w* of tarsus III distinctly lanceolate, most thickened in medial part, shorter than seta *s* and noticeably distant from the base of the segment (Figs. 17e, h). *Females*: Arrangement of hysteronotal shields: unpaired or paired opisthosomal sclerites covering posterior one third of hysterosoma, central sclerite absent or present (Figs. 19c, e); if central sclerite present (*P. promeropis*), it is partly connected with opisthosomal sclerites (Fig. 22d).

The group includes three species (Table 3).

Pteronyssoides (Pteronyssoides) garioui GAUD & MOUCHET, 1959 (Figs. 17a-e, 18c, 19c, d)

MATERIAL EXAMINED: Male holotype, 1 male and 3 female paratypes (MRAC 180 218), ex *Deleornis fraseri* (JARDINE & SELBY, 1843) (Nectariniidae), Cameroon, XI.1955, coll. unknown; 16 male and 16 female paratypes (MRAC 180 219 - 180 224), same data; 2 males, 3 females (UGA 9284 AMNH 703 458) ex *D. f. cameroonensis* (BANNERMAN, 1921), Zaire, Vungu, 5° 30' S, 13° 23' E, date and coll. unknown.

This species is known from the type host *Deleornis (=Anthreptes) fraseri* in Cameroon and Zaire (GAUD & MOUCHET, 1959). The most clear diagnostic feature of this species within the subgenus *Pteronyssoides* s. str. is a unique form of the opisthosomal shield and the presence of adanal shields in females (Fig. 19c, d).

Pteronyssoides (Pteronyssoides) nectariniae MIRONOV, 2001 (Figs. 17f-h, 18d, 19e)

MATERIAL EXAMINED: Male holotype and 3 female paratypes (NMB 00368) ex *Cinnyris afer* (BOCAGE, 1868) (Nectariniidae), South Africa, Lydenburg, 19.VI.1989, D.H. DE STEWART.

Pteronyssoides nectariniae is known only from the type host, *Cynniris (=Nectarinia) afer*, in South Africa (MIRONOV, 2001). The clear diagnostic feature of this species within the *nectariniae* group is the paired opisthosomal sclerites in females (Fig. 19e).

Pteronyssoides (Pteronyssoides) promeropis MIRONOV & KOPIJ, 2000 (Figs. 22d, 23a-d, 25a)

MATERIAL EXAMINED: 2 male and 2 female paratypes (ZISP 4205) from *Promerops gurneyi* VERRAUX, 1871 (Promeropidae), South Africa, Free State, Waterual, 24 III 1989, D.H. DE STEWART.

This species is known only from the type host, *Promerops gurneyi*, in South Africa (MIRONOV & KOPIJ, 2000); it easily distinguishable from other species of the genus *Pteronyssoides* by the unique structure of hysteronotal shield in females: central sclerite connected with opisthosomal sclerites (Fig. 22d).

Group *parinus*

Diagnosis: *Both sexes*: Prodorsal shield with straight or slightly convex posterior margin and bluntly rounded posterior angles. Solenidion $\sigma 2$ of genu I absent. *Males*: Setae *f2* situated dorsally, above bases of setae *ps2*; outer margin of tarsus III convex; seta *w* of tarsus III setiform or spiculiform, longer than seta *s* and situated in basal quarter of the segment. *Females*: Arrangement of hysteronotal shield: pair of large opisthosomal sclerites with bluntly rounded anterior ends and rudimentary lateral sclerites; central sclerite absent (*P. parinus*) or present and represented by plate with acute posterior angles.
The group includes four species (Table 3).

Pteronyssoides(Pteronyssoides) parinus (Koch, 1841) (Figs. 20a-d, 21a-b, 22a)

Material examined: 4 males, 4 females (ZISP 1437) ex *Parus caeruleus* Linnaeus, 1758 (Paridae), Russia, Kaliningrad Province, Rybachy, 4 VI 1980, S.V. Mironov; 3 males, 4 females (ZISP 1441), same host, Russia, Leningrad Province, Gumbaritzy, 8.IX.1981, S.V. Mironov; 5 males, 2 females (AMU 00331 and 00333), same host, Poland, Kopan, 7.X.1983, P. Daszkiewicz.

This species is very common for its type host, the blue tit *Parus caeruleus*, in Europe (Faccini & Atyeo, 1981; Mironov, 1985, 1989, 1996, 1997), and it was also reported from *P. flavipectus* Severtsov, 1873 in Tadjikistan (Dubinin & Sosnina, 1952). The most clear diagnostic feature differentiating *P. parinus* from all other species of the *parinus* group is the absence of the central sclerite in females (Fig. 22a). As was found in the course of our study, the population of *Parus caeruleus* in northern Africa bears a different *Pteronyssoides* species (see below).

Pteronyssoides (Pteronyssoides) pari (Linnaeus, 1758)

A taxonomic problem is related with *Pteronyssoides pari*, because currently it is not clear for expert, how this species actually looks like. This species, originally named as *Pediculus pari* Linnaeus, 1758 and placed among lice, was based on a very poor description and drawings by Fritsch of a mite found on the great tit, *Parus major* Linnaeus, 1758, in Germany in 1730. Based on the original drawings reproduced by Oudemans (1926), it is possible only to guess that this creature belongs to the Pteronyssidae, because it does not resemble any other feather mite suprageneric taxa (Analgidae and Proctophyllodidae) commonly associated with Paridae (Faccini & Atyeo, 1981). It is quite important to stress that since that time, in spite of extensive investigations of feather mites from passerines of Europe (see references in: Mironov, 1996), this mite has never been recollected from the big tit in Europe, a very common bird in this area. This raises a serious doubt that the recorded host association is natural; it is quite reasonable to suggest that there was an accidental contamination or that the type host was identified incorrectly. Revising the earlier acarological publications, Oudemans (1926, 1929, 1937) proposed to synonymize *Pteronyssoides parinus* (Koch, 1841), a species commonly occurring on the blue tit *Par. caeruleus* Linnaeus, 1758 in Europe (Mironov, 1985, 1989, 1996, 1997), with *P. pari*. However, in the generic revision of pteronyssids, Faccini & Atyeo (1981) did not agree with this synonymy, considering *P. pari* and *P. parinus* as different species. The main reason for this solution was a finding of a *Pteronyssoides* species on "a subspecies of *Par. major* from Korea" that differed from *P. parinus* ex *Par. caeruleus* and, therefore, those specimens were referred to *P. pari*. Unfortunately, *P. pari* was not redescribed based on this material and its present location is unknown. Besides, one may doubt that *Par. major* from Korea bears the same species as in Europe. Thus, for example, our study shows that populations of *P. caeruleus* from Europe and northern Africa bear different species of *Pteronyssoides* (see below *P. triangularis*). If there actually was an accidental contamination or misidentification of the type host of *P. pari*, a problem would arise: what well-known *Pteronyssoides* species from tits of Europe, *P. parinus* or *P. piscinotus*, should be synonymized with it? Based on the facts described above and for the stability of nomenclature, we suggest following Faccini & Atyeo (1981) and treating *P. pari* and *P. parinus* as separate species.

Pteronyssoides (Pteronyssoides) piscinotus Mironov, 1985 (Figs. 20e, 21c, 22b)

Material examined: Holotype male, 2 male and 3 female paratypes (ZISP 963) ex *Parus montanus* (Conrad von Baldenstein, 1827) (Paridae), Russia, Leningrad Province, Gumbatritzy, 13.IX.1981, S.V. Mironov.

This species is known from the tits *Parus montanus* (type host) and *Par. palustris* Linnaeus, 1758 in North-Western Russia (Mironov, 1985; 1996). The most characteristic feature easily differing *P. piscinotus* from all other *Pteronyssoides* species is the fishtail-shaped central sclerite in females (Fig. 22b).

Pteronyssoides (Pteronyssoides) triangularis sp. n. (Figs. 20f, 22c)

Type material: Male holotype, 2 male and 4 female paratypes (MRAC 180 258) ex *Parus caeruleus* Linnaeus, 1758 (Paridae), Morocco, Rabat, I.1952, coll. unknown. Holotype, paratypes – MRAC.

Description: *Male (holotype)*: Idiosoma length x width 380 x 275 (in 2 paratypes 380-382 x 275-285). Length of hysterosoma 245. Prodorsal shield: posterior angles rounded, lateral margins with incisions around setae *se*, posterior margin slightly convex, size 108 x 118, setae *se* separated by 98. Setae *c2* hair-like, about 130 long, situated in anteromedian angles of humeral shield; setae

c3 lanceolately thickened in basal part, about 125 in length, 8 in width. Hysteronotal shield: anterior margin almost straight, anterior angles rectangular, size 198 x 118. Distance between prodorsal and hysteronotal shields about 70. Opisthosomal lobes with bluntly rounded posterior margin, with slightly extending bases of setae *h2*, *h3*. Setae *f2* situated dorsally, above bases of setae *ps2*, 55-65 long (Fig. 20f). Setae *ps1* long, extending to level of tarsi III. Terminal cleft wide V-shaped, with narrow membrane, 14 long, length including supranal concavity 37. Dorsal measurements: *c2:d2* 86, *d2:e2* 101, *d2:gl* 22, *gl:e1* 46, *e2:h3* 52, *e2:e2* 78, *h3:h3* 32. Transventral sclerite 14 in length; tips of epiandrium extending to base of genital apparatus; genital arch 24 x 13; aedeagus about half as long as genital arch. Setae *4a* at midlevel of genital apparatus, bases of setae *g* adjacent to each other. Adanal shield T-shaped, extending to trochanters IV. Adanal membranes long, extending beyond level of setae *ps3*. Diameter of anal discs 18. Ventral measurements: *ps2:ps2* 65, *ps3:ps3* 41, *ih:ih* 51. Ventral membrane of tarsus I about half as long as segment. Tarsus III 75 in length, with bidentate apex, without membrane; setae *w* spiculiform, 41 in length; setae *s* narrowly lanceolate 12 in length; setae *f* slightly thickened; setae *r* about 2.5 longer than segment. Tarsus IV about half as long as tibia IV, modified seta *d* closer to seta *f* than to base of the segment.
Female (paratype): Idiosoma length x width 435 x 275 (in 3 paratypes 420-425 x 250-260). Length of hysterosoma 300. Prodorsal shield as in the male, 110 x 104, setae *se* separated by 104. Setae *c2* long hair-like, about 110 in length. Setae *c3* thickened, with very thin apex, about 78 in length, 6.5 in width. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites extending to bases of setae *h2, h3*, pair of rudimentary lateral shields, and terminal sclerite (Fig. 22c). Central sclerite triangular, 46 x 56 (in other paratypes 47-79 x 45-50), anterior end extending to midlevel between trochanters III and IV. Opisthosomal shields as irregular triangles, extending to level of lateral sclerite rudiments; length of opisthosomal shields 84. Posterior margin of opisthosoma between setae *h3* almost straight, extended bases of setae *h2, h3* with bidentate apex. Setae *d1, d2, e1, e2* and openings *gl* on striated tegument; setae *e1* posterior to central sclerite. Setae *ps1* situated terminally. Dorsal measurements: *c2:d2* 118, *d2:e2* 107, *d2:gl* 40, *gl:e1* 40, *e2:h3* 67, *h3:h3* 124. Epigynium semicircular, 49 x 95.

DIFFERENTIAL DIAGNOSIS: This species is very close to *Pteronyssoides parinus*. Males differ by longer setae *f2* (55-65), which are equal to the opisthosoma width at the level of setae *ps2* (Fig. 20f); females are distinguished by having a central sclerite of triangular form (Fig. 22c). In males of *P. parinus*, setae *f2* are 32-40 (n=12) that is about half as wide as the opisthosoma (Fig. 20a, d); in females, the central sclerite is absent (Fig. 22a).

ETYMOLOGY: Specific epithet refers to the form of central sclerite in female.

Ungrouped species

Pteronyssoides (Pteronyssoides) lambda GAUD & MOUCHET, 1959 (Figs. 16d-f, 18b, 19b)

MATERIAL EXAMINED: Male holotype, 2 male and 5 female paratypes (MRAC 180 232) ex *Amblyospiza albifrons saturata* SHARPE, 1908 (Ploceidae), Cameroon, XI.1955, coll. unknown; 3 males, 2 females (YSU 2083 AMNH 725 388) ex *A. a. tandae* BANNERMAN, 1921, Angola, N Dallo Tando, 18.XII.1908, coll. unknown; 2 males, 2 females (YSU 2075 AMNH 298 022) ex *Ploceus nigricollis brachypterus* SWAINSON, 1837 (Ploceidae), Fernando Po Island, 17.VII.1929, J.G. CORREIA.

Pteronyssoides lambda was originally described from *A. a. saturata* in Cameroon (GAUD & MOUCHET, 1959); *Ploceus nigricollis* is a new host genus for this mite. This species easily differs from all other known *Pteronyssoides* species by two unique features: the lambda-shaped central sclerite in females (Fig. 19b) and a rectangular ledge on the outer margin of tarsus III in males (Fig. 16f).

Pteronyssides (Pteronyssoides) striatus (ROBIN, 1877) (Figs. 21d, e, 23e, f, 25b, 26a)

MATERIAL EXAMINED: 4 males, 5 females (ZISP 1452) ex *Fringilla coelebs* LINNAEUS, 1758 (Fringillidae) Russia, Kaliningrad Province, Rybachy, 20 V 1979 S.V. MIRONOV; 3 males, 4 females (ZISP 1457), same host, Russia, Leningrad Province, Gumbaritzy, 28 VII 1981, S.V. MIRONOV; 6 males, 5 females (MRAC 180 271 and 180 272) ex *F. c. spodiogenys* BONAPARTE 1841, Morocco, Rabat, VIII.1954, coll. unknown; 3 males, 2 females (MRAC 180 273), same host, Morocco, Bouznika, IV.1952, coll. unknown;

Pteronyssoides striatus, the type species of the genus *Pteronyssoides*, is widely known from its type host, the chaffinch *Fringilla coelebs*, in Europe and Northern Africa (ROBIN & MEGNIN, 1877; GAUD, 1952; FACCINI & ATYEO, 1981; MIRONOV, 1989, 1996, 1997). The diagnostic features easily differing this species from all other species of the genus are the heavily sclerotized ledge on the lateral margins of opisthosoma in males (Fig. 21d) and the absence of hysteronotal shield in females (Fig. 26a).

Subgenus *Holonyssoides* MIRONOV, 1993

TYPE SPECIES: *Pteronyssoides holoplax* GAUD & MOUCHET, 1959.

DIAGNOSIS: *Both sexes*: Prodorsal shield with acute or rectangular posterior angles, which are commonly extended laterally; scapular shields large and close to prodorsal shield, in most species these shields separated by a single furrow only (Figs. 24a, e, 26b, 27a, 28a, d).

Females: Almost entire dorsal surface of hysterosoma covered with large one-pieced hysteronotal shield extending by anterior end to level of humeral setae (Fig. 26b-d, 30b, c), or this shield split into anterior and posterior parts by narrow transverse band of soft tegument (Fig. 30a).

The subgenus includes 5 species (Table 3).

Pteronyssoides (Holonyssoides) desmiphorus (Gaud, 1952) (Figs. 24a-d, 25c, 26b)

Material examined: Male holotype and 1 male paratype (MRAC 180 217) ex *Hypsipetes madagascariensis* (Statius Muller, 1776) (Pycnonotidae), Cameroon, Tulear, XI.1951, coll. unknown; 1 male, 1 female (UGA 9626 USNM 128 659) ex *H. m. rostratus* (Ridgway, 1893), NW of Madagascar, Aldabra Island, 8.XI.1892, W.L. Abbot; 1 male, 1 female (UGA 9638 USNM 296 537) ex *H. leucocephalus stresmanni* (Mayr, 1942), China, NW Yunnan Prov., LiKiang Mts., VIII.1923, J.F. Rock.

This species is restricted to bulbuls of the genus *Hypsipetes* Vigors, 1831, and was originally described from two males from the Madagascar bulbul, *H. madagascariensis,* in Madagascar (Gaud, 1952; Faccini & Atyeo, 1981). The drawing of the female (Fig. 26b) in the present study is based on the specimen from *H. M. rostratus*.

Pteronyssoides (Holonyssoides) holoplax Gaud & Mouchet, 1959 (Figs. 24e-i, 25d, e, 26c)

Material examined: Male holotype and 1 female paratype (MRAC 180 225) ex *Pycnonotus barbatus* (Desfontaines, 1789) [ssp. *gabonensis*?] (Pycnonotidae), Cameroon, Yaounde, IX.1955, coll. unknown; 1 male, 1 female (NU 4181, SAIMR FMT-4-29-62) ex *Pycnonotus xanthopygos* (Hemprich & Ehrenberg, 1833), Mozambique, Buzi, XI.1961, coll. unknown; 1 male (MRAC 180 229) ex *Chlorocichla simplex* (Harlaub, 1855) (Pycnonotidae) Cameroon, VIII.1955, coll. unknown; 3 males, 4 females (MRAC 180 230) ex *Chlorocichla flavicollis* (Swainson, 1837), Cameroon, XI.1956, coll. unknown.

This species is the smallest in size within in the genus; it is associated with bulbuls (Pycnonotidae) of the genera *Pycnonotus* Boie, 1826 and *Chlorocichla* Sharpe, 1882 distributed in Africa (Gaud & Mouchet, 1959; Gaud & Till, 1961). The type host given in the original description (Gaud & Mouchet, 1959) was named *Pycnonotus barbatus gabonensis* Sharpe, 1871; however, any subspecies is not indicated in the type slide. *Pycnonotus xanthopygos* is a new host record for this species.

Pteronyssoides (Holonyssoides) latior (Trouessart, 1887) (Figs. 28a-c, 29a, 30c-f)

Material examined: 14 males and 21 females, syntypes (TRT 37F10 – 37F14) ex *Astrapia nigra* (Gmelin, 1788) (Paradisaeidae), New Guinea, no date, coll. Laglaise. Lectotype is now marked in the slide TRT 37F11.

This species is known only from the type host, *Astrapia nigra,* in New Guinea (Trouessart, 1887; Faccini & Atyeo, 1981). *Pteronyssoides latior* may be easily distinguished from other known *Pteronyssoides* species by the following unique features: in both sexes, tips of epimerites I connected; in males, opisthosomal lobes are elongated, tarsus III has enlarged apex and big triangular tooth on inner margin (Figs. 28a-c)

Pteronyssoides (Holonyssoides) oxylabis sp. n. (Figs. 27a-f, 29b-e, 30a)

Type material: Heteromorph male holotype and 1 female paratype (UGA 4254 AMNH 412 103) ex *Oxylabes madagascariensis* (Gmelin, 1789) (Timaliidae), Madagascar, near Fito and Didy, Forest Sianaka, 1926, coll. unknown; 1 homeomorph male and 1 female paratypes (UGA 4256 AMNH 589 210), same data except for the date, V.1926. Holotype and 1 female paratype – MZUM, other paratypes – ZISP.

Description: *Heteromorph male (holotype)*: Idiosoma length x width 413 x 252. Length of hysterosoma 274. Prodorsal shield: posterior angles almost rectangular, lateral margins without incisions, posterior margin straight, size 121 x 116, setae *se* separated by 90. Setae *c2* thin hair-like, situated in anteromedian angle of humeral shields; setae *c3* about 135 in length, lanceolately thickened in basal part, greatest width 6.5. Hysteronotal shield: anterior margin straight, anterior angles extending laterally, size 258 x 140. Distance between prodorsal and hysteronotal shields about 30. Opisthosoma almost rectangular, posterior angles slightly rounded, posterior margin of lobes lightly convex; bases of setae *h2*, *h3* only slightly extended. Setae *f2* situated dorsally, lateral to setae *ps2*. Terminal cleft small V-shaped, with narrow membrane occupying the cleft and all posterior margins of lobes, 14 long, length of cleft including supranal concavity 32 (Fig. 27a, c). Dorsal measurements: *c2:d2* 77, *d2:e2* 115, *d2:gl* 34, *gl:e1* 28, *e2:h3* 56, *e2:e2* 67, *h3:h3* 44. Transventral sclerite thick, 16 in length; tips of epiandrium long, extending beyond base of genital apparatus; genital arch 22 x 16; aedeagus about one third length of genital arch. Setae *4a* slightly posterior of genital apparatus. Adanal shield large cross-shaped, extending to trochanters IV; median longitudinal bulk of the shield and lateral rectangular areas heavily sclerotized. (Fig. 27d). Adanal membranes short. Diameter of anal discs 19. Ventral measurements: *ps2:ps2* 86, *ps3:ps3* 25, *ih:ih* 52, *g:g* 7. Tarsus III with bidentate apex, 90 long; setae *w* thick setiform 41 in length; setae *s* narrowly lanceolate, slightly curved, 16 in length; setae *f* slightly thickened, setae *r* about 2.5 times longer than the segment (Fig. 27e). Tarsus IV about half as long as tibia IV; modified seta *d* at midlevel of the segment (Fig. 27f).

Homeomorph male (paratype): Idiosoma length x width 361 x 248. Length of hysterosoma 236. Prodorsal shield as in heteromorph male, size 108 x 105, setae *se* separated by 87. Setae *c2* thin hair-like, situated in anteromedian angle of humeral shields; setae *c3* about 110 in length, narrowly lanceolate in basal two thirds, greatest width 6. Hysteronotal shield: as in heteromorph male, size 234 x 136. Distance between prodorsal and hysteronotal shields about 25. Opisthosoma almost rectangular, terminal cleft barely expressed, posterior margin of lobes slightly convex, with narrow membrane along all the posterior margins of opisthosoma (Fig. 29c). Length of cleft including supranal concavity 32. Position of setae *h2, h3, ps2, f2* as in the heteromorph male (Figs. 27a-c). Dorsal measurements: *c2:d2* 62, *d2:e2* 90, *d2:gl* 28, *gl:e1* 25, *e2:h3* 54, *e2:e2* 79, *h3:h3* 43. Transventral sclerite 14 in length; tips of epiandrium long, extending beyond base of genital apparatus; genital arch 21 x 15; aedeagus about one third length of genital arch. Setae *4a* slightly posterior to genital apparatus base. Adanal shield as a silhouette of flying bird: longitudinal bulk extending to trochanters IV and lateral parts of wings well sclerotized (Fig. 29b). Adanal membranes short. Diameter of anal discs 17. Ventral measurements: *ps2:ps2* 89, *ps3:ps3* 28, *ih:ih* 62, *g:g* 6.Tarsus III with bidentate apex, 68 in length; setae *w* thick setiform 34 in length; setae *s* narrowly lanceolate, slightly curved, 15 in length; setae *r* about 2.5 times longer than segment. Tarsus IV as in the heteromorph male.

Female (paratype): Idiosoma length x width 475 x 265 (in other paratype 460 x 258). Length of hysterosoma 330. Prodorsal shield as in the males, 130 x 140, setae *se* separated by 93. Setae *c2* short hair-like, situated in anteromedian angle of humeral shields. Setae *c3* setiform, slightly enlarged in basal part, about 135 in length, 6 in greatest width. Dorsal shields of hysterosoma: large hysteronotal shield covering almost entire median area of hysterosoma split by narrow transverse band at level of setae *e1* into anterior piece (main body of hysteronotal shield) and posterior piece (opisthosomal sclerite); pair of lateral sclerites present (Fig. 30a). Central sclerite large rectangular, anterior end at level of setae *c2*, posterior margin at level of setae *e1*, greatest length 212, width at anterior margin 146. Opisthosomal sclerite covering posterior half of opisthosoma, length from anterior margin to setae *h3* 105. Lateral sclerites as long longitudinal bars with acute anterior and posterior ends, with openings *gl* situated approximately at midlevel of these sclerites. Posterior end of opisthosoma with a pair of short widely separated lobe-like extensions bearing setae *h3;* posterior margin between these extensions almost straight. Setae *d1, d2, f2* and openings *gl* on shield surface; setae *c1* on anterior margin of central sclerite; setae *d2* on lateral margin of central sclerite, setae *f2* on lateral margin of opisthosomal shield; setae *e2* on anterior angles of opisthosomal sclerite, setae *e1* posterior to openings *gl*, situated between central and opisthosomal sclerites. Setae *ps1* at level of setae *h2*. Dorsal measurements: *c2:d2* 100, *d1:d2* 50, *d2:e2* 106, *d2:gl* 56, *gl:e1* 38, *e2:h3* 95, *h3:h3* 77. Epigynium bow-like, 41 x 105.

DIFFERENTIAL DIAGNOSIS: This species is the only known species of *Pteronyssoides* so far with two forms of males, which differ from each other by the structure of the terminal cleft and transventral sclerite and may be treated as heteromorph and homeomorph. *Pteronyssoides oxylabis* clearly differs from all other species of the subgenus *Holonyssoides* by he following characters: in both sexes, posterior angles of prodorsal shied not extending laterally (Fig. 27a); in females, the hysteronotal shield is split by the narrow transverse band of striated tegument into anterior and posterior pieces (central and opisthosomal sclerites), and lateral shields are present and bear openings *gl* (Fig. 30c); in both forms of males, the adanal shield is cross-shaped with heavily sclerotized median and most lateral areas (Figs. 27b, d, 29b).

ETYMOLOGY: The specific epithet derives from the generic name of the type host.

Pteronyssoides (Holonyssoides) pycnonoti MIRONOV, 1993 (Fig. 26d)

MATERIAL EXAMINED: Female holotype (ZISP 3742) ex *Pycnonotus aurigaster* (VIEILLOT, 1818) (Pycnonotidae), Vietnam, Ha Tay Province, Ba Vi District, 9.VIII.1989, S.V. MIRONOV.

Pteronyssoides pycnonoti was described only from a single female from *Pycnonotus aurigaster* in Vietnam (MIRONOV, 1993). This species is very close to *P. holoplax* associated with African bulbuls; females of *P. pycnonoti* differ from that species by the narrowed hysteronotal shield, anterior margin of which is as wide as distance between scapular setae *se*.

Pteronyssoides (Holonyssoides) timaliae MIRONOV, 1993 (Figs. 28d-f, 29f, g, 30b)

MATERIAL EXAMINED: Male holotype, 2 male and 5 female paratypes (ZISP 3739) ex *Timalia pileata* HORSFIELD, 1821 (Timaliidae), Vietnam, Ha Tay Province, Ba Vi District, 27.V.1989, S.V. MIRONOV.

This species is known only from *Timalia pileata* in Vietnam (MIRONOV, 1993). *Pteronyssoides timaliae* is very similar to previous species associated with bulbuls, *P. holoplax, P desmiphorus* and *P. pycnonoti* (Figs. 24a, e, 26b-d), and differs from them by more elongated idiosoma in both sexes and apically enlarged bases of setae *h3* in females (Figs. 28d, 30b).

Phylogeny

The branch-and-bound search produced 6 shortest trees having length 87 steps and standard indices, excluding uninformative characters, as follows: CI=0.6506, RI=0.8304, RC=0.5536. Strict consensus of these trees is shown in Fig. 31. The trees differ in the position of

Sturnotrogus subtruncatus and in branching of species within the *parinus* group cluster. *Sturnotrogus subtruncatus* is either a sister clade of *Scutulanyssus dasyrhitidis* or the *Pteronyssoides* branch, or clades *Pteronyssoides*, *Sturnotrogus*, and *Scutulanyssus* arise from an unresolved node as in the consensus tree. In the cluster of the *parinus* group, relationships between three species either are unresolved, or *Pteronyssoides piscinotus* and *P. triangularis* form a sister clade. Monophyly of the genus *Pteronyssoides* is supported by four unambiguous synapomorphies: loss of the lateral sclerites (character 16.3) and disposition of openings *gl* on striated integument (18) in females, development of the bidentate apex on tarsus III (39.2), and the dorsobasal spine on tarsus IV (45) in males. The *Pteronyssoides* branch splits into two major clusters corresponding to our taxonomic concept of subdivision the genus into subgenera *Holonyssoides* and *Pteronyssoides* s. str. (Mironov, 1993). The *Holonyssoides* cluster is supported by two synapomophies in the structure of the prodorsum in both sexes: narrowed space between prodorsal and scapular shields and extended acute angles of prodorsal shields (1, 2). The cluster uniting relatively small-sized species (*P. desmophorus*, *P. holoplax*, *P. timaliae*) is characterized by five synapomorphies: development of sclerotized patches on prodorsal shield (4), reduction of ventral membrane on tarsus I (5.2), development of longitudinal opisthosomal lacuna in females (20), development of wide adanal apodemes (29) and reduction of lateral parts of adanal shield in males (31). Two large-sized species, *P. latior* and *P. oxylabis*, belong to weakly supported lineage characterised only by the anterior position of setae *ps1* in females (24); each of this species could probably represent a particular evolutionary lineage within *Holonyssoides*.

The major cluster *Pteronyssoides* s. str. is characterized by three synpomorphies in females: reduction or loss of hysteronotal shield in anterolateral area of hysteronotum (7), formation (splitting) of opisthosomal shield (8), and loss of lateral areas of opisthosomal shield that leads to the placement of setae *e2* on striated tegument (23). The *nectariniae* group splitting from the base of the *Pteronyssoides* cluster is supported by three synapomorphies representing structures of tarsus III in males: shortening of seta *w* regarding seta *s* (41), moving of seta *w* to the midlevel of the segment (42) and bending of tarsus to form a blunt angle on the outer margin (44.1). The most noticeable tendency in the *nectariniae* cluster is a subsequent reduction of the hysteronotal of shield in females. In this regard, *P. promeropis* is probably the most primitive within this group and the whole *Pteronyssoides* s. str., because only in this species, the central sclerite remains attached to the opisthosomal shield. In the two other species of the cluster, *P. garioui* and *P. nectariniae*, the central sclerite is lost (12.2), and in the latter species, the opisthosomal shield is split longitudinally into two pieces (9).

The branch bearing the remaining species of the subgenus *Pteronyssoides* s.str. is supported by four synapomorphies: loss of solenidion $\sigma 2$ on genu I in both sexes (6), separation of entire opisthosomal sclerite into a pair of sclerites (9), splitting of central sclerite from opisthosomal sclerite (12.1), and placement of setae *el* on striated tegument (21) in females. This branch splits into the cluster of the *parinus* group and the crown of *Pteronyssoides* s. str. branch, which includes the *ovoscutatus* group and two unique species, *P. lambda* and *P. striatus*, not referred to any group.

The *parinus* group is characterized by three synapomorphies representing female characters: the development of triangular central sclerite (13.2), and formation of small-sized lateral sclerites (16.2), having ovate form (17.2). Although relationships among three species of this cluster remain unresolved, based on the extent of development of the central sclerite it is possible to suggest that *P. piscinotus*, having the largest central sclerite (Fig. 22b), is the most primitive species in the group, while *P. parinus*, which has lost it entirely (Fig. 22a), is the most derived one.

The crown of the *Pteronyssoides* s. str. is supported by a single but relatively rare character state, movement of setae *f2* to a ventral position in males (33). The first of the ungrouped species, *P. striatus* is characterized by the complete loss of the hysteronotal shield fragments in females, both the opisthosomal and central sclerites (10.3, 12.2). The second ungrouped species, *P. lambda*, has several unique character states: in females, the central sclerite is lambda-shaped (13.3), and pygidial fragments of opisthosomal shields are fused to each other (10.2); in males, tarsus III has a rectangular ledge on outer margin (44.2).

The cluster of the *ovoscutatus* group, uniting almost half of known species, is supported by the formation of the central sclerite of ovate form in females (13.1) and loss of lateral parts of the adanal shield in males (31). The core of this cluster, the sister lineage to *P. motacillae*, is characterized by the development of a membrane on the inner margin of tarsus III in males (40). The core of the *ovoscutatus* cluster splits into three subclusters that we term *eupasseris*, *pytiliae* and *euplecti*. The first subcluster unites species having extending lobar apices in males (34); its sister clade bearing subclusters *pytiliae* and *euplecti* is characterizeed by the acute anterior ends of opisthosomal shields in females (11). In turn, the subcluster *pytiliae* is characterised by a large ovate central sclerite that extends to the level of trochanters IV (14, 15.1), the subcluster *euplecti* is characterized by cupules *ih* moved closer to midline than setae *ps3* (36). It is interesting to note that the two most-derived species of the *pytiliae* subcluster, *P. faini* and *P. queleae*, have tarsus III with a claw-like apex in male (39.1) (Figs. 5e, 13d), an obvious reversion of the derived state. The bidentate form of apex is a synapomorphy for the genus *Pteronyssoides* as whole; this reversion may be related to the diminution in size of these species. The general morphological tendency of the *ovoscutatus* group is a reduction of hysteronotal sclerites in the opisthosomal region. The maximal reduction of the central sclerite is demonstrated in

Table 3 — Host associations and geographic locations of *Pteronyssoides* species.

Mite taxa	Host species	Host family	Locality	Reference
***Pteronyssoides* s.str.**				
Group ***ovoscutatus***				
P.(P.) emberizae	*Emberiza flaviventris*	Emberizidae	Rwanda	Present study
P.(P.) eupasseris	*Passer griseus*	Passeridae	Central African republic	Present study
P.(P.) euplecti	*Euplectes hordaceus*	Ploceidae	Sao Tome Island, Cameroon, Ghana	Present study
"	*E. ardens*	Ploceidae	South Africa	Present study
P.(P.) faini	*Lonchura bicolor poensis*	Estrildidae	Fernando Po Island	Present study
P.(P.) foudiae	*Foudia madagascariensis*	Ploceidae	Madagascar	Present study
"	*F. eminentissima aldabrana*	Ploceidae	Aldabra Island	Present study
P.(P.) lonchurae	*Lonchura malacca formosana*	Estrildidae	Taiwan	SUGIMOTO, 1940
P.(P.) microscutatus	*Euplectes axillaris*	Ploceidae	Swaziland	Present study
P.(P.) motacillae	*Motacilla flava*	Motacillidae	NW Russia, Kirgyzia	MIRONOV, 1985, 1989
"	*M. alba leucopsis*	Motacillidae	Russia: Primorye	MIRONOV, 1985, 1989
"	*M. citreola*	Motacillidae	Kyrgyzia	MIRONOV, 1985, 1989
P.(P.) ovoscutatus	*Cyanomitra verticalis**	Nectariniidae	Cameroon	Present study
P.(P.) passeris	*Dicrurus forficatus*	Dicruridae	Madagascar	GAUD, 1952
	Dicrurus atripennis	Dicruridae	Cameroon	Present study
	Dicrurus adsimilis	Dicruridae	South Africa	Present study
P.(P.) plocei	*Ploceus superciliaris*	Ploceidae	Rwanda	Present study
P.(P.) pytiliae	*Pytilia melba belli*	Estrildidae	Mozambique, Uganda	Present study
P.(P.) queleae	*Quelea quelea*	Ploceidae	South Rhodesia, Senegal, Cameroon, Marocco	Present study
P.(P.) serini	*Serinus sulphuratus*	Fringillidae	South Africa	Present study
"	*S. mozambicus*	Fringillidae	South Africa	Present study
P. (P). viduinus	*Vidua macroura*	Viduidae	Cameroon	Present study
Group ***nectariniae***				
P.(P.) garioui	*Deleornis fraseri*	Nectriniidae	Cameroon	GAUD & MOUCHET, 1959
"	*D. f. cameroonensis*	Nectriniidae	Zaire	Present study
P. (P.) nectariniae	*Cynniris afer*	Nectariniidae	South Africa	MIRONOV, 2001
P.(P.) promeropis	*Promerops gurneyi*	Promeropidae	South Africa	MIRONOV & KOPIJ, 2000
Group ***parinus***				
P.(P.) parinus	*Parus caeruleus*	Paridae	Europe, NW Russia	FACCINI & ATYEO, 1981; MIRONOV, 1989, 1996
"	*Parus flavipectus*	Paridae	Tadjikistan	DUBININ & SOSNINA, 1952
P.(P.) pari	*Parus major*	Paridae	Europe, Korea	OUDEMANS, 1926; FACCINI & ATYEO, 1981
P.(P.) piscinotus	*Parus montanus*	Paridae	NW Russia	MIRONOV, 1985
	Parus palustris	Paridae	NW Russia	MIRONOV, 1985
P.(P.) triangularis	*Parus caeruleus*	Paridae	Marocco	Present study
Ungrouped species				
P.(P.) lambda	*Amblyospiza albifrons saturata*	Ploceidae	Cameroon	GAUD & MOUCHET, 1959
"	*A. a. tandae*	Ploceidae	Angola	Present study
"	*Ploceus nigricollis*	Ploceidae	Fernando Po Island	Present study
P. (P). striatus	*Fringilla coelebs*	Fringillidae	Europe, NW Russia	ROBIN & MEGNIN, 1877; FACCINI & ATYEO, 1981; MIRONOV, 1989, 1996
"	*Fringilla coelebs spodiogenys*	Fringillidae	Morocco	GAUD, 1952

Mite taxa	Host species	Host family	Locality	Reference
Holonyssoides				
P.(H.) desmiphorus	*Hypsipetes madagascariensis*	Pycnonotidae	Cameroon	GAUD, 1952
"	*H. m. rostratus*	Pycnonotidae	Aldabra Island	Present study
"	*H. leucocephalus stresmanni*	Pycnonotidae	China: Yunnan Prov.	Present study
P.(H.) holoplax	*Pycnonotus barbatus gabonensis*	Pycnonotidae	Cameroon	GAUD & MOUCHET, 1959
"	*P. xanthopygos*	Pycnonotidae	Mozambique	Present study
"	*Chlorocichla flavicollis*	Pycnonotidae	Cameroon	GAUD & MOUCHET, 1959
"	*Ch. simplex*	Pycnonotidae	Cameroon	GAUD & MOUCHET, 1959
P.(P.) latior	*Astrapia nigra*	Paradisaeidae	New Guinea	TROUESSART, 1887
P.(H.) oxylabis	*Oxylabes madagascariensis*	Timaliidae	Madagascar	Present study
P.(H.) pycnonoti	*Pycnonotus aurigaster*	Pycnonotidae	Vietnam	MIRONOV, 1993
P.(H.) timaliae	*Timalia pileata*	Timaliidae	Vietnam	MIRONOV, 1993

* Questionable host association.

P. microscutatus, which has a very small rod-shaped central sclerite (15.2) (Fig. 11a). The reduction of opisthosomal sclerites by splitting them into the main and pygidial fragments is observed in *P. emberizae, P. eupasseris* and *P. serini* (10.1) (Figs. 3a, 7a, 15d). Taking into account this tendency it is possible to suggest the unique species *P. striatus*, displaying the maximum degree of the hysteronotal shield reduction in female, could derive from the *ovoscutatus* group, particularly from the *eupasseris* subcluster. However, to support this hypothesis it is necessary to admit that the lateral parts of the adanal shield in *P. striatus* has been restored and the inner membrane on tarsus III has been secondary lost in males, i.e. characters 31 and 40 have been reversed to plesiomorphic states. To a lesser extent a suggestion about the origin within the *ovoscutatus* group could be made for *P. lambda*, because this species also has opisthosomal sclerites split into fragments. However, the large central sclerite of a unique form (Fig. 19b) is in a serious contradiction with the general pattern in the *ovoscutatus* group.

In tracing the main evolutionary changes in the genus *Pteronyssoides* (Fig. 31) it is worthy to note that its subgenera demonstrate contrasting trends in morphological modifications. The subgenus *Holonyssoides* represents the evolutionary lineage characterized by the progressive strengthening of dorsal shields in both sexes, particularly in the prodorsum; in the most derived species (e.g. *P. holoplax*), the prodorsal and scapular shields are almost joined in both sexes (Figs. 24a, e, 26 b-d). In contrast to this, members of the subgenus *Pteronyssoides* s. str. show a strong tendency to reduce the hysteronotal shield in females. This trend in various extents is realized independently in several lineages. In the *nectariniae* group, the extreme of reduction is observed in *P. nectariniae*, females of which retain only a pair of opisthosomal sclerites (Fig. 19e). In the *parinus* group, *P. parinus* also has only a pair of opisthosomal sclerites and rudimentary lateral sclerites (Fig. 22a); in the *ovoscutatus* group, *P. microscutatus* has a pair of opisthosomal shields and the rudimentary central sclerite (Fig. 10a); and finally, the unique species *P. striatus* has completely lost all hysteronotal shields (Fig. 26a).

Host associations

Analysis of host associations of the genus *Pteronyssoides* (Table 3) shows that it is primarily distributed on the most derived grouping of passerines, the parvorder Passerida, with exceptions for two species, *Pteronyssoides latior* and *P. passeris,* associated with hosts from the parvorder Corvida. Regarding the host range at species level, most *Pteronyssoides* species are known so far as monoxenous parasites, eight species occur on hosts of one genus and two species are recorded on a few genera of one family. Pteronyssoides species-groups recognized in the course of our analysis are mainly restricted to a single bird family or superfamily. This suggests that this pattern of distribution of the genus *Pteronyssoides* in significant extent is the result of cospeciation process. Realising that species diversity of *Pteronyssiodes* is known so far quite incompletely, nevertheless, it is possible to propose a very provisional co-phylogenetic hypothesis (Fig. 32), based on the currently known host associations (Table 3), and a direct comparison of the phylogeny of *Pteronyssoides* species (Fig. 31) with a phylogenetic hypothesis for suprageneric taxa of passerine hosts. Owing to numerous molecular based studies in passed five years (BARKER *et al.*, 2002, 2004, ERICSON *et al.*, 2001, ERICSON & JOHANSON, 2003), significant progress in has been achieved in phylogeny of passerine birds, and relationships among most superfamilies have become relatively clear. However, a number of questions still remain unresolved even at familial/superfamilial levels of this huge avian group, particularly, the relationships between the dozen of families forming the "core Passeroidea" (Emberezidae, Fringillidae, Motacillidae, etc.) (SORENSON & PAYNE, 2001; ERICSON & JOHANSON, 2003). Because of this uncertainty, in our hypothesis we have mainly used species groups of *Pteronyssoides*, on the one hand, and families or superfamilies of passerines on the other hand. As the basis for the phylogeny of passerines, we use the most comprehensive phylogenetic hypothesis of Barker *et al.* (2004), combined with the hypothesis for Sylvioidea of BERESFORD *et al.* (2005).

According to our hypothesis, the genus *Pteronyssoides* originated on the ancestor of the parvorder Passerida, branching out from the common stalk of pteronyssid genera restricted to this host group such as *Scutulanyssus, Sturnotrogus* and *Mouchetia* GAUD, 1961. The basal split of *Pteronyssoides* coincided with the splitting of Passeroidea and Sylvioidea, two of five major lineages recognized within Passerida (ERICSON & JOHANSON, 2003; BARKER *et al.*, 2004). This primary splitting led to the origin of two lineages classified as subgenera, *Pteronyssoides* s. str. and *Holonyssoides*. On three other lineages, Muscicapoidea, "Paridae and allies" and "Sittidae and allies" (ERICSON & JOHANSON, 2003), these mites probably missed the boat or have been extinct on these host lineages by some other reasons.

Representatives of the subgenus *Holonyssoides* dispersed on three lineages of Sylvoidea. The lineage of small-sized species (*P. holoplax, P. desmiphorus, P. pycnonoti*) and its sister lineage represented by *P. timaliae* were formed on bulbuls (Pycnonotidae) and babblers (Timaliidae), respectively. These host families represent the most derived and species-rich groupings within the Sylvioidea. *Pteronyssoides oxylabis*, representing the third lineage of *Holonyssoides* associated with Sylvoidea, inhabits the white-throated oxylabes, *Oxylabes madagascariensis,* which is an endemic sylvioid bird in Madagascar. This bird was traditionally assigned to Timaliidae (HOWARD & MOORE, 1991); however it has been recently shown that *O. madagascariensis* belongs to so-called "Malgasy endemic warblers", ancient sylvioid migrants to Madagascar, which are neither Timaliidae nor Pycnonotidae (CIBOIS *et al.*, 2001; BERESFORD *et al.*, 2005). *Pteronyssoides latior* inhabits a bird of paradise, *Astrapia nigra* (Paradisaeidae), in New Guinea; this host family is phylogenetically quite distant from Sylvioidea and belongs to the "core Corvoidea" within the paraphyletic parvorder Corvida (BARKER *et al.*, 2004). As the association with Paradisaeidae is a unique case for the genus *Pteronyssoides*, we suppose that this is the result of some earlier host shift from sylvioid hosts.

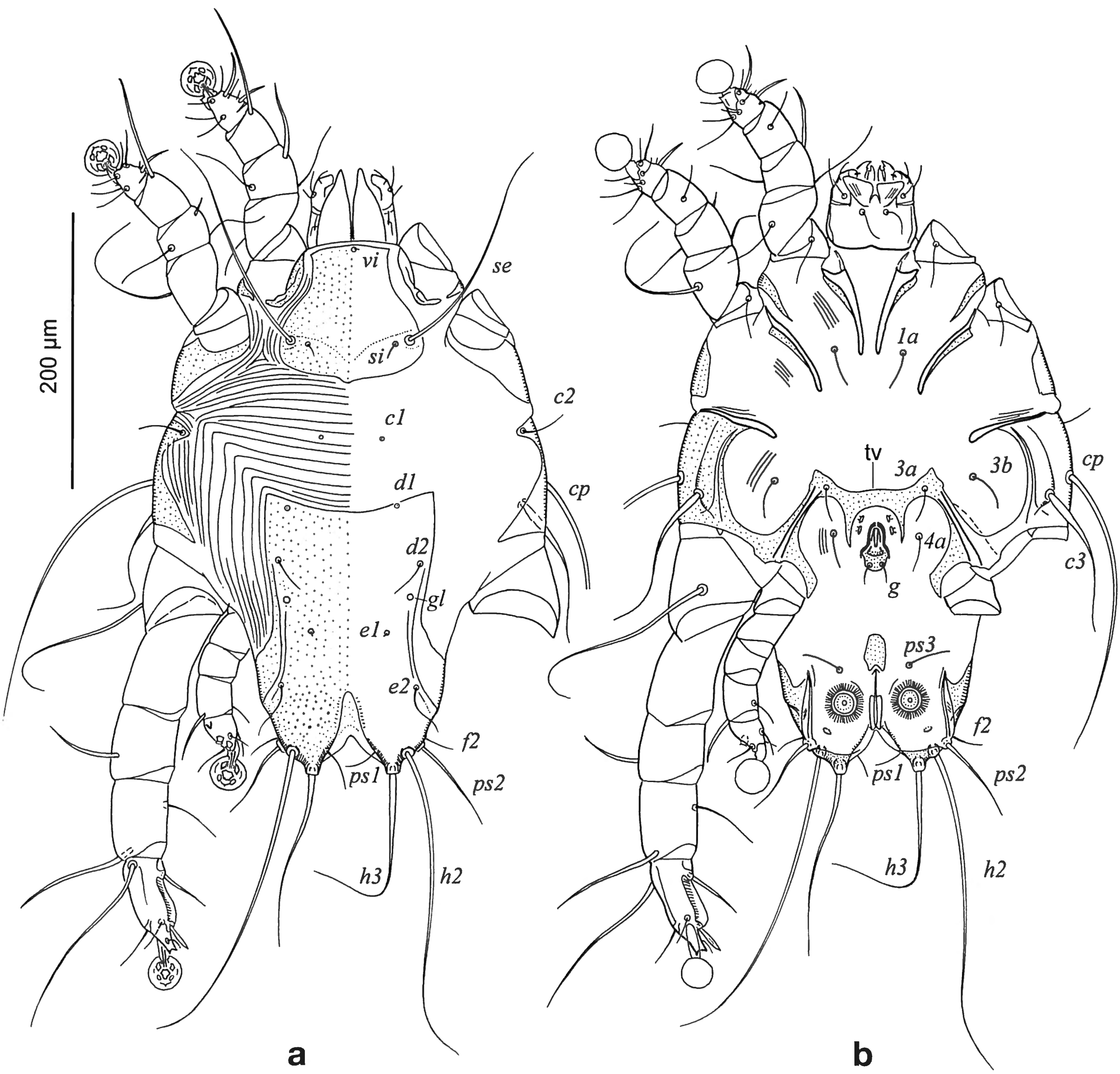
Representatives of the subgenus *Pteronyssoides* s. str. associated with Passeroidea dispersed on two branches of these birds. The *nectariniae* group was formed on the sunbirds (Nectariniidae) and sugarbirds (Promeropidae), an early derivative group of passeroids. It is necessary to note that although these families are typically considered as closely related (HOWARD & MOORE, 1991; DICKINSON, 2003), some recent phylogenetic investigations suggest that this bird lineage may be paraphyletic (BARKER *et al.*, 2004; BERESFORD *et al.*, 2005).

The lineage uniting the species-rich group *ovoscutatus* and "unique species" was formed on the ancestor of the core Passeroidea (BARKER *et al.*, 2004), in which at least 13 families are recognized (DICKINSON, 2003). Representatives of the *ovoscutatus* group are distributed on seven of eight families of this branch occurring in the Old World (Fig. 32), namely on finches, buntings, sparrows, wagtails, weavers, waxbills and widow finches; they are not known from the accentors, Prunellidae. As the hypotheses for relationships between the families of this branch are not clear (SORENSON & PAYNE, 2001) and diversity of the *ovoscutatus* group on these hosts is obviously quite poorly explored, it is difficult to conclude whether this group mainly cospeciated with hosts or if there have been horizontal transfers between or within host families. It is possible only to point out that mites belonging to the *euplecti* and *pytiliae* subclusters probably originated on the families Estrildidae, Ploceidae and Viduidae, which according to all recent hypotheses form a monophyletic clade within the core Passeroidea. Representatives of the subcluster *eupasseris* are distributed on the remaining host families of the core Passeroidea. *Pteronyssoides passeris*, a member of the *eupasseris* subcluster, is an exception in host associations, because it is distributed on drongos Dicruridae. Like Paradisaeidae, this family is phylogeneteically distant from the main hosts of the genus *Pteronyssoides* and also belongs to the core Corvoidea; therefore we suggest that this association may be explained by the result of ancient transfer from Passeroidea.

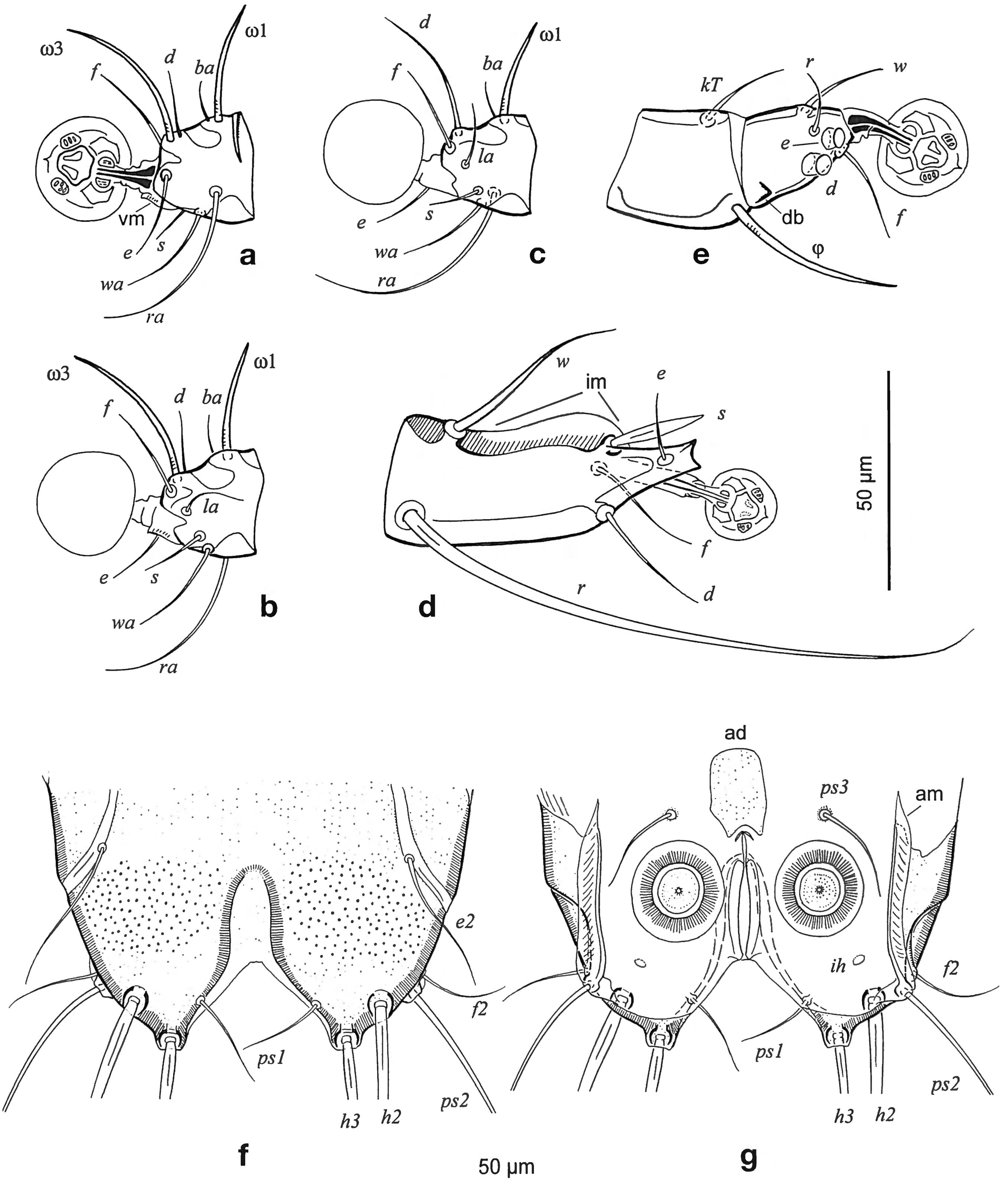
The *parinus* group is associated exclusively with tits, Paridae; this family does not belong to Passeroidea at all, but together with the penduline tits, Remizidae, forms a separate major lineage within Passerida and is most probably related to Sylvoidea (ERICSON & JOHANSON, 2003; BARKER *et al.*, 2004). Taking into consideration that the *parinus* group is closely related to the *ovoscutatus* group, and its representatives occur only on the subgenera *Cyanistes* KAUP, 1829, *Poecile* KAUP, 1829 and *Parus* LINNAEUS, 1858 and is reliably absent on other subgenera represented in Palaearctic (MIRONOV, 1996), we suggest that the associations of this group with Paridae is most probably the result of earlier host shift from some ancestors of Passeroidea.

Regarding host associations of the *parinus* group, interestingly to add that European and African populations of the blue tit, *Parus caeruleus*, bear different species, *Pteronyssoides parinus* and *P. triangularis*, respectively. It means that these host populations have been isolated long enough to allow the primary *Pteronyssoides* species diverging into two distinct species (Figs. 22a, c).

Thus, according our hypothesis, the genus *Pteronyssoides* originated on the ancestor of the parvorder Passerida and owing to cospeciation diversified on hosts of two major lineages (Passeroidea and Sylvoidea); due to host switching events in the course of evolution, these mites conquered another major lineage (Paridae and allies) within Passerida and a few phylogenetically distant host belonging to the Corvoidea (parvorder Corvida). We expect that subsequent extensive studies of the mite fauna of the Old World passerines, especially those from tropical region such as Africa and southern Asia, would reveal many more pteronyssid species, which will lead to better understanding of the phylogenetic relationships within this mite group and their evolution on these hosts.

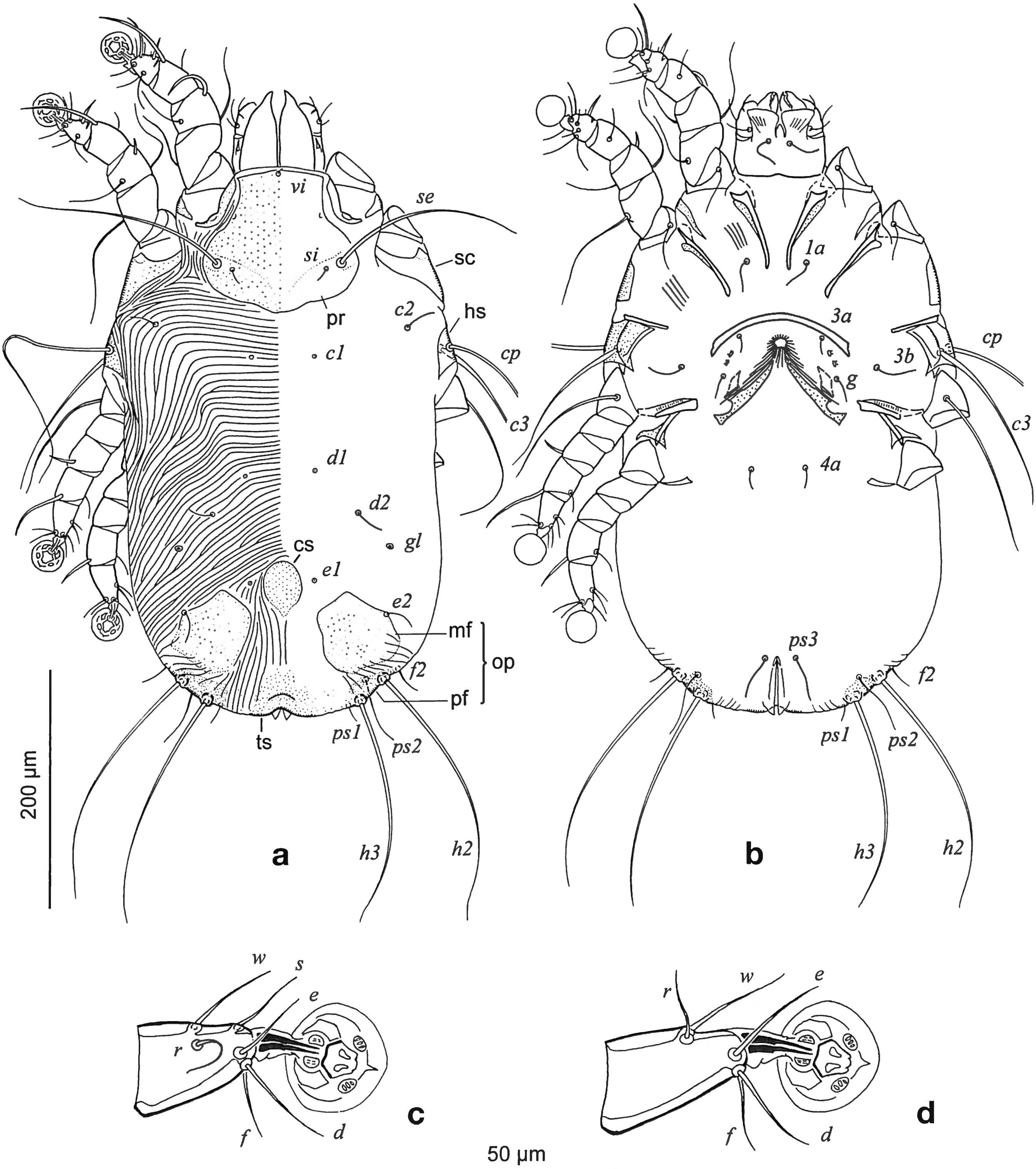


Figs. 1a-b — *Pteronyssoides emberizae*, male. **a.** Dorsal view. **b.** Ventral view. tv – transventral sclerite.

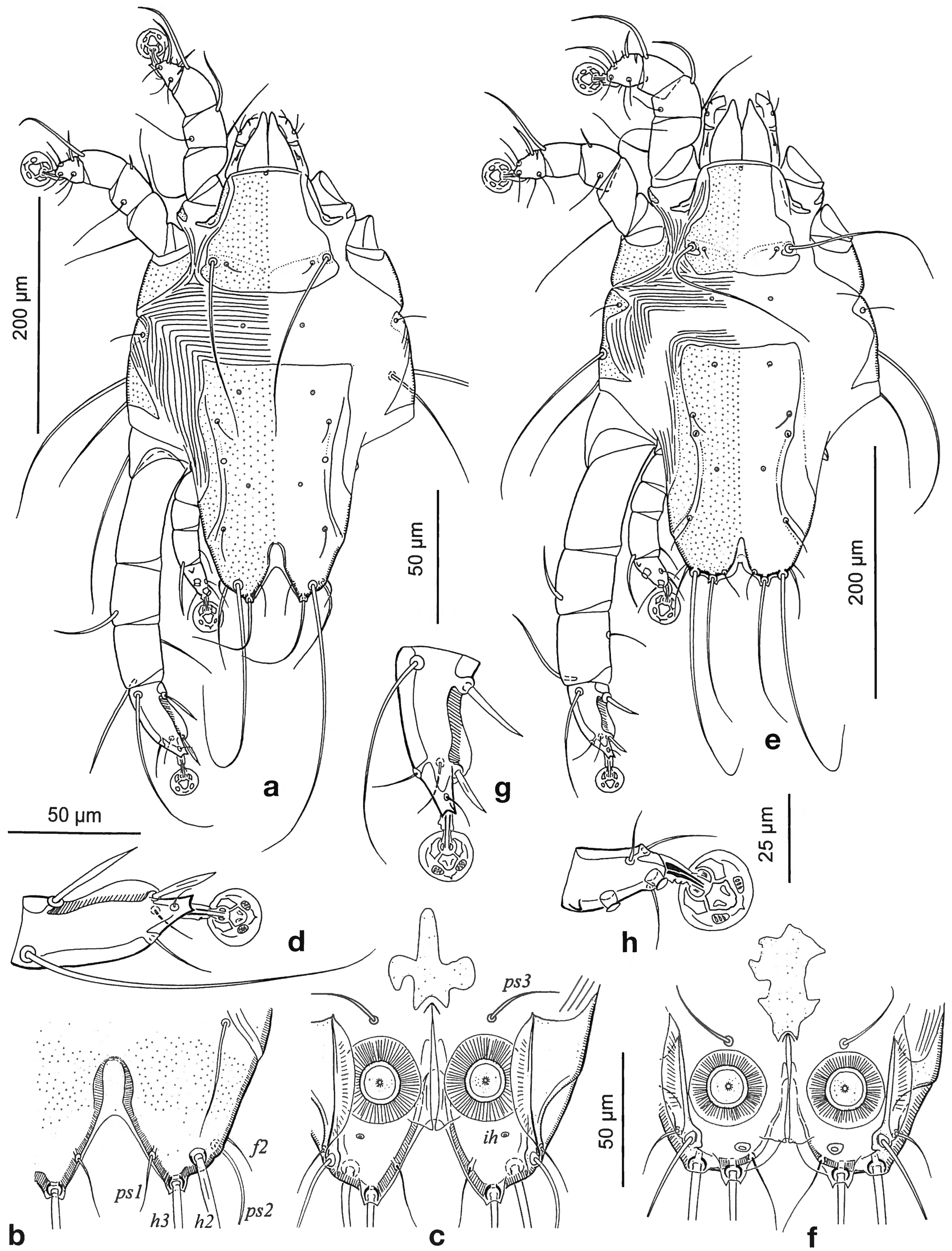


Figs. 2a-g — *Pteronyssoides emberizae*, male. **a**. Tarsus I, dorsal view. **b**. Tarsus I, ventral view. **c**. Tarsus II, ventral view. **d**. Tarsus III, dorsal view. **e**. Tibia and tarsus IV, dorsal view. **f**. Opisthosoma, dorsal view. **g**. Opisthosoma, ventral view.

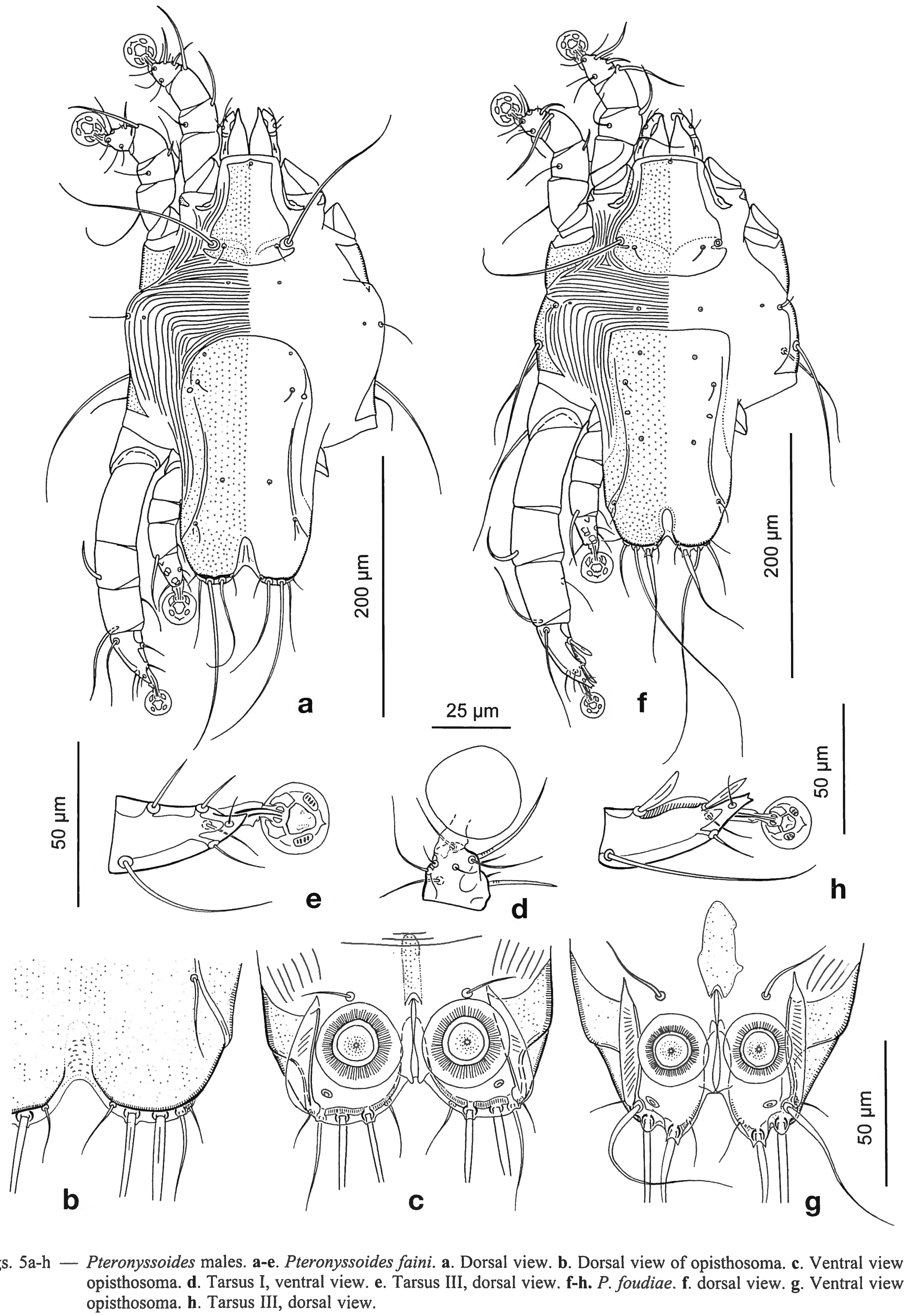
am – adanal membrane, as – adanal shield, db – dorsobasal spine of tarsus IV, im – membrane on inner margin of tarsus III, vm – ventral membrane of tarsus.



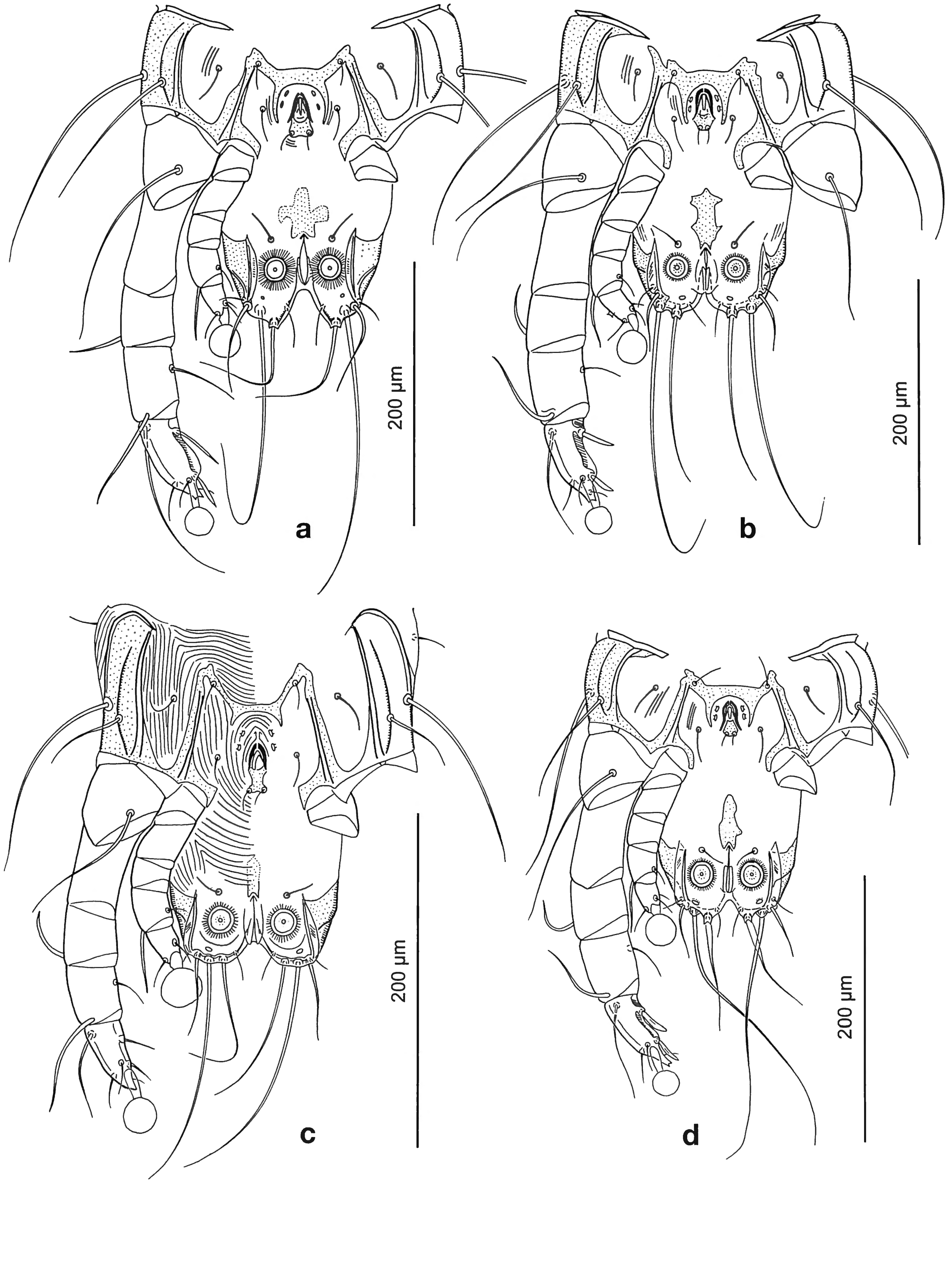
Figs. 3a-d — *Pteronyssoides emberizae*, female. **a**. Dorsal view. **b**. Ventral view, **c**. Tarsus III, dorsal view. **d**. Tarsus IV, dorsal view.
cs – central sclerite, hs – humeral shield, mf – main fragment of opisthosomal sclerite, op – opisthosomal sclerite, pf – pygidial fragment of opisthosomal sclerite, pr – prodorsal shield, sc – scapular shield, ts – terminal sclerite.



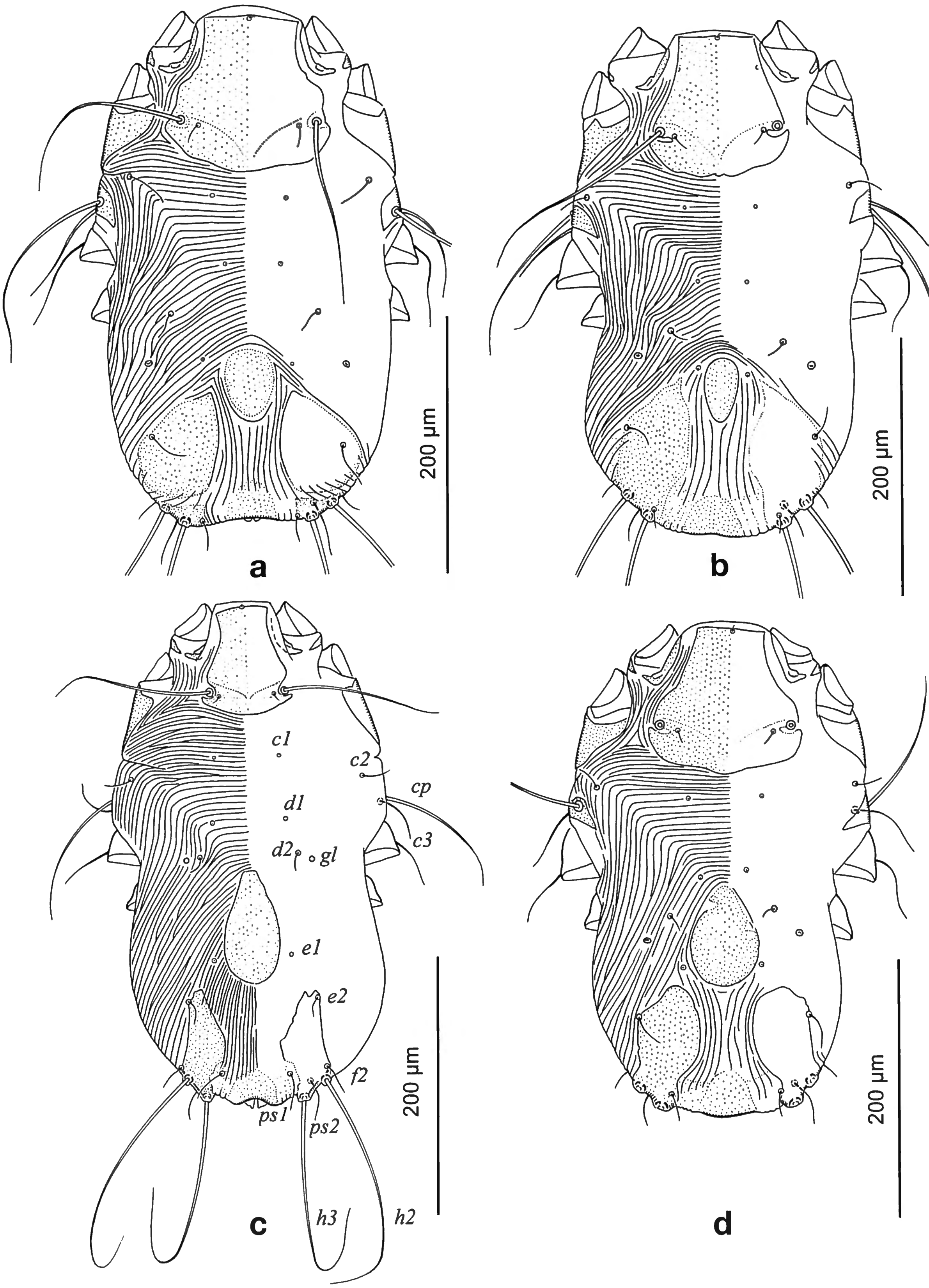
Figs. 4a-h — *Pteronyssoides* males. **a-d**. *Pteronyssoides eupasseris*. **a**. Dorsal view. **b**. Dorsal view of opisthosoma. **c**. Ventral view of opisthosoma. **d**. Tarsus III, dorsal view. **e-h**. *P. euplecti*. **e**. Dorsal view. **f**. Ventral view of opisthosoma. **g**. Tarsus III, dorsal view. **h**. Tarsus IV, dorsal view.



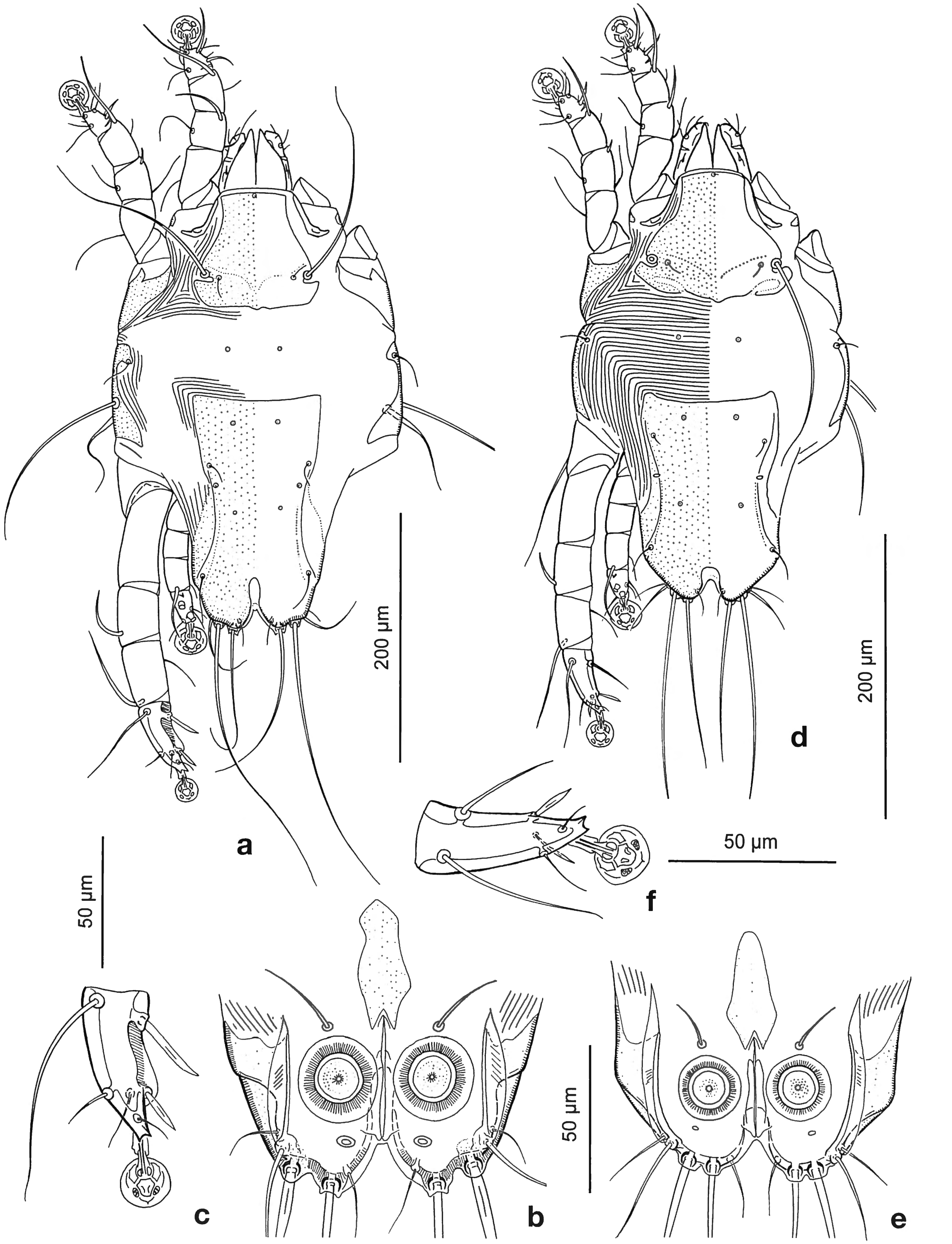
Figs. 5a-h — *Pteronyssoides* males. **a-e**. *Pteronyssoides faini*. **a**. Dorsal view. **b**. Dorsal view of opisthosoma. **c**. Ventral view of opisthosoma. **d**. Tarsus I, ventral view. **e**. Tarsus III, dorsal view. **f-h.** *P. foudiae*. **f**. dorsal view. **g**. Ventral view of opisthosoma. **h**. Tarsus III, dorsal view.



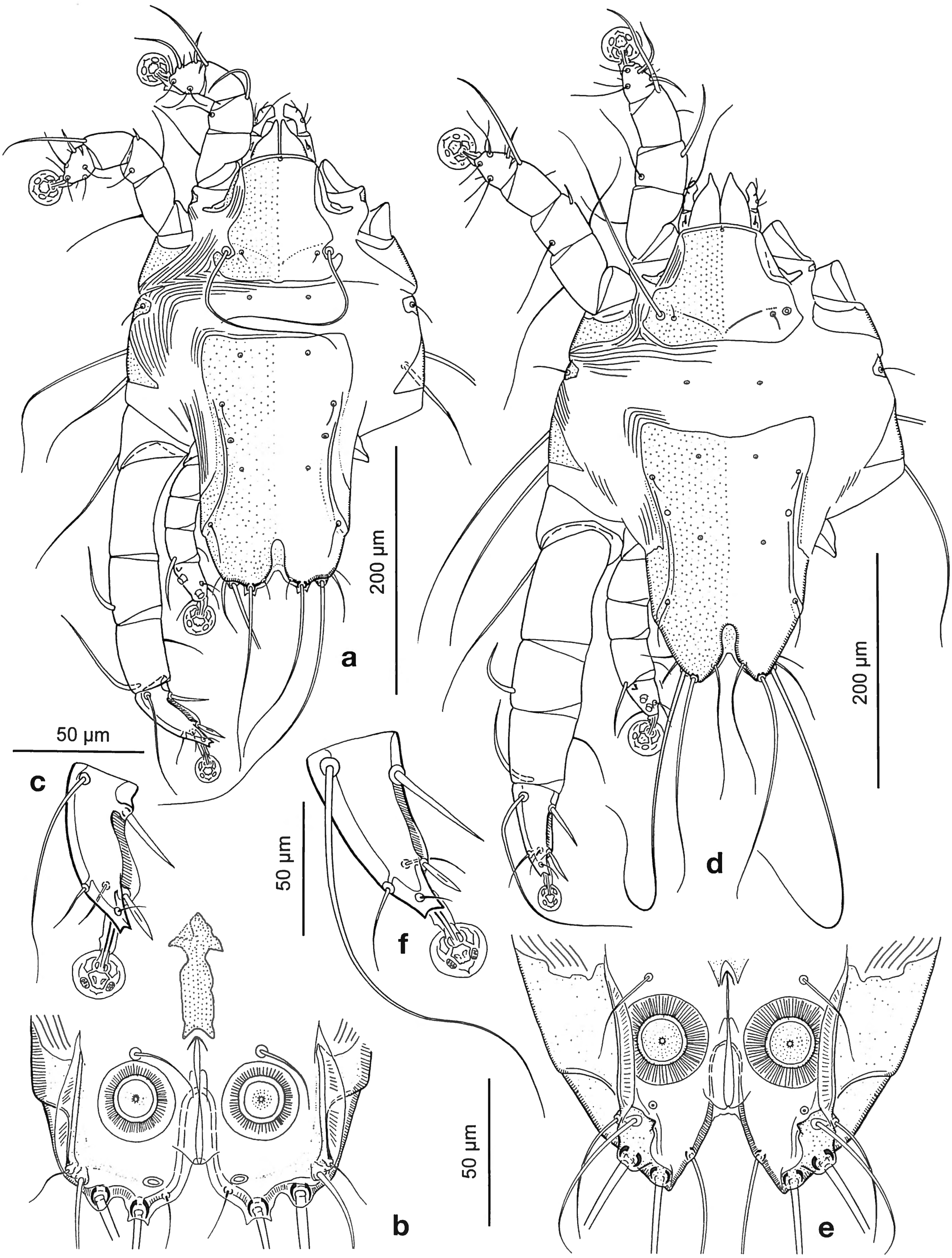
Figs. 6a-d — *Pteronyssoides* males, ventral view of hysterosoma. **a**. *Pteronyssoides eupasseris*. **b**. *P. euplecti*. **c**. *P. faini*. **d**. *P. foudiae*.



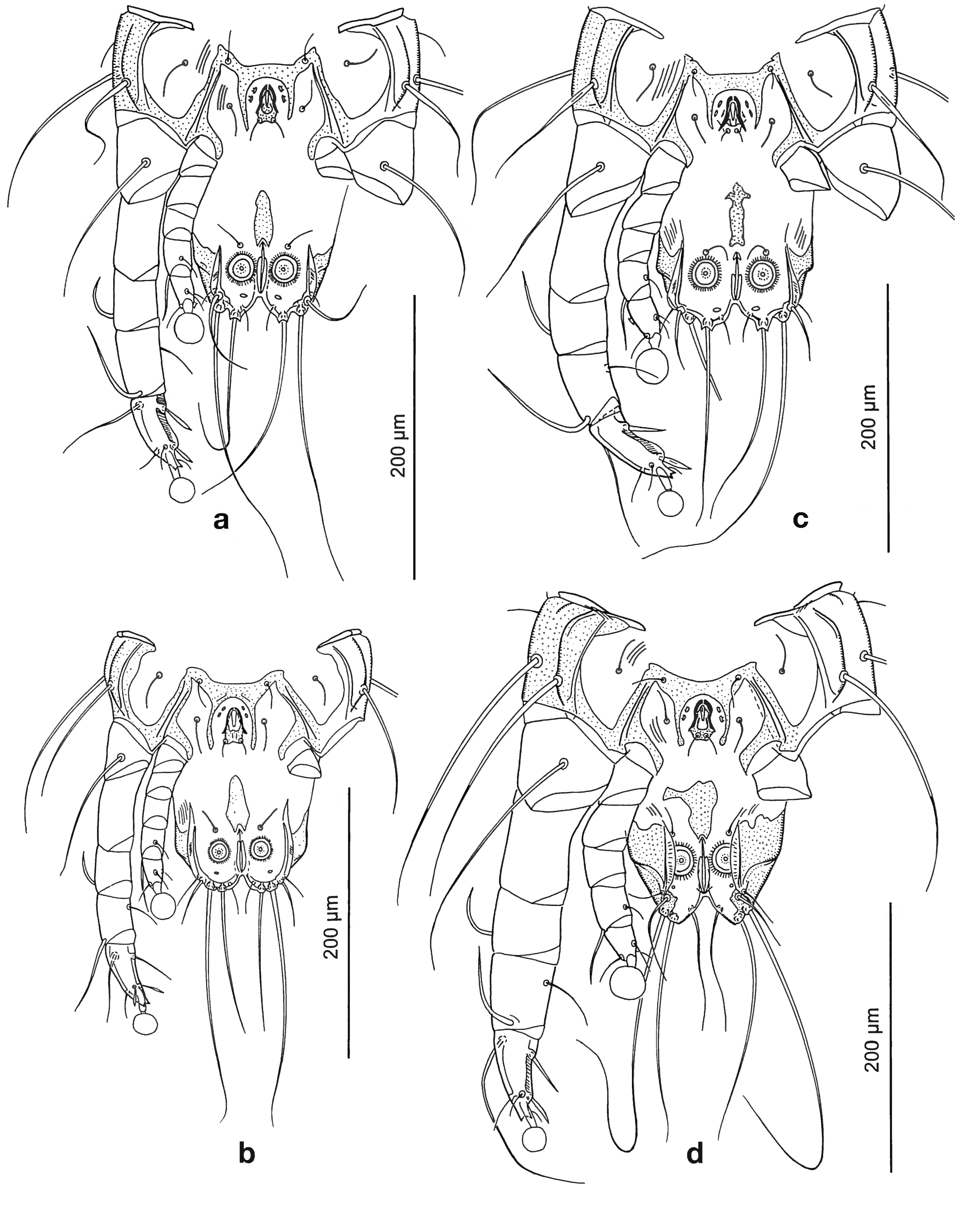
Figs. 7a-d — *Pteronyssoides* females, dorsal view of idiosoma. **a**. *Pteronyssoides eupasseris*. **b**. *P. euplecti*. **c**. *P. faini*. **d**. *P. foudiae*.



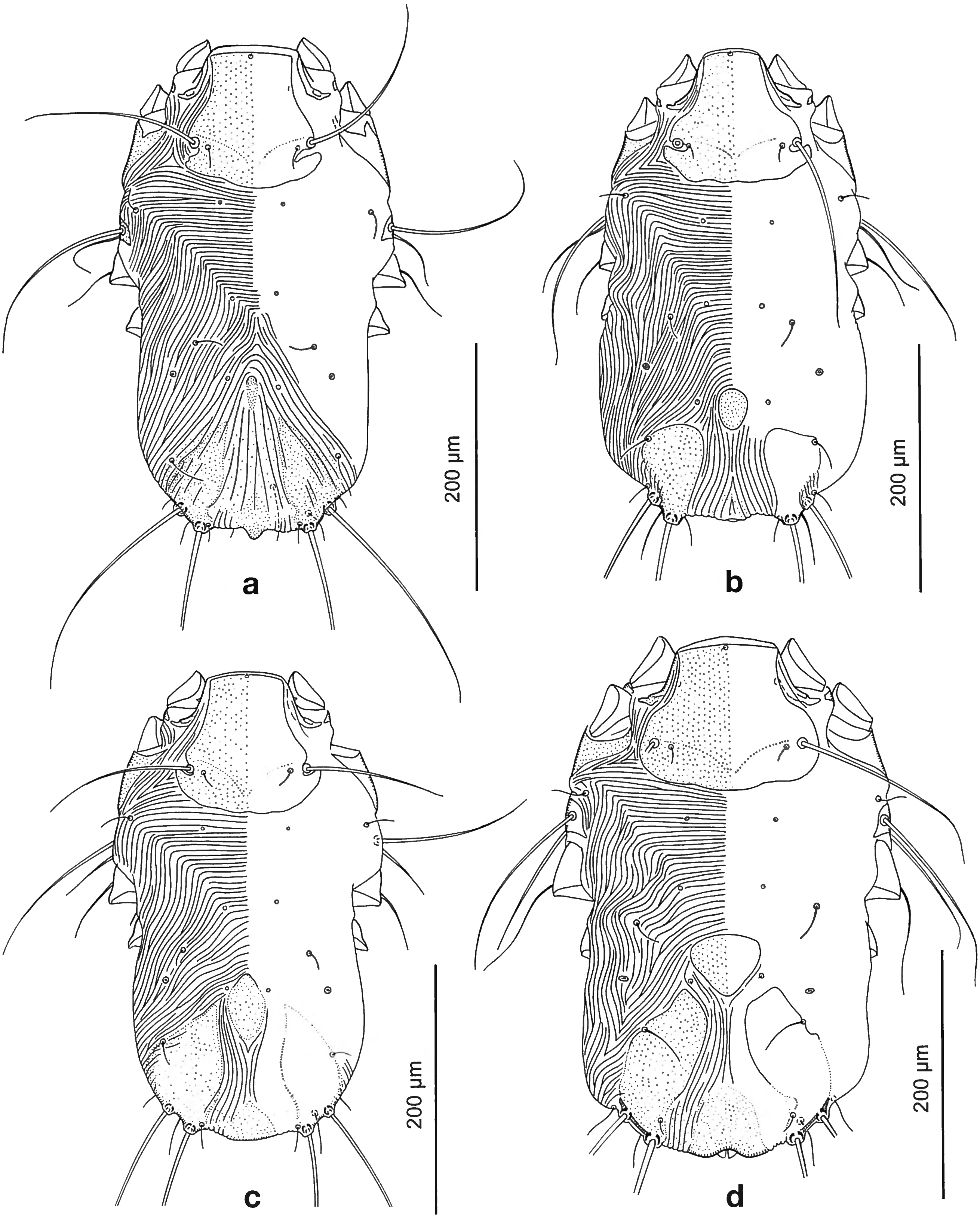
Figs. 8a-f — *Pteronyssoides* males. **a-c**. *Pteronyssoides microscutatus*. **a**. Dorsal view. **b**. Opisthosoma, ventral view. **c**. Tarsus III, dorsal view. **d-f**. *P. motacillae*. **d**. Dorsal view. **e**. Ventral view of opisthosoma. **f**. Tarsus III, dorsal view.



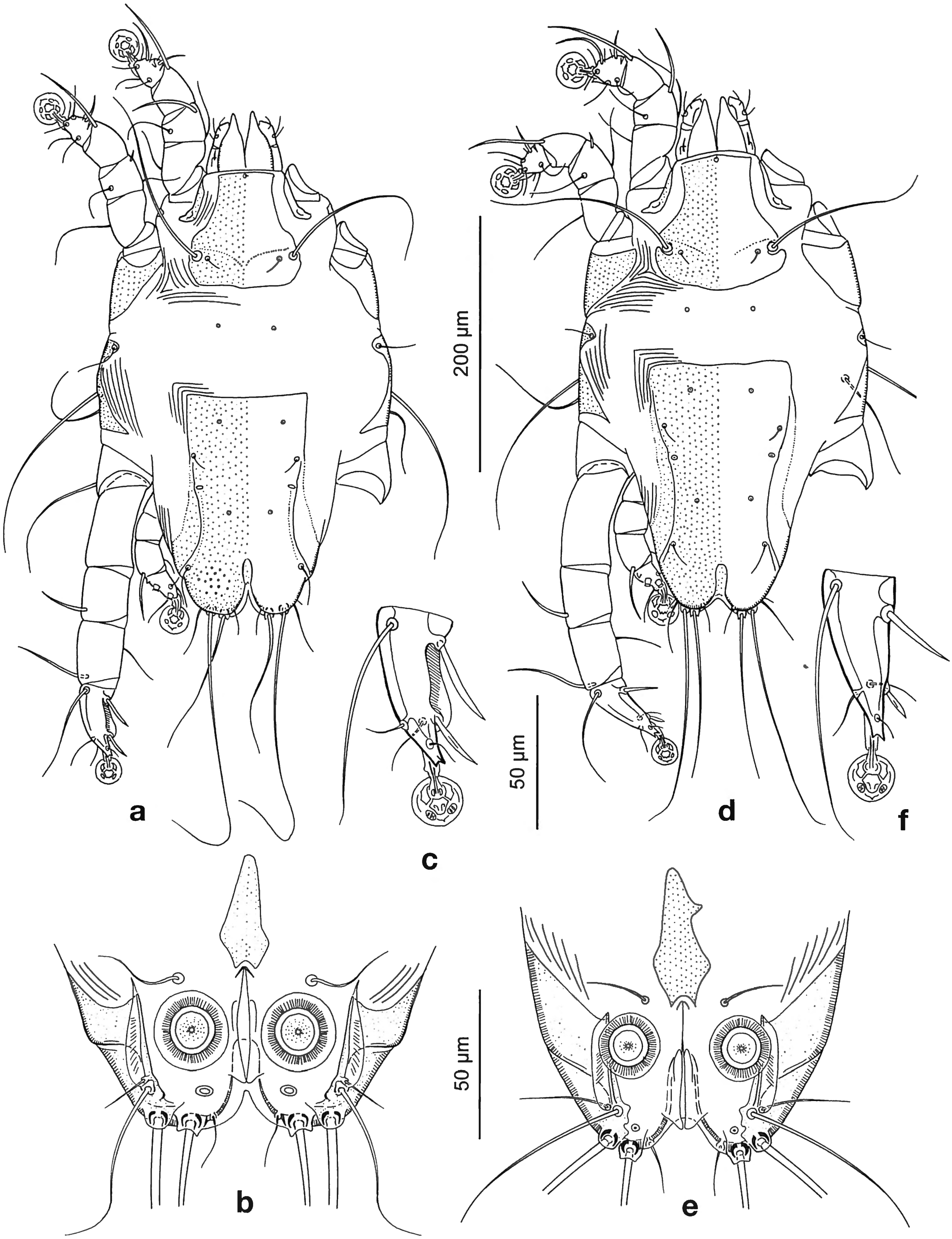
Figs. 9a-f — *Pteronyssoides* males. **a-c**. *Pteronyssoides ovoscutatus*. **a**. Dorsal view. **b**. Ventral view of opisthosoma. **c**. Tarsus III, dorsal view. **d-f**. *P. passeris*. **d**. Dorsal view. **e**. Ventral view of opisthosoma. **f**. Tarsus III, dorsal view.



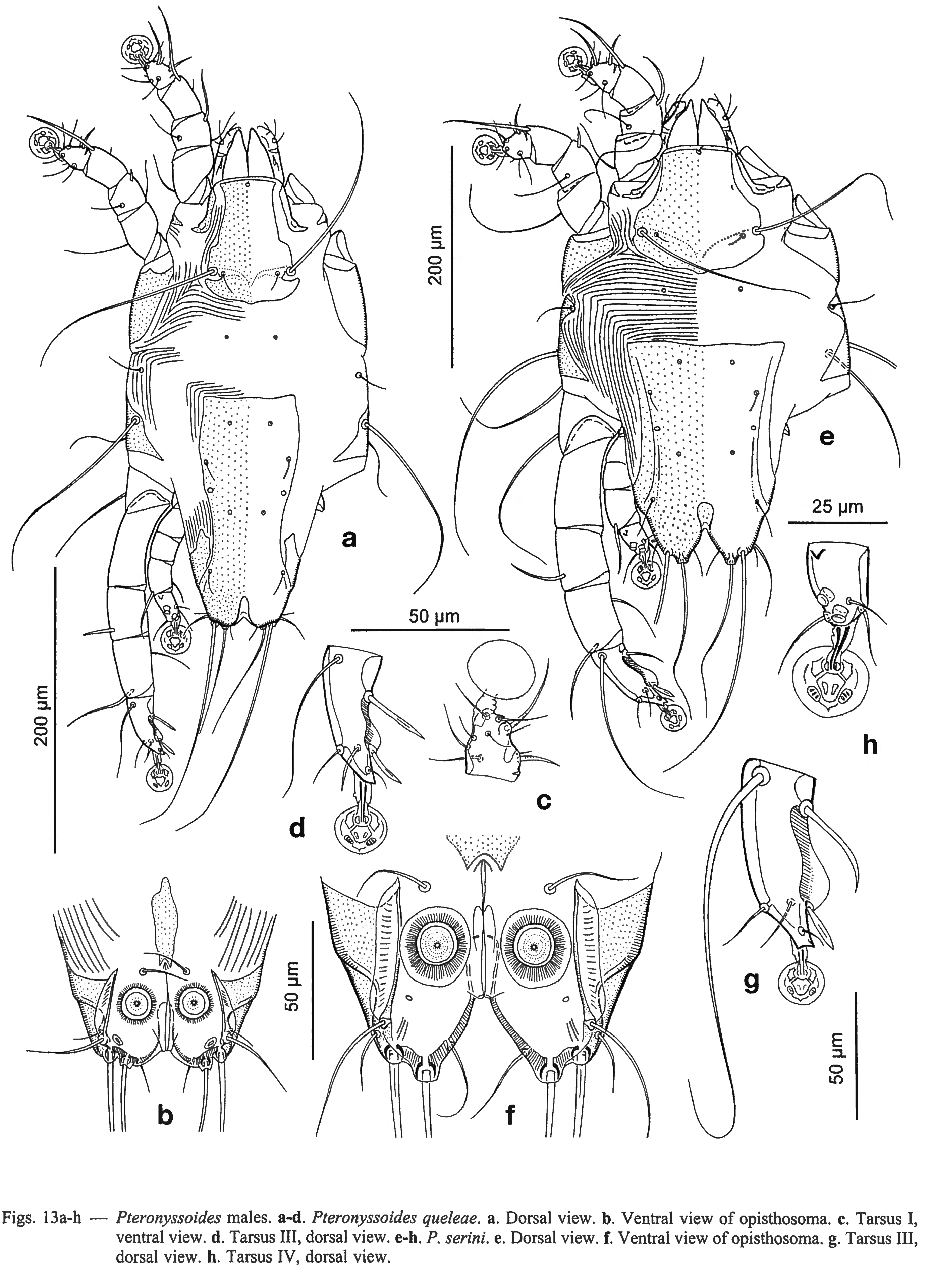
Figs.10a-d — *Pteronyssoides* males, ventral view of hysterosoma. **a**. *Pteronyssoides microscutatus*. **b**. *P. motacillae*. **c**. *P. ovoscutatus*. **d**. *P. passeris*.



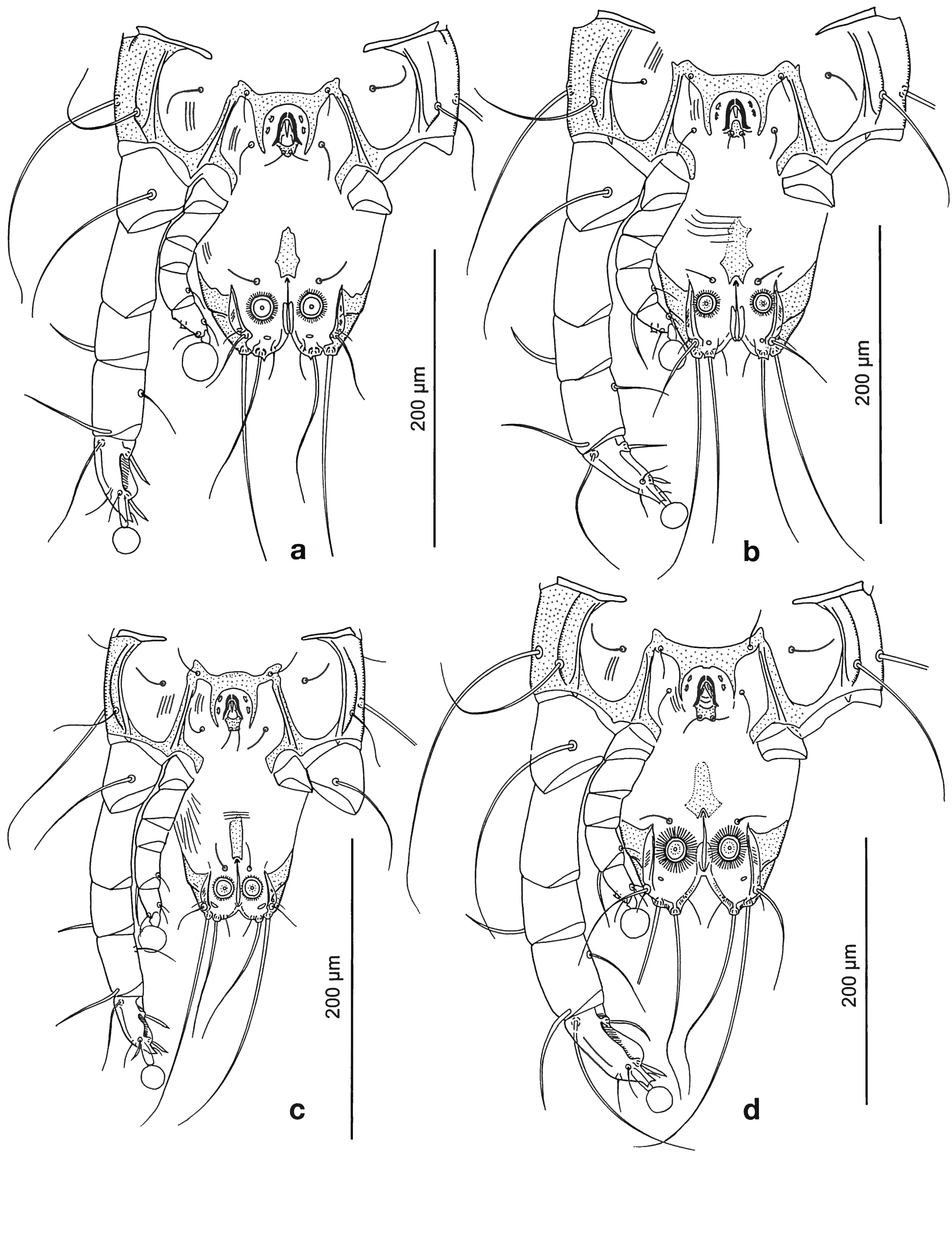
Figs. 11a-d — *Pteronyssoides* females, dorsal view of idiosoma. **a**. *Pteronyssoides microscutatus*. **b**. *P. motacillae*. **c**. *P. ovoscutatus*. **d**. *P. passeris*.



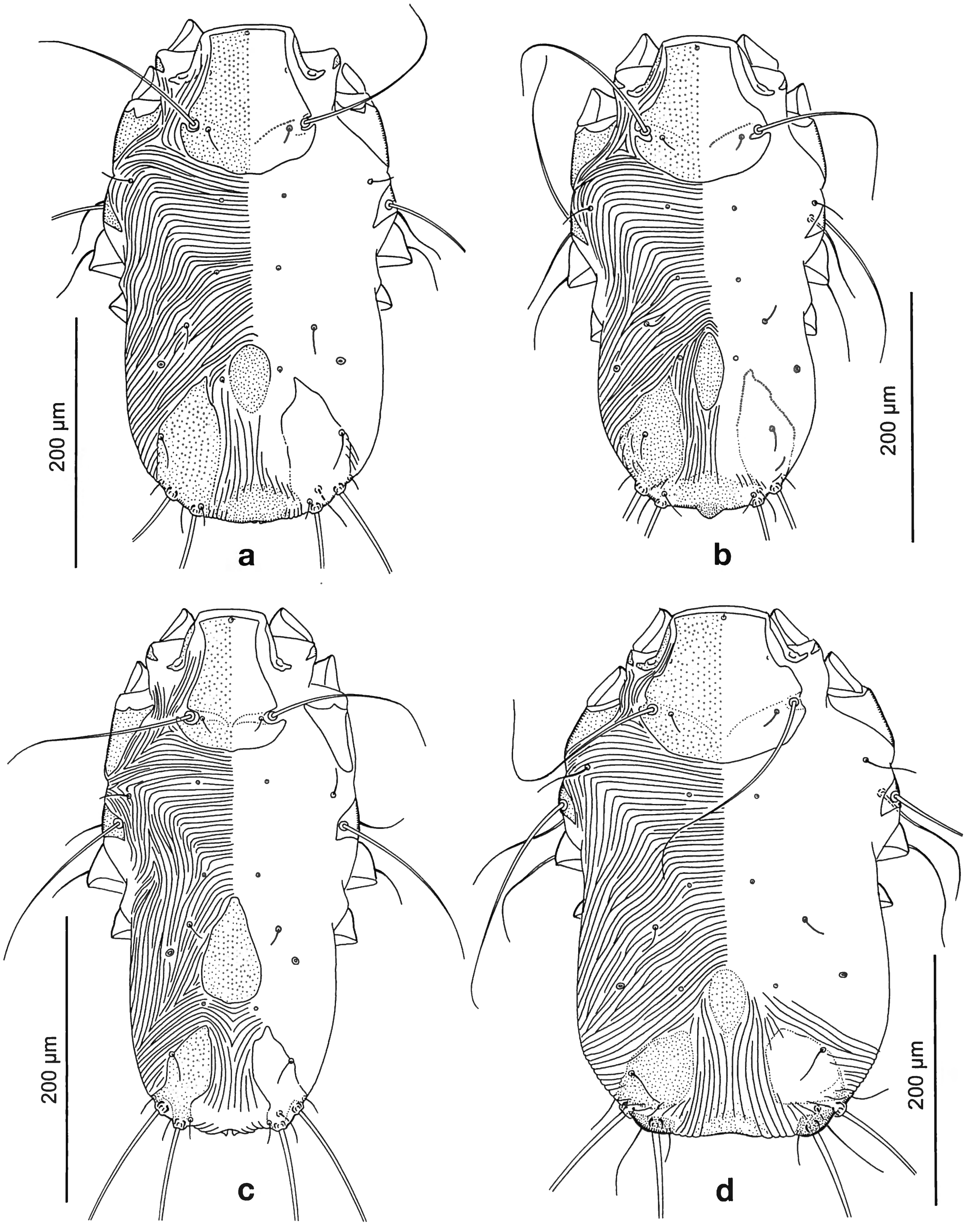
Figs. 12a-f — *Pteronyssoides* males. **a-c**. *Pteronyssoides plocei*. **a**. Dorsal view. **b**. Ventral view of opisthosoma. **c**. Tarsus III, dorsal view. **d-f**. *P. pytiliae*. **d**. Dorsal view. **e**. Ventral view of opisthosoma. **f**. Tarsus III, dorsal view.



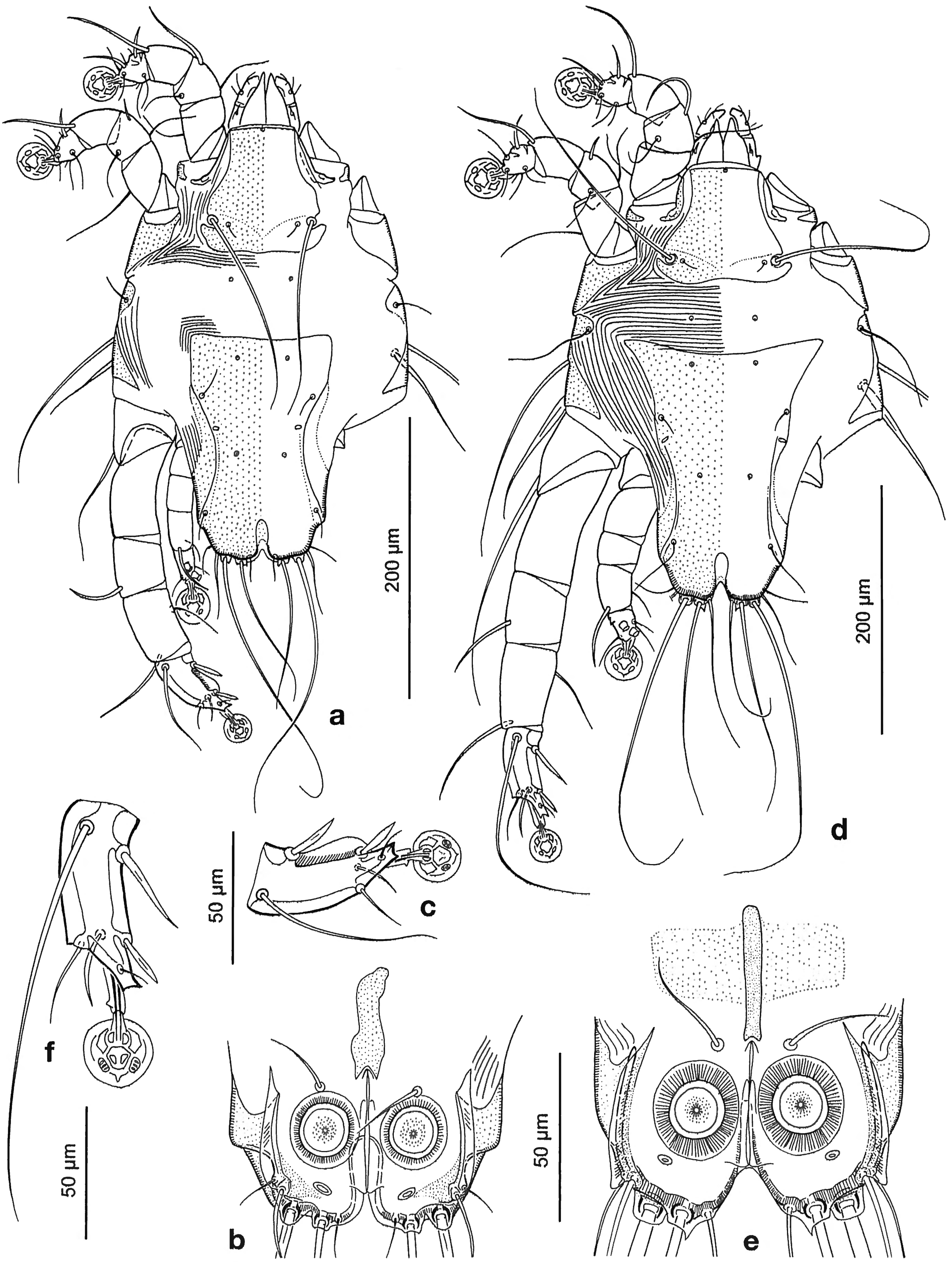
Figs. 13a-h — *Pteronyssoides* males. **a-d**. *Pteronyssoides queleae*. **a**. Dorsal view. **b**. Ventral view of opisthosoma. **c**. Tarsus I, ventral view. **d**. Tarsus III, dorsal view. **e-h**. *P. serini*. **e**. Dorsal view. **f**. Ventral view of opisthosoma. **g**. Tarsus III, dorsal view. **h**. Tarsus IV, dorsal view.



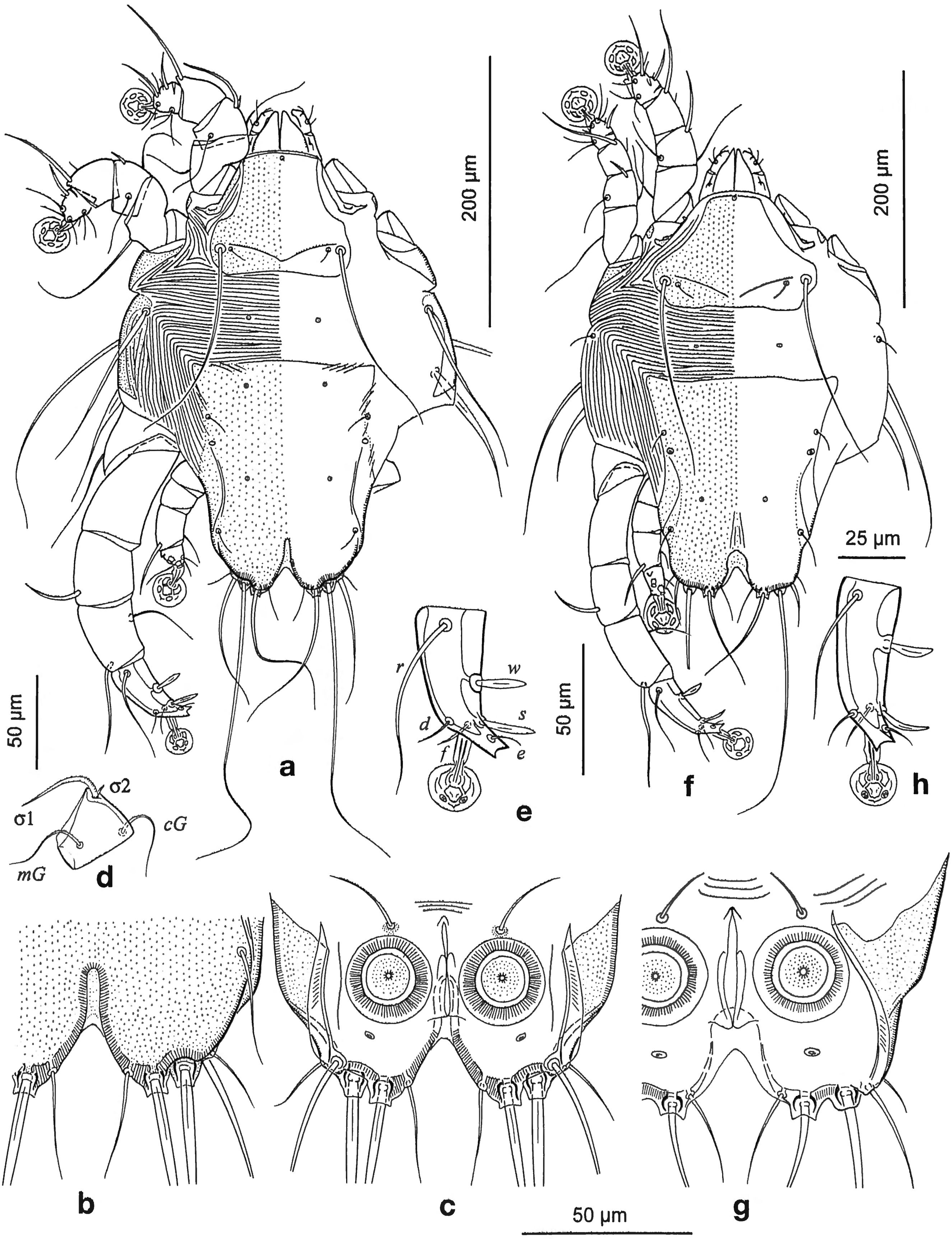
Figs. 14a-d — *Pteronyssoides* males, ventral view of hysterosoma. **a**. *Pteronyssoides plocei*. **b**. *P. pytiliae*. **c**. *P. queleae*. **d**. *P. serini*.



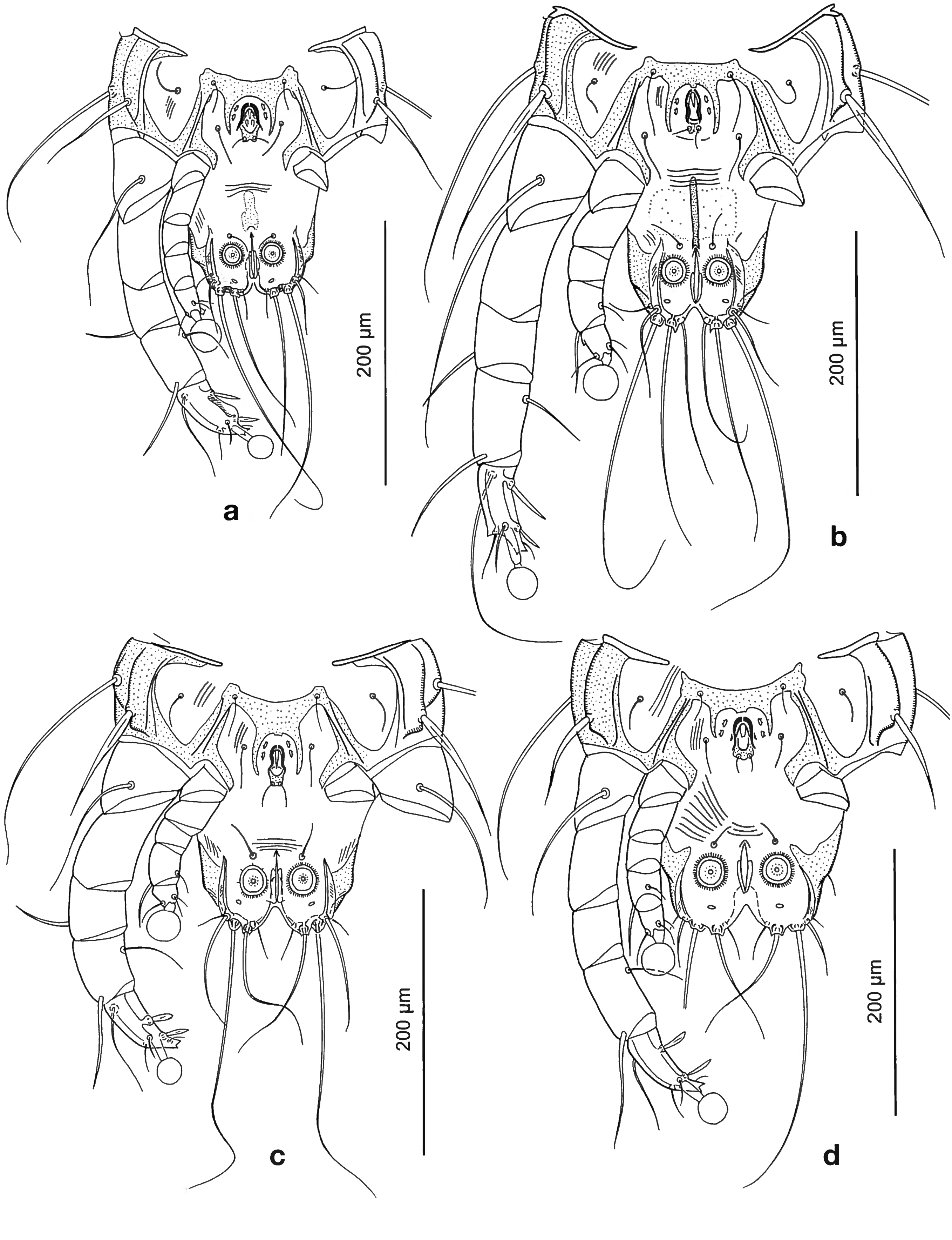
Figs. 15a-d — *Pteronyssoides* females, dorsal view of idiosoma. **a**. *Pteronyssoides plocei*. **b**. *P. pytiliae*. **c**. *P. queleae*. **d**. *P. serini*.



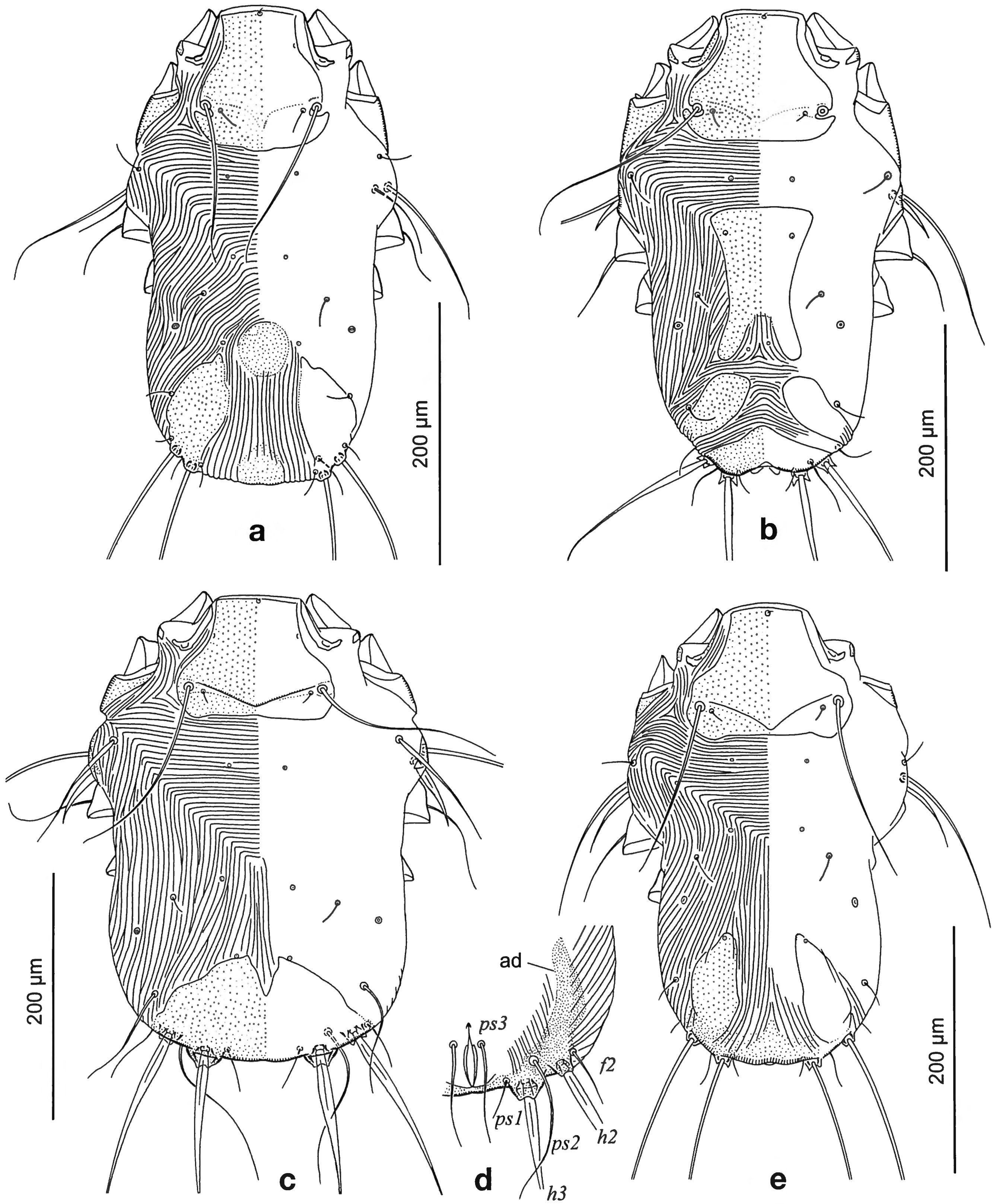
Figs. 16a-f — *Pteronyssoides* males. **a-c**. *Pteronyssoides viduinus*. **a**. Dorsal view. **b**. Ventral view of opisthosoma. **c**. Tarsus III, dorsal view. **d-f**. *P. lambda*. **d**. Dorsal view. **e**. Ventral view of opisthosoma. **f**. Tarsus III, dorsal view.



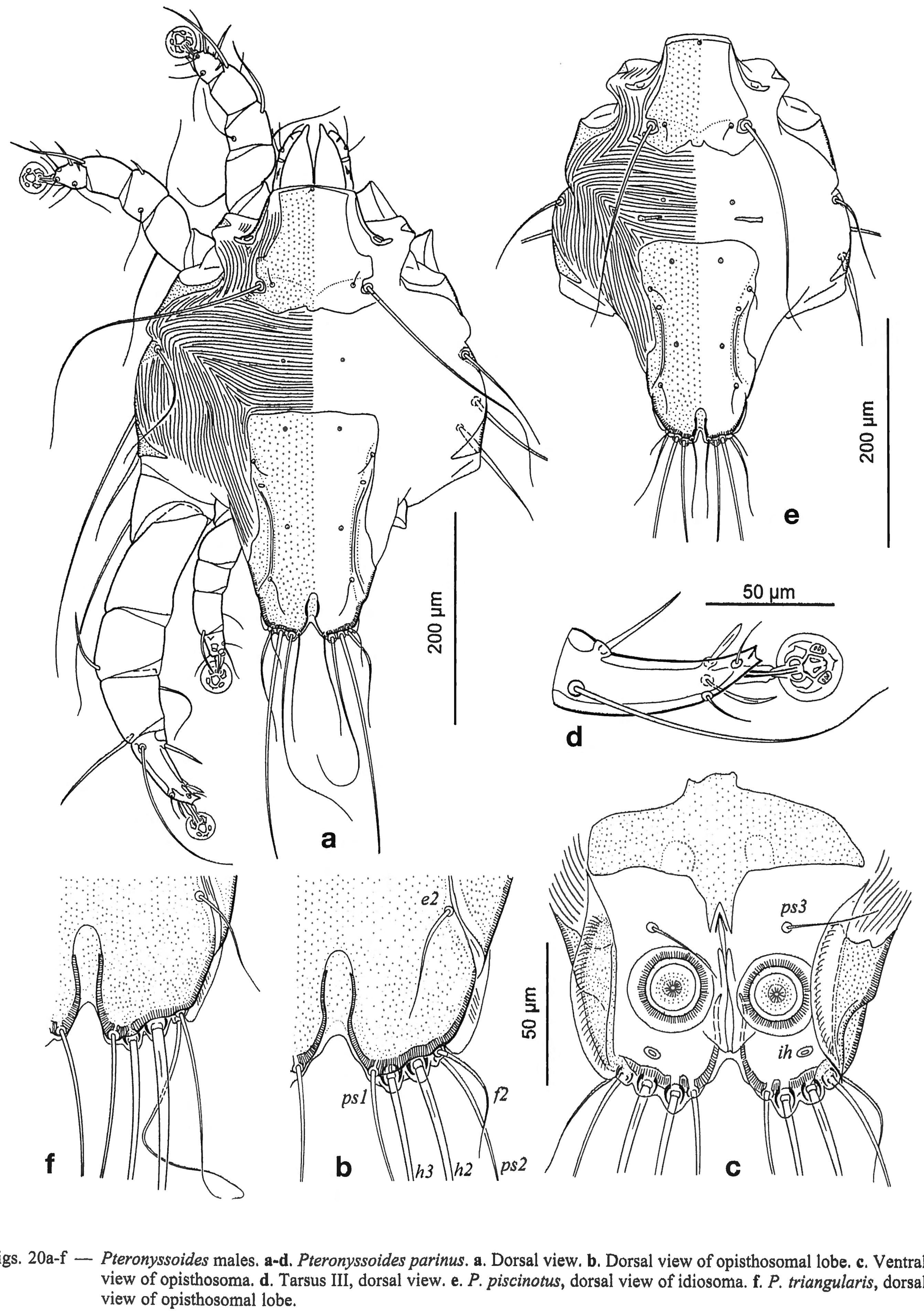
Figs. 17a-h — *Pteronyssoides* males. **a-e**. *Pteronyssoides garioui*. **a**. Dorsal view. **b**. Dorsal view of oisthosoma. **c**. Ventral view of opisthosoma. **d**. Genu I, dorsal view. **e**. Tarsus III, dorsal view. **f-h**. *P. nectariniae*. **f**. Dorsal view. **g**. Ventral view of opisthosoma. **h**. Tarsus III, dorsal view.



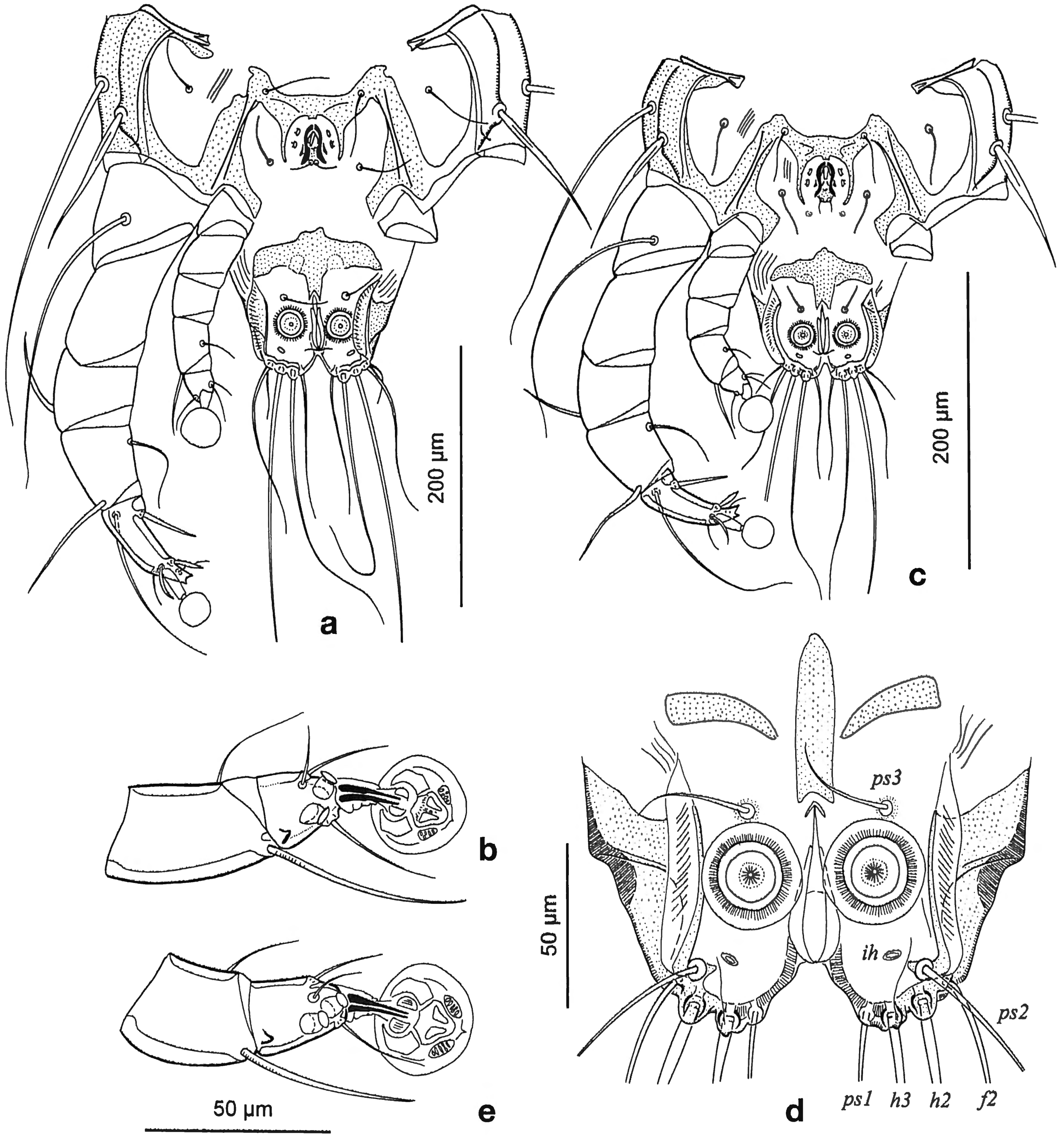
Figs. 18a-d — *Pteronyssoides* males, ventral view of hysterosoma. **a**. *Pteronyssoides viduinus*. **b**. *P. lambda*. **c**. *P. garioui*. **d**. *P. nectariniae*.



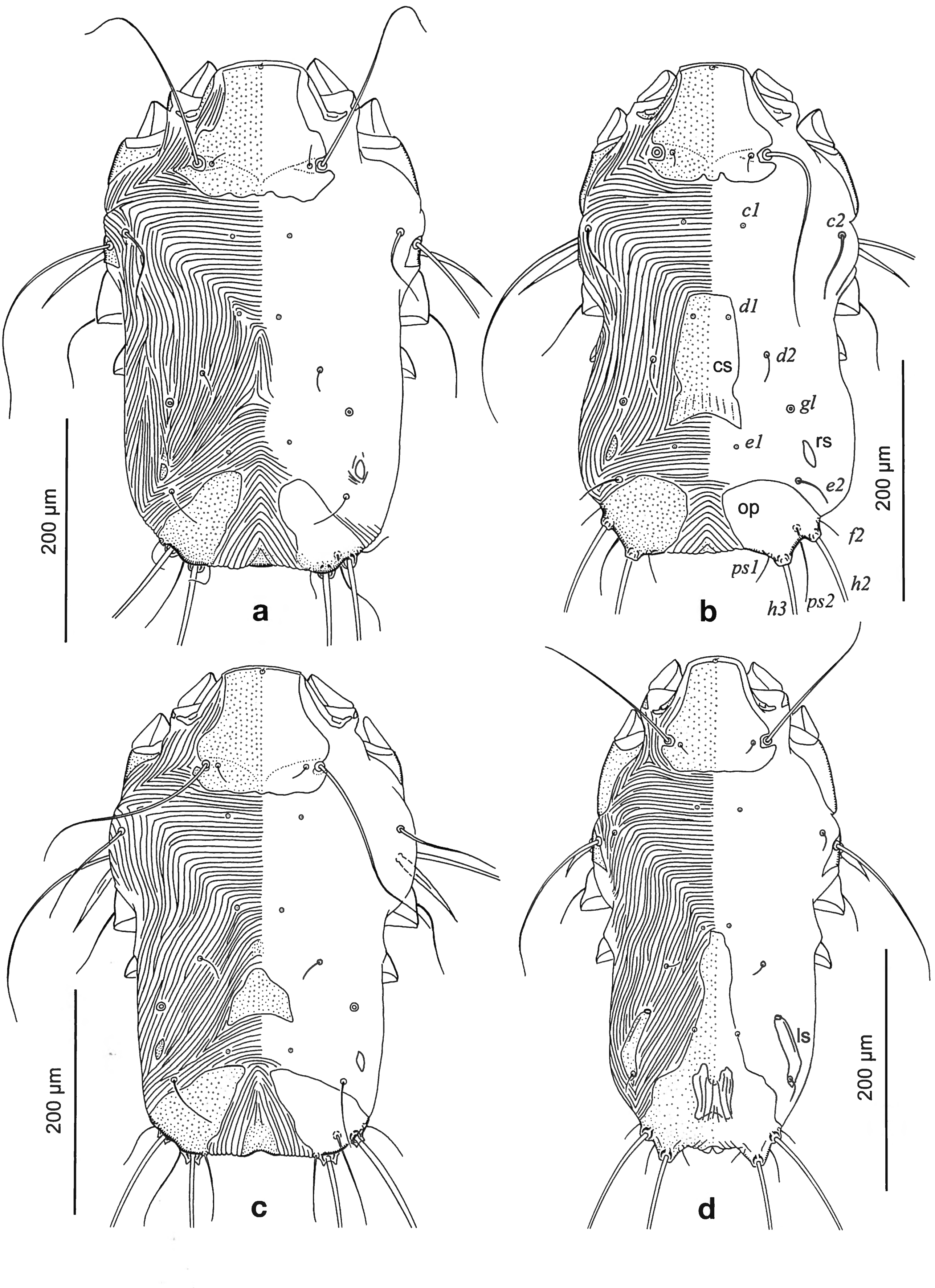
Figs. 19a-e — *Pteronyssoides* females. **a**. *Pteronyssoides viduinus*, dorsal view of idiosoma **b**. *P. lambda*, dorsal view of idiosoma. **c-d**. *P. garioui*. **c**. Dorsal view of idiosoma. **d**. Ventral view of opisthosoma. **e**. *P. nectariniae*. ad – adanal shield.



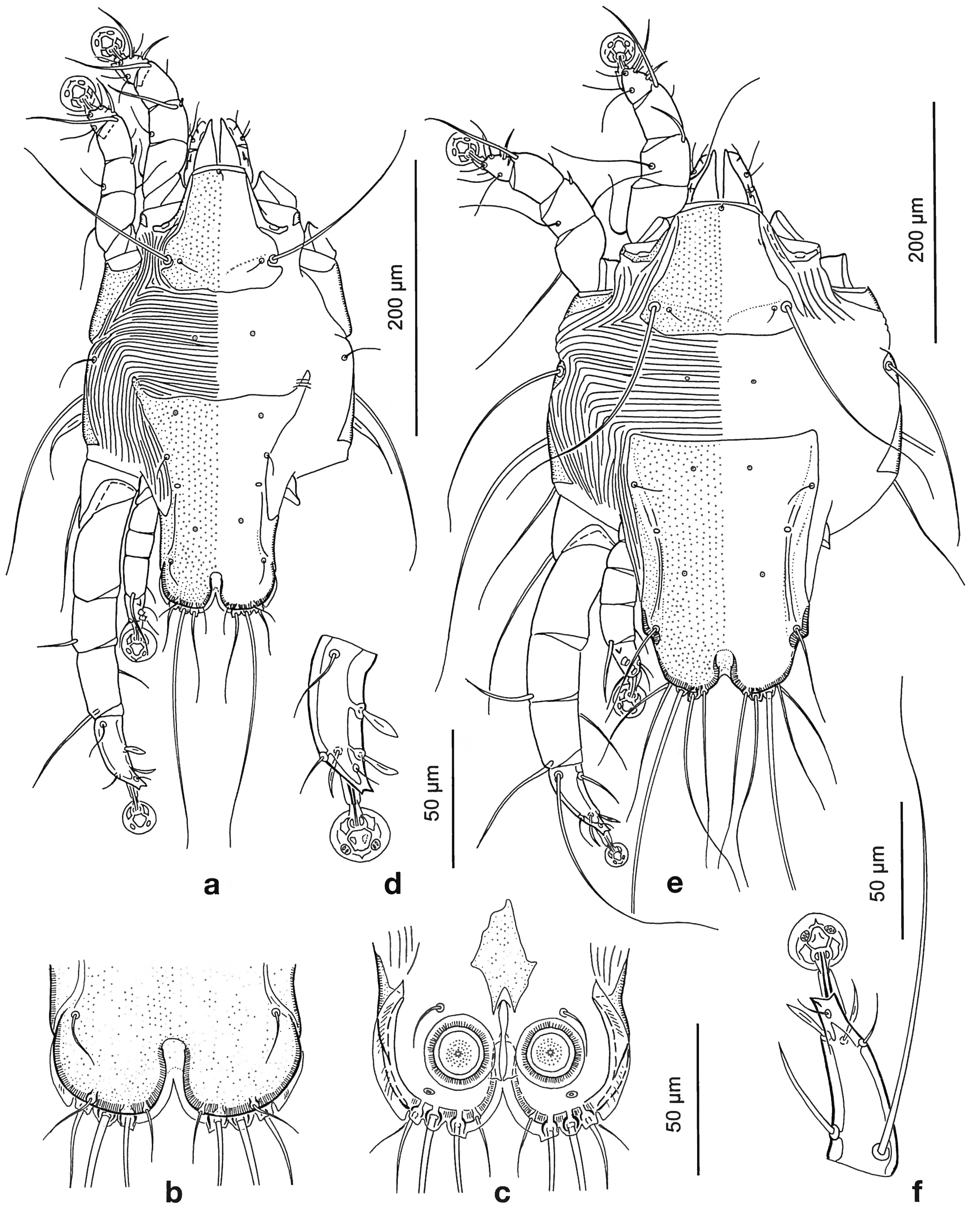
Figs. 20a-f — *Pteronyssoides* males. **a-d.** *Pteronyssoides parinus*. **a.** Dorsal view. **b.** Dorsal view of opisthosomal lobe. **c.** Ventral view of opisthosoma. **d.** Tarsus III, dorsal view. **e.** *P. piscinotus*, dorsal view of idiosoma. **f.** *P. triangularis*, dorsal view of opisthosomal lobe.



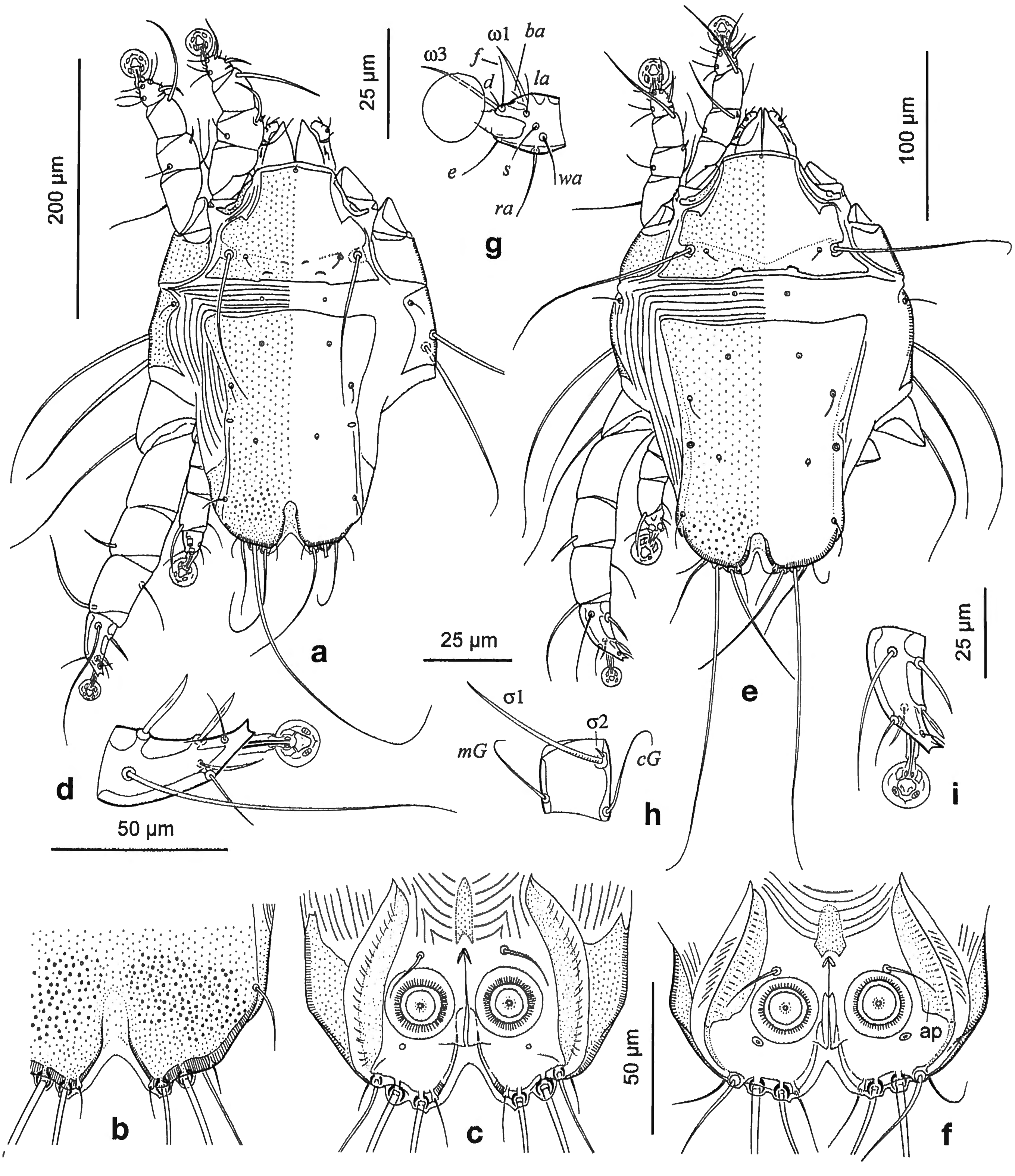
Figs. 21a-e — *Pteronyssoides* males. **a-b**. *Pteronyssoides parinus*. **a**. Ventral view of hysterosoma. **b**. Tibia and tarsus IV, dorsal view. **c**. *P. piscinotus*, ventral view of hysterosoma. **d–e**. *P. striatus*. **d**. Ventral view of opisthosoma. **e**. Tibia and tarsus IV, dorsal view.



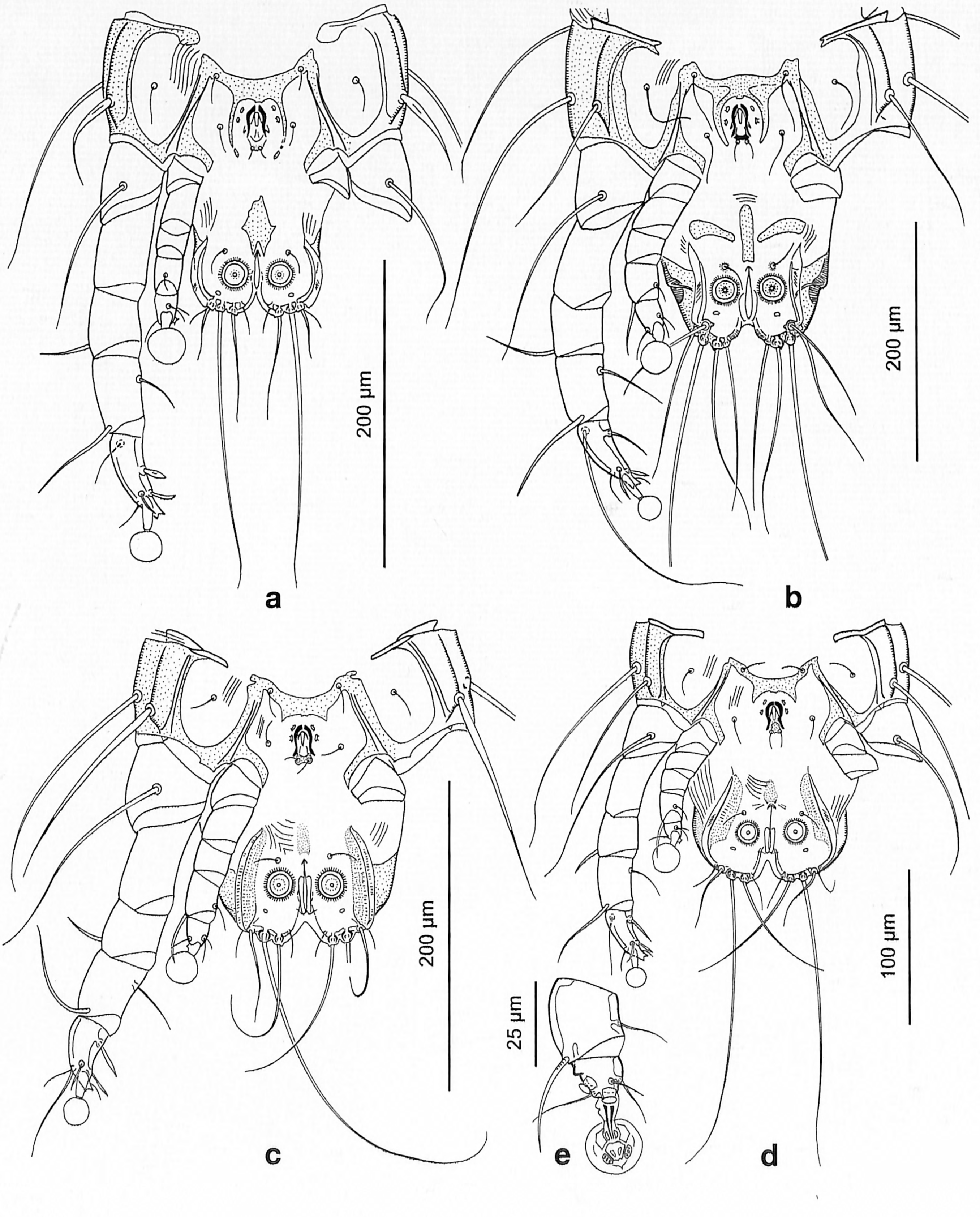
Figs. 22a-d — *Pteronyssoides* females, dorsal view of idiosoma. **a.** *Pteronyssoides parinus*. **b.** *P. piscinotus*. **c.** *P. triangularis*. **d.** *P. promeropis*. cs – central sclerite, ls – lateral sclerite, op – opisthosomal sclerite, rs – rudimentary lateral sclerite.



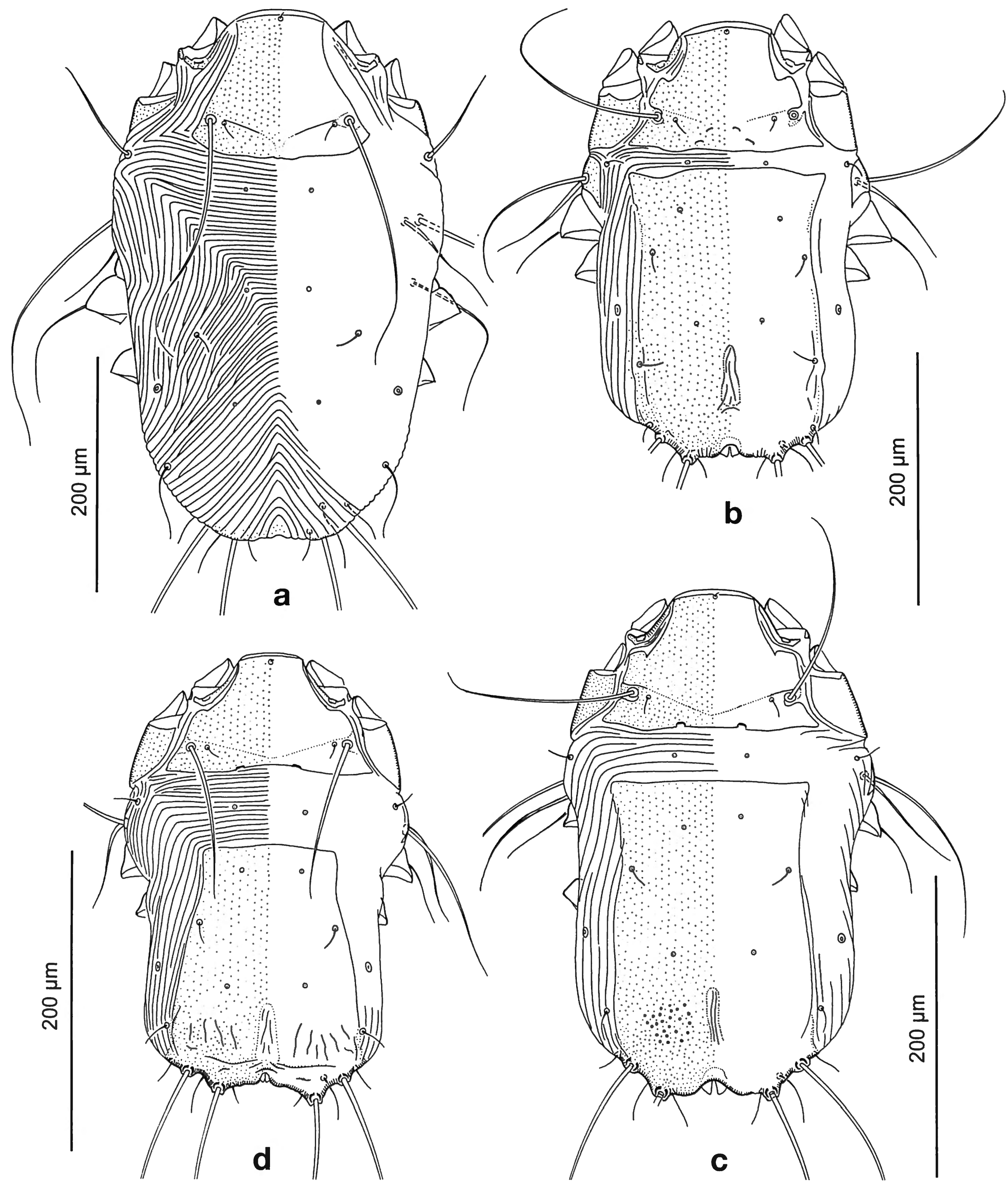
Figs. 23a-f — *Pteronyssoides* males. **a–c**. *Pteronyssoides promeropis*. **a**. Dorsal view. **b**. Dorsal view of opisthosoma. **c**. Ventral view of opisthosoma. **d**. Tarsus III, dorsal view. **e-f**. *P. striatus*. **e**. Dorsal view. **f**. Tarsus III, dorsal view.



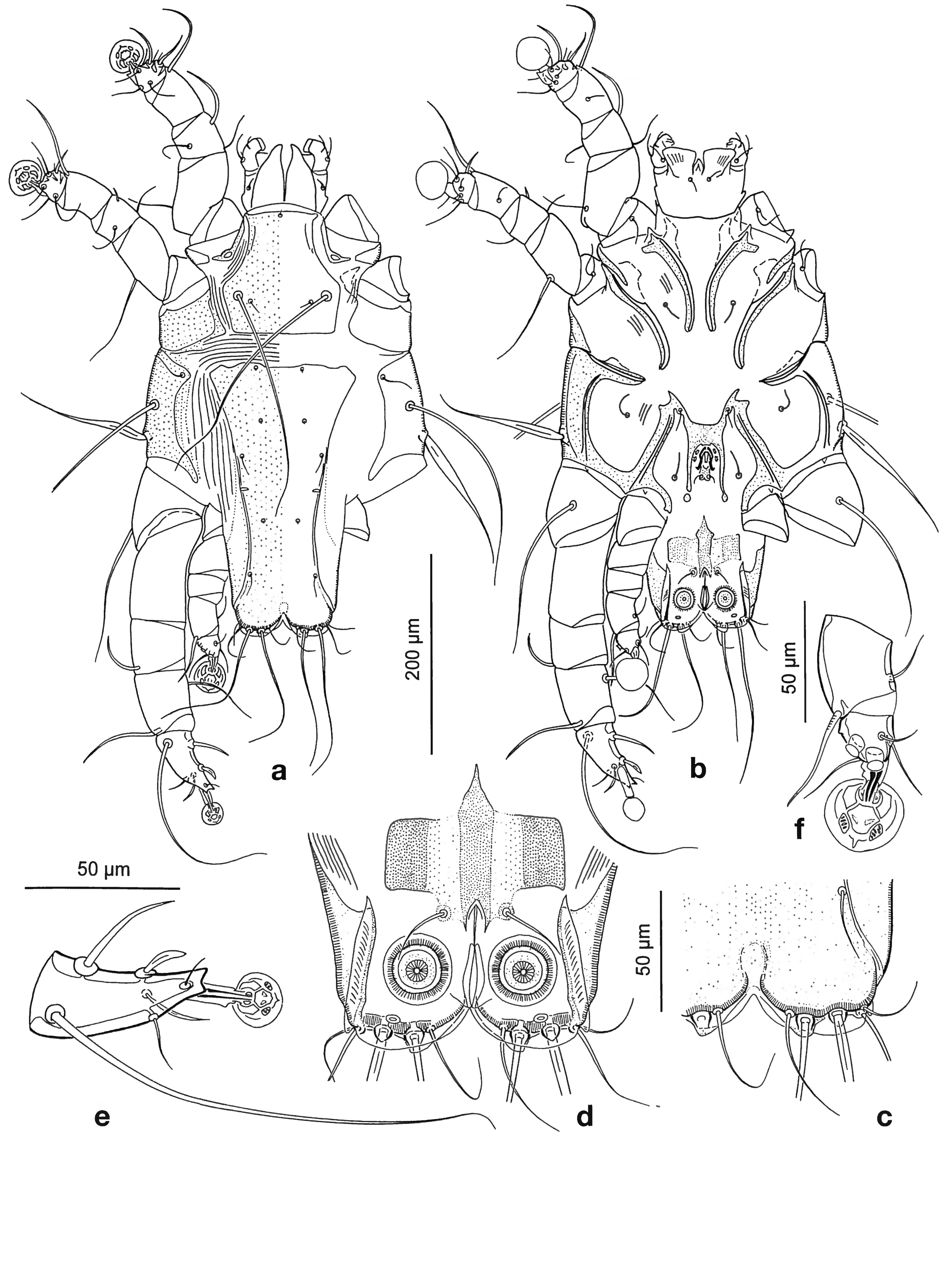
Figs. 24a-i — *Pteronyssoides* males. **a-d.** *Pteronyssoides desmiphorus*. **a.** Dorsal view. **b.** Dorsal view of opisthosoma. **c.** Ventral view of opisthosoma. **d.** Tarsus III, dorsal view. **e-i.** *P. holoplax*. **e.** Dorsal view. **f.** Ventral view of opisthosoma. **g.** Tarsus I, ventral view. **h.** Genu I, dorsal view. **i.** Tarsus III, dorsal view. ap – adanal apodeme.



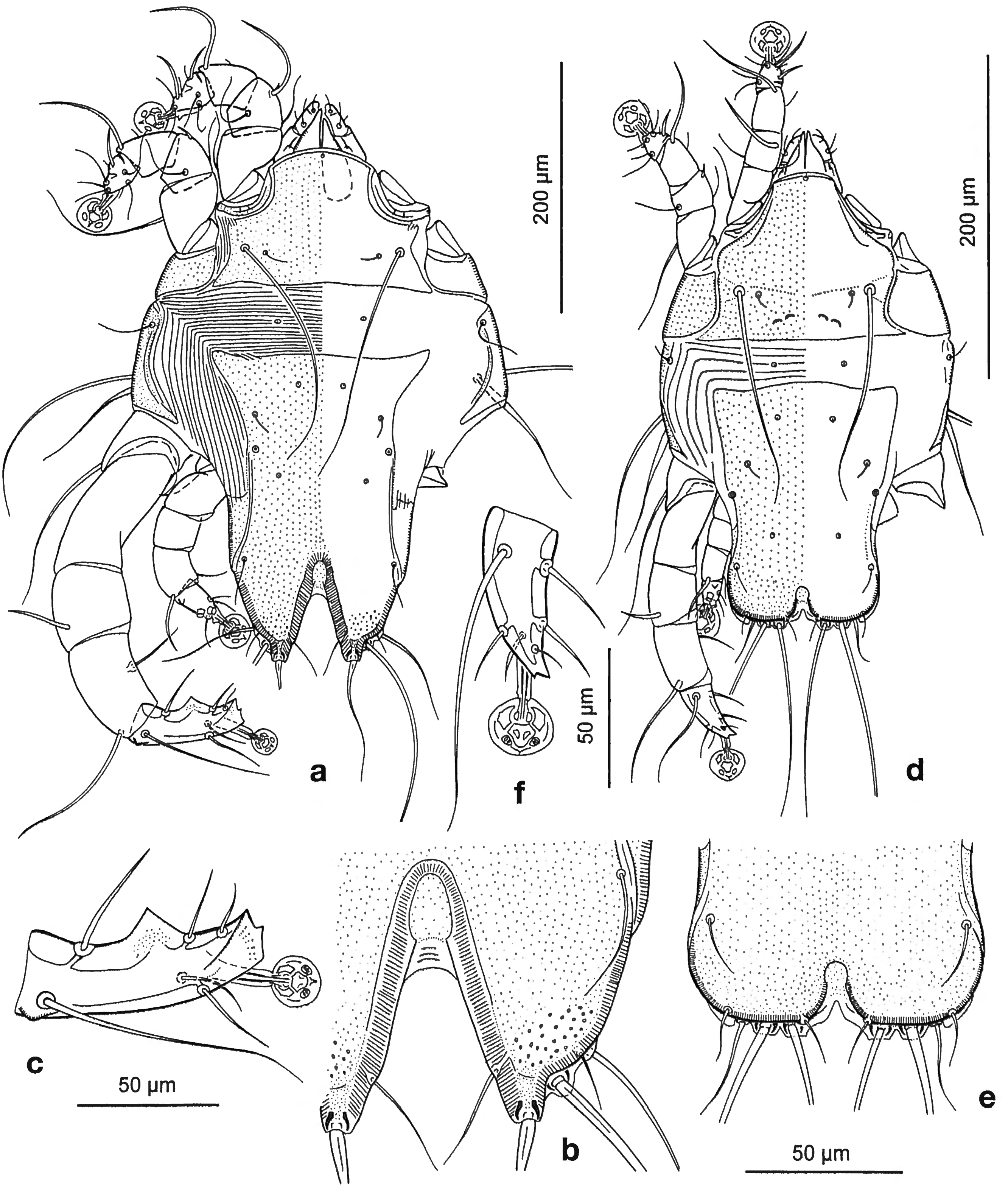
Figs. 25a-e — *Pteronyssoides* males. **a**. *Pteronyssoides promeropis,* ventral view of hysterosoma. **b**. *P. striatus*, ventral view of hysterosoma. **c**. *P. desmiphorus*, ventral view of hysterosoma. **d-e**. *P. holoplax*. **d**. Ventral view of hysterosoma. **e**. Tibia and tarsus IV, dorsal view.



Figs. 26a-d — *Pteronyssoides* females, dorsal view of idiosoma. **a**. *Pteronyssoides striatus*. **b**. *P. desmiphorus*. **c**. *P. holoplax*. **d**. *P. pycnonoti*.

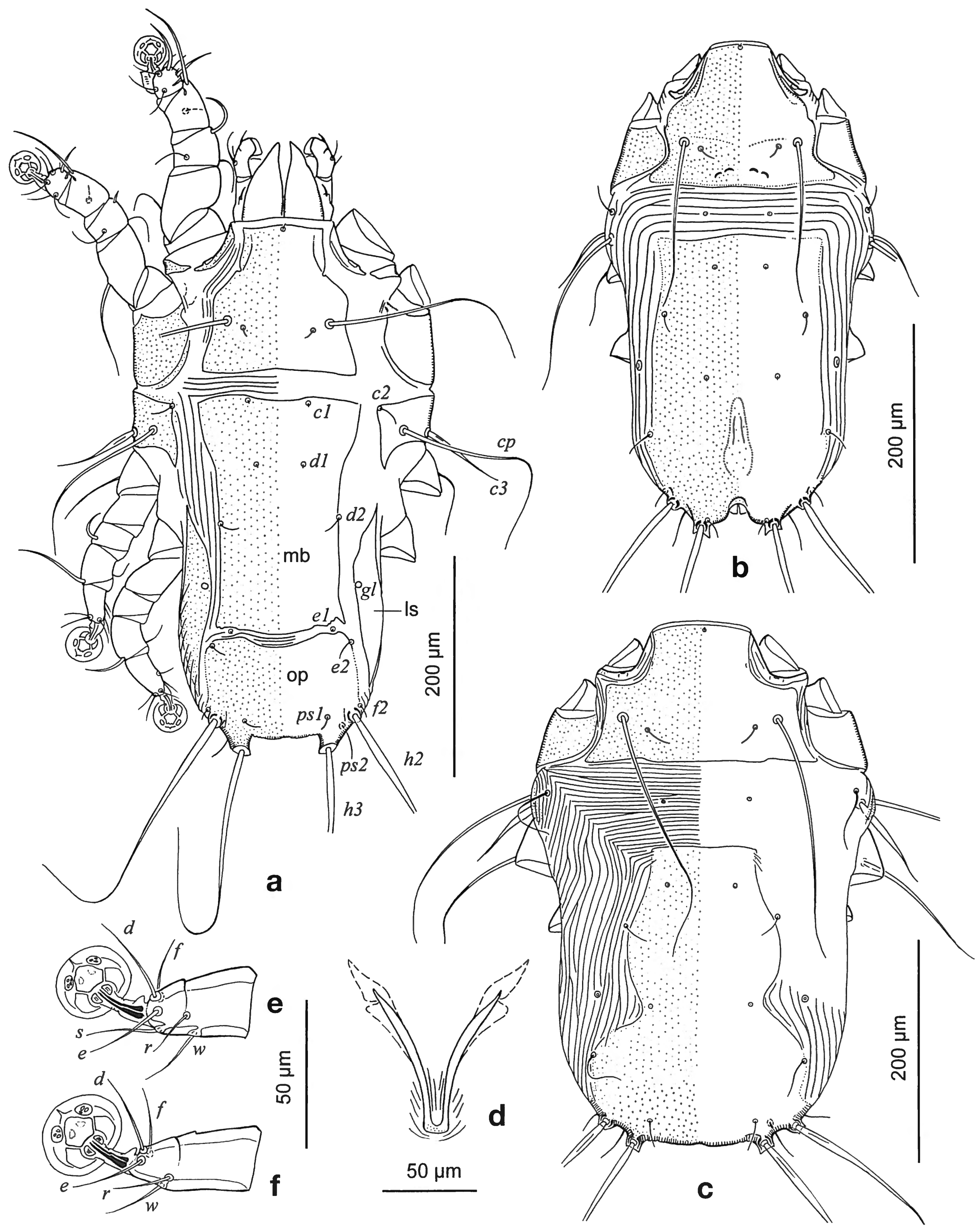


Figs. 27a-f — *Pteronyssoides oxylabis*, heteromorph male. **a**. Dorsal view. **b**. Ventral view. **c**. Dorsal view of opisthosomal lobe. **d**. Ventral view of opisthosoma. **e**. Tarsus III, dorsal view. **f**. Tibia and tarsus IV, dorsal view.



Figs. 28a-f — *Pteronyssoides* males. **a-c**. *Pteronyssoides latior*. **a**. Dorsal view. **b**. Dorsal view of opisthosomal lobe. **c**. Tarsus III, dorsal view. **d-f**. *P. timaliae*. **d**. Dorsal view. **e**. Dorsal view of opisthosoma. **f**. Tarsus III, dorsal view.

Figs. 29a-g — *Pteronyssoides* males. **a**. *Pteronyssoides latior,* ventral view. **b-e**. *P. oxylabis*, homeomorph male. **b**. Ventral view of hysterosoma. **c**. Dorsal view of opisthosoma. **d**. Tarsus I, dorsal view. **e**. Tarsus I, ventral view. **f-g**. *P. timaliae*. **f**. Ventral view of hysterosoma. **g**. Ventral view of opisthosoma.



Figs. 30a-f — *Pteronyssoides* females. **a**. *Pteronyssoides oxylabis*, dorsal view. **b**. *P. timaliae*, dorsal view of idiosoma. **c-f**. *P. latior*. **c**. Dorsal view of idiosoma. **d**. Epimerits I. **e**. Tarsus III dorsal view. **f**. Tarsus IV, dorsal view. ls – lateral sclerite, mb – main body of hysteronotal shield, op – opisthosomal sclerite.

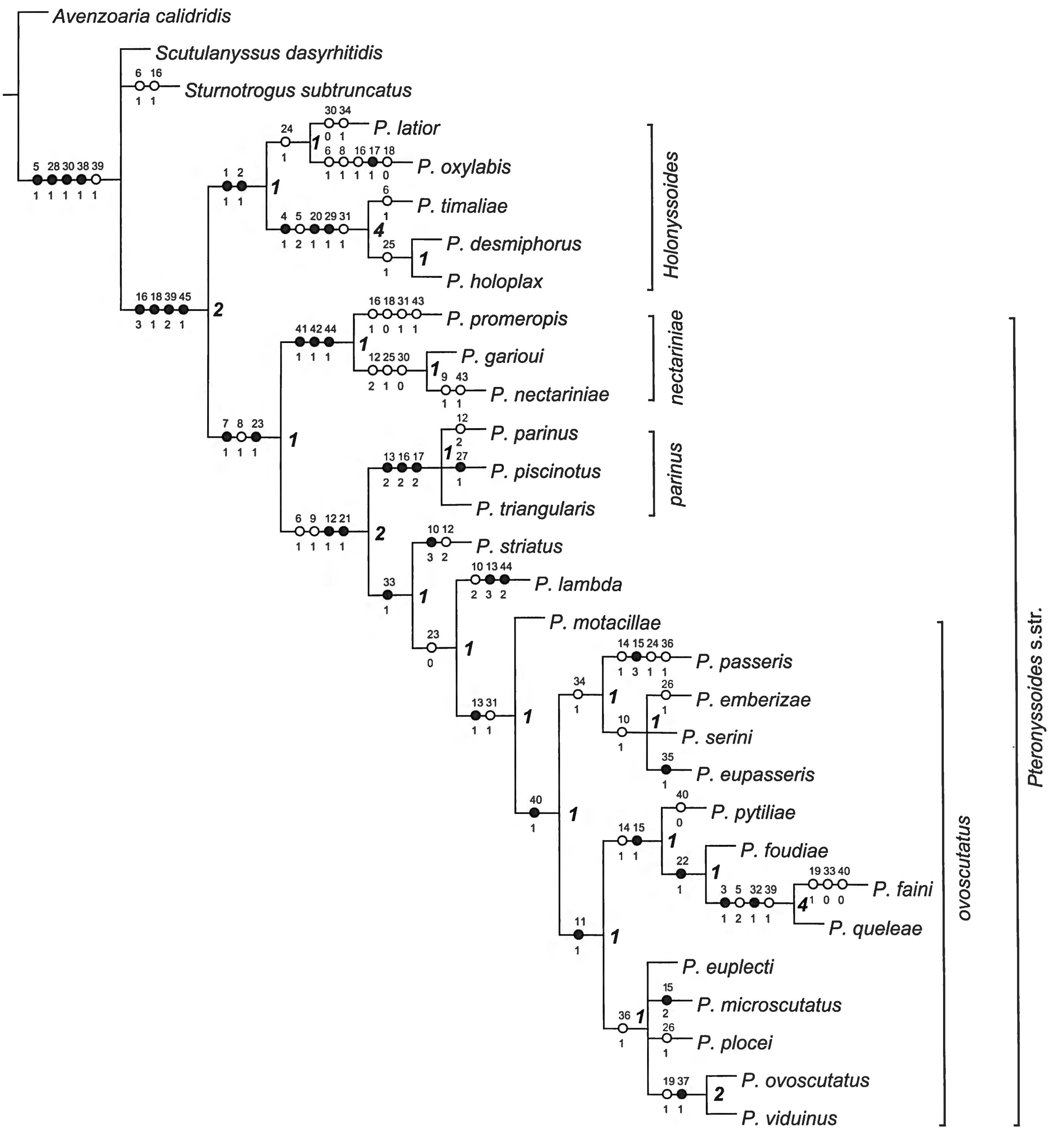


Fig. 31 — Phylogeny of *Pteronyssoides*. Strict consensus of six most parsimonious trees. DELTRAN character optimisation. Numbers above dots (black – unique apomorphy, white – homoplasy) refer to characters; numbers under dots refer to a character state achieved in the respective node. Numbers in bold Italics near nodes are Bremer indices.

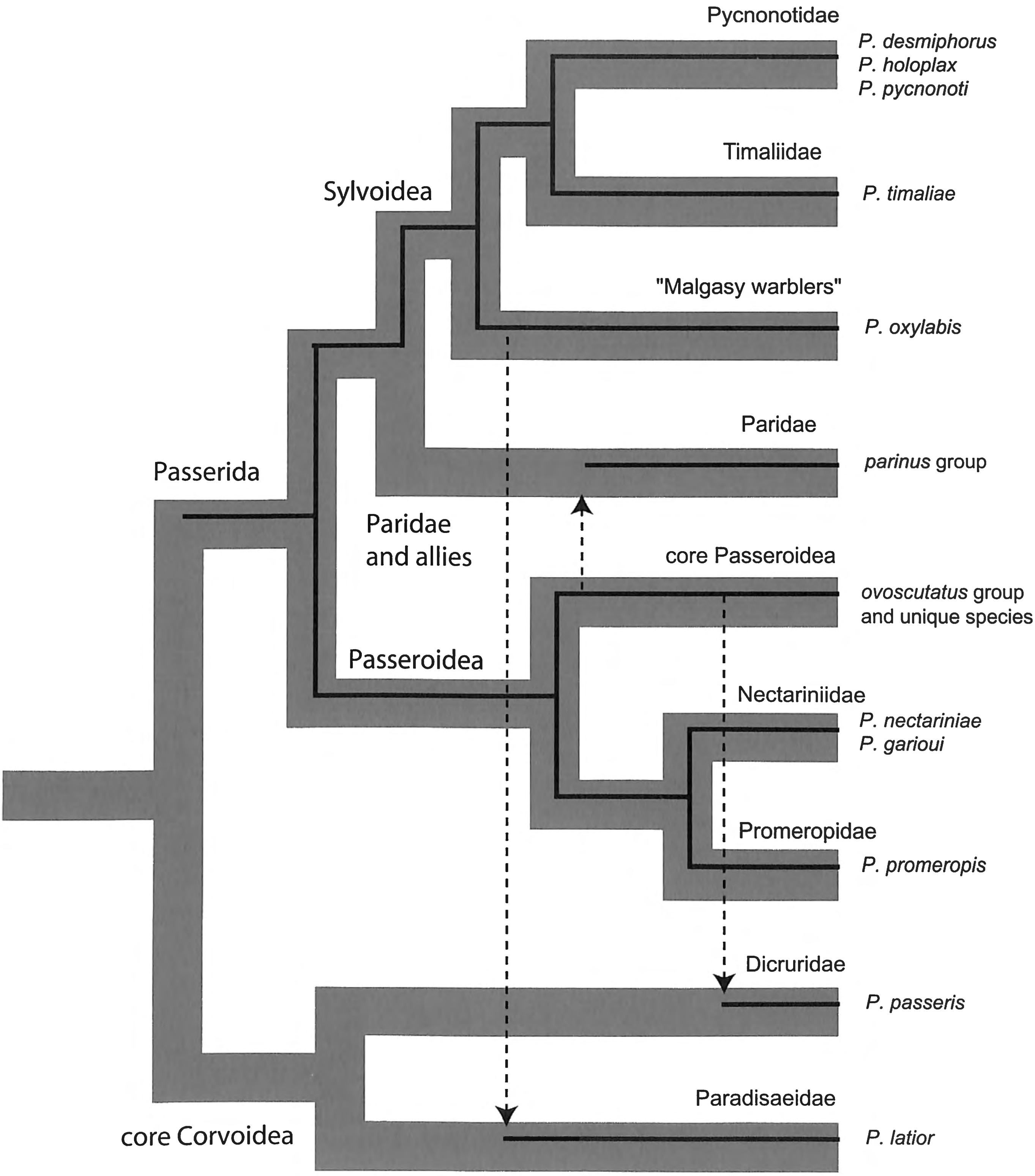


Fig. 32 — Hypothetical scheme of evolution of *Pteronyssoides* on passerines hosts. Phylogenetic hypothesis for passerines after BARKER *et al.* (2004) and BERESFORD *et al.* (2005); host lineages not bearing *Pteronyssoides* species are omitted; dashed lines with arrow are host shifting events.

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