SYSTEMATIC REVIEW AND PHYLOGENY OF THE
FEATHER MITE GENUS *METAPTERONYSSUS GAUD*,
1981 (ASTIGMATA: PTERONYSSIDAE) ASSOCIATED
WITH AFRICAN PASSERINES


A systematic review of the feather mite genus *Metapteronyssus* Gaud, 1981 is given, including an improved diagnosis of the genus, revised key to species, description of four new species from African passerines, cladistic analysis of the genus, and a brief discussion of associations with passerine hosts. The type species *Metapteronyssus glossifer* (Gaud, 1953) is redescribed based on the type material from *Euplectes franciscanus* (Isert, 1789) (Ploceidae); new species found in the course of study are described as follows: *Metapteronyssus amadinae* sp. n. from *Amadina fasciata alexanderi* Neumann, 1908 (Estrildidae), *M. anaplecti* sp. n. from *Anaplectes rubriceps* (Sundevall, 1850) (Ploceidae), *M. bordacei* sp. n. from *Euplectes bordaceus* Linnaeus, 1758 (Ploceidae), and *M. pseudonigritae* sp. n. from *Pseudonigrita cabanisi* (Fischer et Reichenov, 1884) (Passeridae). Brief diagnoses are provided for all formerly described species.

Maximum parsimony based on 34 morphological characters revealed three phylogenetic lineages treated as species groups: *angolensis*, *glossifer*, and *plocepasseri*. Two clear morphological tendencies realized independently in these lineages are traced. One tendency is a progressive reduction of the central hysteronotal sclerite in females; in most derived species of each lineage it is reduced to a thin rod-shaped sclerite or is completely lost. The other tendency is a narrowing of the opisthosomal terminus and development of terminal membranous lobules in males that is realized in each lineage in a different way.

Based on the phylogenetic relationships among mite species, their currently known distribution among passerines, and taking into consideration phylogenetic relationships between higher passerine host families, we hypothesize that the genus *Metapteronyssus* originated on the ancestors of the superfamily Passeroidea (parvorder Passerida). We suggest that owing to subsequent cospeciation, its representatives have been dispersed on estrildid finches (Estrildidae), weavers (Ploceidae), and sparrows (Passeridae), and apparently have gone extinct on other families of Passeroidea.

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Feather mites of the family Pteronyssidae Oudemans, 1941 (Astigmata: Analgoidea) currently include over 130 species in 22 genera (Faccini & Atyeo 1981, Gaud & Atyeo 1996, Mironov 2001, Mironov & Wauthy 2005a). Within this family, the genus Metapteronyssus Gaud, 1981 represents small-sized pteronyssid mites known from three families of passerine birds, Estrildidae, Passeridae, and Ploceidae. As for most pteronyssids, representatives of this genus inhabit the ventral surfaces of vanes of primary and secondary flight feather of their hosts.

This genus initially included a single species, Metapteronyssus glossifer (Gaud, 1953), described from Euplectes franciscanus (Isert, 1789) (Ploceidae) and also reported from several other ploceids and estrildid finches in Africa (Gaud 1953, Faccini & Atyeo 1981). Later, Mironov and Kojip (2000) described the second species, M. angolensis Mironov et Kojip, 2000, from the blue waxbill Uraeginthus angolensis (Linnaeus, 1758) (Estrildidae). Finally,
nine more new species were described from various African sparrows, weavers, and estrildid finches and a key to species was proposed for the first time by Mironov (2002).

In the course of our systematic study of feather mites associated with African passerines (Mironov & Wauthy 2005a-c) we have found four new species of Metapteronyssus and also re-examined type material of all formerly described species. Our examination of the type series of *M. glossifer* and additional material revealed that in the generic revision of pteronyssids (Faccini & Atyeo 1981) this species was redescribed incorrectly. These authors actually redescribed another species and gave incorrect data on host associations that has also led to inappropriate interpretation of *M. glossifer* in subsequent publications (Mironov & Kopij 2000, Mironov 2002).

The main goal of our paper is a taxonomic review and phylogenetic analysis of the genus *Metapteronyssus* based on morphological characters. The taxonomic part contains an improved diagnosis of the genus *Metapteronyssus*, a revised key to species, descriptions of four new species, redescription of the true type species, and brief diagnoses and taxonomic remarks for all formerly known species. We also briefly discuss known host associations of *Metapteronyssus* and, based on the phylogeny of this genus, provide a preliminary hypothesis for its evolution on passerines.

### Material and methods

**Specimens**

The main part of material used in the present study was received from the Musée royal de l’Afrique central (Tervuren, Belgium), other material was obtained from the Institut royal des Sciences naturelles de Belgique (Brussels, Belgium), National Museum of Bloemfontein (Free State, South Africa), and University of Georgia (Athens, USA).

Diagnoses for the genus and species 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 initially elaborated for the genus *Pteroherpus* Gaud, 1981.

For membranous structures of the opisthosoma in males of *Metapteronyssus* species we propose the following terms, based in part on terms used by previous authors. The entire membrane along all the posterior margin of the opisthosoma between bases of setae *ps2* (figs. 18a, b) is referred to as the ‘opisthosomal membrane’ following Faccini & Atyeo (1981). Two small lobe-like extensions with membranous margins developed on the posterior end of the opisthosoma between setae *h3* (figs. 1a, b, 2a, b) are referred to as ‘terminal lobules’. In some species the border between the membranous marginal part and scarcely sclerotized basal part of the lobules may be not clearly expressed. In any case, only the membranous part of these lobules is referred to as the ‘terminal membrane’.

Two small semicircular membranous extensions situated between the bases of setae *h2* and *h3* are referred to as ‘subterminal membranes’ (Mironov 2002) (fig. 2b). The anal area bearing anal discs and anal opening is flanked from lateral sides by a pair of the adanal membranes.

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.

Specimen depositories and reference accession numbers are given using the following abbreviations: AMNH – American Museum of Natural History, New York, USA; IRSNB – uncatalogued collection of Prof. A. Fain, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MRAC – Musée royal de l’Afrique central, Tervuren, Belgium; NMB – National Museum of Bloemfontein, Free State, South Africa; UGA – University of Georgia, Athens, USA; USNM – US National Museum of Natural History, Beltsville, Maryland, 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 indicated; the second is a collection number of the respective host specimen. In those cases where the recent country name differs from that given in the slide-mounted specimen, location data also point out the original country name, as written on the slide label; the abbreviation ‘coll.’ means ‘collector’. Taxonomy and scientific names of birds follow Dickinson (2003), passerine phylogeny used in the discussion of host associations follows recent conceptions based on molecular studies (Sorenson & Payne 2001, Ericson & Johanson 2003, Barker et al. 2004).

**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). Two autapomorphic characters (unique features of hysteronotal shield in females of *M. gaudi* Mironov, 2002 and *M. puylaerti* Mironov, 2002) were included to stress peculiarity of these species and also taking into consideration that
these features may potentially represent characteristics for species groupings, which could be recognised in future investigations of diversity.

Representatives of three closely related pteronyssid genera also associated with passerine hosts, *Scutulanysys das yrithidis* (Gaud & Atyeo, 1981) from *Patlodeslura fuliginosa* Shelley, 1887 (Hirundinidae), *Sturnotractorus subtruncatus* (Trouessart, 1885) from *Gracula religiosa* Linnaeus, 1758 (Sturnidae), and *Pteronyssoides* (Holonyssoides) holoplax (Gaud et Mouzil, 1959) from *Pycnonotus barbatus* (Desfontaines, 1789) (Pycnonotidae) were used as outgroups to test monophyly of the genus *Metapteronyssus*.

In total, 18 taxa and 34 characters, two of which represent autapomorphies in outgroups and one in the ingroup (*Metapteronyssus* spp.), 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). Constructing and editing of tree were accomplished with Winclada, version 1.0 (Nixon 1999).

**Systematics**

**Family Pteronyssidae** Oudemans, 1941

**Genus Metapteronyssus** Gaud, 1981


**Diagnosis**

Both sexes. – Epimerites I fused as a narrow U, connection of posterior tips may be very thin. Unpaired vertical seta *vi* absent. Prodorsal shield occupies antero-median part of pronotum, not developed posterior to scapular setae, postero-lateral extensions present or absent, setae *se* on these extension or on striated tegument. Setae *c2* setiform, short. Setae *c3* commonly lanceolate. Setae *dp2* of palpae simple, hair-like. Setae *ba* of tarsi I, II as small spine, rarely absent (*M. amadinae, M. pseudonigratae*). Solenidion *α1* of genu I longer than *α1* on tarsus I; solenidion *α2* of genu I absent. Ventral membrane of tarsus I about ½ length of the segment. Coxal fields I, II with striated tegument.

Male. – Opisthosomal lobes not expressed, opisthosa gradually attenuate to posterior end (figs. 1a, 4a, 18a), or with strongly convex postero-lateral margins (*placepasseri group*) (figs. 13a, 15a, b). Most posterior end of opisthosoma between setae *h3* with a pair of small tongue-like membranous extensions (terminal lobules), with or without subterminal membranes between setae *h2* and *h3* (figs. 2a, 13a), or posterior end of opisthosoma bluntly rounded and bears entire opisthosomal membrane between bases of setae *ps2* (some species of the angolensis group) (figs. 18a, b, e). Terminal incision between terminal lobules small, usually slit-like. Supranal concavity long and narrow, with well-sclerotized margins, open postero-riorly. Setae *c2* on inner margin of humeral shields. Setae *ps1* anterior to setae *h3*. Hysteronotal shield free from humeral shields, with pair of bow-shaped heavily sclerotized ridges, anterior ends of which reach antero-lateral angles of the shield, and with median sclerotized ridge extending anterior from supranal concavity (fig. 1a). Hysteronotal gland openings *gl* in posterolateral incisions of hysteronotal shield. Coxal fields III closed. Transventral sclerite present, anterior margin concave, tips of epandrium short or scarcely expressed. Anal discs circular. Adanal shield T-shaped, or split into three separate pieces, or represented only by median or transverse fragment (figs. 2a, 9d, 11a, 13a). Adanal membranes present. Setae *h3* setiform, long. Cupules *ih* indistinct. Tarsus III straight or with slightly curved apical part, with bidentate apical process; seta *r* shorter or subequal in length to tarsus III. Tarsus IV without dorosobasal tooth.

Female. – Idiosoma moderately elongated. Arrangement of hysteronotal shield fragments commonly consists of large central sclerite of ovate or bar-shaped form occupying median part of hysterosoma, pair of lateral sclerites, and pair of small pygidial sclerites (fig. 3a); rarely central sclerite lost (*M. anoplonotus*) (fig. 12b). Hysteronotal gland openings *gl* on anterior end or antero-lateral margin of lateral sclerites. Posterior margin of opisthosoma may have small lobe-like extensions bearing setae *h3*. External copulatory tube usually present, commonly cone-shaped, occupies terminal position (figs. 3a, b, 6a-c); the tube absent in *M. placepasseri* (fig. 14b). Epignyum semicircular or bow-shaped, thick; sclerotized folds of oviporus short, not extending beyond epimerites IIIa (fig. 3b).

The genus currently includes 15 species arranged into three species groups (*angolensis, glossifer, and placepasseri*).
Key to *Metapteronyssus* species

**Males**

1. Posterior margin of opisthosaoma with slightly convex opisthosomal membrane between setae ps2 (fig. 18d) ................................................................. *M. longichurae*
   - Posterior margin of opisthosaoma with a pair of small lobules between setae h3 or with large bilobate membrane between setae ps2 (figs. 2a, 15a, 16a, 18a) ................................................................. 2

2. Posterior margin of opisthosaoma with large bilobate membrane between setae ps2 (figs. 18a, b) ................................................................. *M. angolensis*
   - Posterior margin of opisthosaoma with a pair of small lobules between setae h3, margins of these lobules membranous (figs. 2a, 15a, 16a) ............... 3

3. Opisthosaoma lobules finger-shaped, 2.5-3 times longer than wide (figs. 16a, b) ................................................................. *M. amadiniae* sp.n.
   - Opisthosomal lobules short, tongue-like, approximately as long as wide (figs. 2b, 4b, 15b) ............. 4

4. Postero-lateral margins of opisthosoma strongly convex (figs. 11d, 13a, d) ................................................................. 5
   - Opisthosoma moderately or strongly attenuate posteriorly (figs. 2a, 4a) ................................................................. 8

5. Adanal shield T-shaped or cross-like (fig. 13d). Genital setae g at base of genital apparatus or posterior to it ................................................................. 6
   - Adanal shield as transverse band with very thin median part (fig. 13a). Genital setae g approximately at midlevel of genital apparatus .............. 7

6. Setae s and f of tarsus III setiform. Tips of epiandrium short blunter-angular. Seta ba of tarsi I, II present. Subapical membranes between setae ps2 and h2 absent (figs. 13d-f) ............ *M. plocepaseveri*
   - Setae s and f of tarsus III with lanceolate apical part. Tips of epiandrium acute. Seta ba of tarsi I, II absent. Subapical membrane between setae h2 and h3 present (figs. 15a-e) ................................................................. *M. pseudonigrattae* sp. n.

7. Length of idiosoma 295-340. Anterior end of supranal concavity extends to the level of setae p3. Setae c3 18-20 in length (figs. 11d-f) ................................................................. *M. anoplonotus*
   - Length of idiosoma more than 350. Anterior end of supranal concavity not extending to the level of setae p3. Setae c3 longer than 20 (figs. 13a-c) ............ *M. dabeti*

8. Adanal shield cross-like or T-shaped. Setae 3a situated on transversal sclerite. Tarsus III with straight apex. Posterior margin of opisthosoma between setae h2 blunt (figs. 2a, b, f) ............. 9
   - Adanal shield split into median and pair of lateral fragments, or represented only by single median sclerite. Setae 3a situated posterior to transversal sclerite. Apex of tarsus III curved. Posterior margin of opisthosoma between setae h2 noticeably convex (figs. 4a, b, e) ................................................................. 11

9. Epiandrium tips extending to level of genital arch apex (fig. 5a). Setae e1 slightly posterior to openings gl. Length of idiosoma more than 340 .................. *M. babalornis*
   - Epiandrium tips short, not extending to level of genital arch apex (figs. 2a, 7b). Setae e1 anterior to openings gl. Length of idiosoma less than 300 ................................................................. 10

10. Setae c3 lanceolate, 24-27 in length (fig. 2c) .................. *M. glossifer*
   - Setae c3 with setiform apex, 32-35 in length (fig. 7c) .................. *M. hordacei* sp.n.

11. Prodorsal shield with rounded posterior end, without extending posterior angles, scapular setae si, se on striated tegument. Adanal shield represented by single median sclerite (fig. 9d) .................. *M. plocei*
   - Prodorsal shield with extending posterior angles encompassing bases of scapular setae si, se. Adanal shield consisting of three fragments (figs. 4a, 5d) ................................................................. *M. capensis*

12. Transversal sclerite thin, about 4-6 along midline of the mite body, tips of epiandrium scarcely expressed (fig. 5d). Length of idiosoma 330-360 .................. *M. gaudi*
   - Transversal sclerite about 8-10 along midline, with short epiandrium tips on posterior margin (figs. 4a, 9a, 11a). Length of idiosoma less than 330 .............. 13

13. Genital arch 22-26 in length. Lateral fragments of adanal shield with acute posterior ends, almost extending to adanal membranes (fig. 11a) .............. *M. puylaerti*
   - Genital arch 16-18 in length. Lateral fragments of adanal shield of irregular form, not extending to anterior end of adanal membranes .......... 14

14. Setae c3 narrowly lanceolate, about 24-26 in length (fig. 9b) .......... *M. gaudi*
   - Setae c3 with setiform apical part, over 30 in length (fig. 4c) .......... *M. anaplecti* sp. n.

**Females**

1. Central hysterontal sclerite absent (fig. 12b) .................. *M. anoplonotus* sp. n.
   - Central hysterontal sclerite present, represented by one or two pieces (figs. 3a, 6a-c, 12a) ............. 2

2. Central hysterontal sclerite fused with pygidial sclerites forming a fish-shaped shield (fig. 10a) .................. *M. gaudi* sp. n.
   - Central hysterontal sclerites separated from pygidial sclerites (figs. 3a, 8a, b, 10b) ............. 3

3. Central hysterontal sclerite as longitudinal oval. Lateral sclerites as narrow longitudinal bands (figs. 14a, b) ............. 4
Central hysteronotal sclerite represented by entire median band greatly variable in width (figs. 3a, 8b, 17a) or split into anterior and posterior fragments (figs. 6b, 12a). Lateral sclerites of another form .......................................................... 5

4. Posterior margin of opisthosoma with extending terminal region bearing two short lobes. External copulatory tube present, finger-shaped. Small additional sclerites of ovate form near bases of setae d2 present (fig. 14a) .................. M. daberti

– Posterior margin of opisthosoma bluntly rounded, without terminal extension and lobes. External copulatory tube absent. Additional sclerites near lateral margins of central sclerites absent (fig. 14b) .................. M. plocepaseri

5. Anterior end of central hysteronotal sclerite extending to the level of setae c2; its width more than one third of greatest idiosoma width. Lateral sclerites ovate or kidney-shaped (fig. 17a) ... .................................................. M. pseudonigritae sp. n.

– Central hysteronotal sclerite (or its anterior fragment, if this sclerite is split into pieces) not extending to the level of setae c2; width of its anterior end less than one third of idiosoma width. Lateral sclerites as longitudinal plate of irregular form (figs. 3a, 6a, b, 8a, b) .................. 6

6. Central hysteronotal sclerite entire, represented by entire longitudinal sclerite, anterior end of which extends to the level of trochanters III (figs. 3a, 5a, 6c, 8a) .................. 7

– Central hysteronotal sclerite split into anterior and posterior fragments separated by large area of striated tegument (figs. 6b, 12a), or only posterior fragment is developed in posterior third of hysterosoma (fig. 6a) .................. 14

7. External copulatory tube as short apically rounded cone or cylinder, 5-10 in length (figs. 6c, 17b) .................. 8

– External copulatory tube elongated, cone- or finger-shaped, 12-45 in length (figs. 8a, b) ... 11

8. Central hysteronotal sclerite almost parallel sided, its posterior end with narrow and deep incision (figs. 6c, 17b) .................. 9

– Central hysteronotal sclerite strongly narrowed to posterior end, without incision in posterior end (figs. 19a, b) .................. 10

9. Posterior margin of prodorsal shield rounded. Setae e1 mesal from margins of central sclerite (fig. 17b). Seta ba of tarsi I, II absent. Length of idiosoma less than 400 .... M. amadinae sp.n.

– Posterior margin of prodorsal shield as short blunt angle. Setae e1 on lateral margins of central sclerite (fig. 6c). Seta ba of tarsi I, II present. Length of idiosoma 420-460 .... M. bubalornis

10. Width of anterior end of central sclerite 45-50. External copulatory tube button-like, hemispherical (fig. 19b) .................. M. lonchurae

– Width of anterior end of central sclerite 25-30. External copulatory tube is a short cone (fig. 19a) .................. M. angolensis

11. Anterior end of central hysteronotal shield not reaching setae d1, these setae situated on striated tegument (fig. 8a). External copulatory tube finger-like, 34-42 in length .................. M. capensis

– Anterior end of central hysteronotal shield encompassing bases of setae d1 (fig. 9b). External copulatory tube conical, shorter than 25 .... 12

12. Central hysteronotal sclerite almost rod-shaped, width of anterior end 14-20; setae e1 commonly off this sclerite (fig. 8b) .................. M. hordacei sp.n.

– Central hysteronotal sclerite as longitudinal bar, width of anterior end over 30; setae e1 on margin of this sclerite (figs. 3a, 10b) .................. 13

13. Posterior margin of prodorsal shield extending beyond the level of scapular setae; anterior end of central hysteronotal sclerite extending beyond the level of setae d1. Setae e1 approximately at the level of openings gl (fig. 3a) .................. M. glossifer

– Posterior margin of prodorsal shield not extending beyond the level of scapular setae; anterior end of central sclerite not extending beyond the level of setae d1. Setae e1 anterior to the level of openings gl (fig. 10b) .................. M. plocei

14. Central hysteronotal shield represented by two pieces, anterior and posterior fragments (fig. 11a) .................. 15

– Central hysteronotal sclerite represented by single fragment in posterior third of hysterosoma (fig. 6a) .................. M. anaplecti sp.n. (part)

15. Anterior fragment of central hysteronotal sclerite roughly rectangular. Sclerotization around setae se, si poorly developed (fig. 6b) .................. M. anaplecti sp.n. (part)

– Anterior fragment of hysteronotal sclerite as irregular polygon. Posterior angles of prodorsal shield encompassing bases of setae se, si well sclerotized (fig. 11a) .................. M. pulyaerti

Group glossifer

Diagnosis

Male. – Opisthosoma monotonously attenuate to posterior end, its margin between setae p2 blunt or convex (figs. 2a, 4a); posterior margin of part between setae h3 with pair of small terminal lobules having membranous margins; opisthosomal margins between bases of setae h3 and h2 with small subterminal membranes. Adanal shield varies in form from being T-shaped, split into 3 pieces (median and a pair of lateral fragments), or represented by median fragment only. Tarsi III curved or straight.

Female. – Central sclerite commonly represented
by entire median longitudinal band, width of which is less than one third of idiosoma width (figs. 3a, 8a, b); rarely (M. anaplecti, M. puylaerti) central sclerite split into anterior and posterior fragments (figs. 6b, 12a). Lateral shields as longitudinal plate of various shape, commonly with narrowed or acute posterior end.

1. *Metapteronyssus glossifer* (Gaud) (figs. 1a, b, 2a-g, 3a, b)

*Pteronyssus* glossifer Gaud, 1953: 220, fig. 11.


*Metapteronyssus glossifer*: Faccini & Atyeo 1981: 36 (part.); Mironov, 2002: 197 (part.)

Material examined. – CENTRAL AFRICAN REPUBLIC: male lectotype (here designated), 5 male and 1 female paralectotypes ex *Euplectes franciscanus* (Lcrt, 1789) (Ploceidae), Bougouni, October 1950, coll. unknown (MRAC 179 994); 9 male and 1 female paralectotypes, same data (MRAC 179 991).

**Diagnosis**

Setae *ha* of tarsi I, II present (figs. 2d, e). In males, opisthosoma with blunt posterior end, setae *ps2* lateral to setae *h2,* terminal lobules tongue-like, terminal...
membranes poorly sclerotized, not clearly demarked from basal part of lobules; adanal shield T-shaped; transventral sclerite narrow, with slightly expressed epiandrium tips, setae c3 narrowly lanceolate in form, relatively short, 24-27 in length; tarsus III with curved apex (figs. 2a-c, f). In females, central sclerite as longitudinal band extending to the level of trochanters III, greatest width 30-40, posterior end with deep and narrow incision; setae dI, eI on central sclerite; external copulatory tube cone-shaped, short, 15-18 long (figs. 3a, b).

**Description**

Male (lectotype). – Idiosoma length × width 310 × 177 (idiosomal size in 14 paralectotypes 290-315 × 165-180). Length of hysterosoma 172. Prodorsal shield: size 78 × 56, without posterolateral extension, setae se separated by 67. Setae c3 narrowly lanceolate, 24 in length. Hysteronotal shield: anterior margin slightly convex in median part, anterior angles greatly extended laterally, length along midline 158, width at anterior margin 120. Distance between prodorsal and hysteronotal shield along midline
Mironov & Wauthy: Metapteronyssus from African pas


Female (paralectotype). – Idiosoma length×width 383×182 (in other paratype 380×185). Length of hysterosoma 248. Prodorsal shield as in the male, 84×60, setae *se* separated by 73. Setae *c3* narrowly lanceolate, 20 in length. Arrangement of hysteronotal shields: central sclerite, a pair of lateral sclerites and pair of pygidial sclerites. Central sclerite as longitudinal bar (fig. 3a) extending by anterior end to the level of trochanters III, length 176, greatest width

Fig. 3. *Metapteronyssus glossifer*, female. – a, dorsal view; b, ventral view. ct - external copulatory tube, cs - central sclerite, ls - lateral sclerite, py - pygidial sclerite.

Remarks

According to the original description by Gaud (1953), this species was recorded from Euplectes franciscanus (type host), E. hordaceus Linnaeus, 1758, Ploceus cucullatus (Statius Müller, 1776) (Ploceidae), and Uraeginthus bengalus (Linnaeus, 1776) (Estrildidae). This wide host range suggests that the author apparently dealt with a complex of closely related species. Although original drawings (Gaud 1953: fig. 11) are slightly schematic, they correspond well to the specimens from the type host, from which we select a lectotype here to firmly establish its identity. In the generic revisions of pteronyssids, Faccini and Atyeo (1981) pointed out that they re-examined only the material of Gaud from both Euplectes species. Nevertheless, these authors apparently used material from other hosts as well, because the drawings of ‘Metapteronyssus glossifer’ given in the revision (Faccini & Atyeo 1981: figs. 17-20), correspond neither to the specimens from the type host, E. franciscanus, nor to ones from E. hordaceus (specimens from the latter host we consider a new species and describe below). Based on several clearly visible features in the figures given by Faccini and Atyeo, namely, the shape of prodorsal shield in both sexes, structure of terminal membrane in the male, and the shape of hysteronotal sclerites and length of external copulatory tube in the female, we suggest that these authors used for drawing the specimens from U. bengalus, i.e. they actually figured M. angolensis (see below, angolensis species group).
2. *Metapteronyssus anaplecti* sp. n.
(figs. 4a-c, 6a, b)

Type material. – RWANDA: male holotype and 4 male, 11 female paratypes ex *Anaplectes rubriceps* (Sundevall, 1850) (Ploceidae), Akanyaru, 28 October 1955, A. Fain (IRSNB).

Diagnosis

Setae *ba* of tarsi I, II present. In males, opisthosoma with extending convex posterior end, setae *ps2* anterior to setae *h2*; terminal lobules short, terminal membranes semicircular, clearly demarked from lobules; adanal shield split into median and pair of lateral fragments; transventral sclerite narrow, with slightly

Fig. 5. *Metapteronyssus* males. – a, *Metapteronyssus bubalornis*, ventral view of hysterosoma; b, setae *c3*; c, tarsus III, dorsal view; d, *M. capensis*, ventral view of hysterosoma; e, setae *c3*; f, tarsus III, dorsal view.

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expressed epiandrium tips, setae 3a off transventral sclerite; setae e3 narrowly lanceolate in basal part, with setiform apex, 33-38 in length; tarsus III with curved apex (figs. 4a-e). In females, central sclerite represented either by two fragments (anterior fragment of square form at the level of trochanters III and posterior one in posterior part of opisthosoma) or only by the posterior fragment, greatest width of the posterior fragment 35-45, its posterior end with short incision; setae d1 on anterior fragment (if it is present), setae e1 on posterior fragment; external copulatory tube cone-shaped, long, 28-32 in length (figs. 6a, e).

Descriptive Details

Male (holotype). – Idiosoma length × width 305 × 177 (in 4 paratypes 300-310 × 160-190). Length of hysterosoma 172. Prodorsal shield: without
posterior extensions (in some specimens they are poorly expressed), size of proper shield $64 \times 45$, setae se separated by 54. Setae c3 lanceolated enlarged in basal part, 37 in length. Hysteronotal shield: anterior margin slightly convex in median part, anterior angles acute, greatly extended, size $164 \times 127$. Distance between prodorsal and hysteronotal shields about 65. Opisthosoma with convex posterior end, setae ps2 anterior to setae h2. Most terminal part of opisthosoma between setae h3 with pair of small terminal lobules; terminal membranes semicircular, clearly demarked from lobules; margins of opisthosoma between setae h2 and h3 with subterminal membranes. Dorsal measurements: $c2:d2$ 49, $d2:e2$ 75, $d2:gl$ 35, $g:el$ 112, $c2:h3$ 36, $e2:e2$ 49, $h2:h2$ 33. Transvентрal sclerite 5 in length; tips of epiandrium short, not extending to genital apparatus apex; genital arch $16 \times 11$; setae g slightly posterior to genital arch base. Adanal shield consisting of 3 fragments: median fragment and pair of small lateral fragments of irregular form. Diameter of anal discs 10. Ventral measurements: ps2: ps2 40, ps3:ps3 22, ps3:h3 43. Setae ba of tarsi I, II small spiniform. Tarsus III in length, with curved apex; tarsal setae f, w setiform, seta s slightly thickened in basal part; seta r shorter than segment.

Female (paratype). – Idiosoma length × width $384 \times 197$ (in other 10 paratypes $385-405 \times 195-215$). Length of hysterosoma 252. Prodorsal shield as in the male, 77 × 56, setae se separated by 67. Setae c3 narrowly lanceolate, 30 in length. Arrangement of hysteronotal shields: central sclerite, pair of opisthosomal sclerites and pair of pygidial sclerites. Central sclerite as narrow longitudinal bar in posterior half of hysterosoma (fig. 6a), length 78, greatest with 38 (in all other paratypes 75-80 × 35-42; in 3 paratypes, central sclerite represented also by additional anterior fragment of approximately square form, 52-55 × 56-60, situated at level of trochanters III, IV, – fig. 6b). Lateral sclerites as longitudinal plates slightly attenuated to posterior end, which is curved to ventral side of the body 64-66 in length; openings gl in anterior end. Pygidial sclerites small triangular, encompassing bases of setae h2, h3, ps1. Setae d1 on lateral margins of central sclerite; setae d2, e1, e2 on striated tegument (setae d1 in anterior fragment of central sclerite, when present); setae e1 slightly anterior to level of openings gl. External copulatory tube a cone-shaped process slightly curved downward, 30 in length, 20 in width at base. Dorsal measurements: $c2:d2$ 83, $d2:e2$ 113, $d2:gl$ 73, $e1:gl$ 14-17, $e2:h3$ 45, $e2:e2$ 57, $h2:h2$ 80, $h3:h3$ 70. Epigynium bow-shaped, 29 × 78.

Etymology
The specific epithet derives from the generic name of the type host and is a noun in the genitive case.

3. *Metapteronyssus bubalornis* Mironov (figs 5a-c, 6c)


Material examined. – CAMEROON: male holotype and 2 female paratypes ex *Bubalornis albirostris* (Veilliot, 1817) (Ploceidae), Maroua, 1949, coll. unknown (MRAC 180601); 2 male, 4 female paratypes, same data (MRAC 180602–180604).

Diagnosis
Setae ba of tarsi I, II present. In males, opisthosoma with blunt posterior end; setae ps2 lateral to setae h2; terminal lobules tongue-like, terminal membranes short, poorly sclerotized, not clearly demarked from lobules; adanal shield T-shaped; transvентрal sclerite wide, with short epiandrium tips not extending to genital arch apex, setae 3a on transvентрal sclerite; setae c3 narrowly lanceolate, with thin apex, 27-30 in length; tarsus III with straight apex (figs. 5a-c). In females, central sclerite as longitudinal bar extending to level of trochanters III, greatest width 25-32, its posterior end with long narrow incision, setae d1, e1 on margins of central sclerite; external copulatory tube button-shaped, short, about 7 in length (fig. 6c).

Remarks
This species is known only from the white-billed buffalo weaver *Bubalornis albirostris*.

4. *Metapteronyssus capensis* Mironov (figs. 5d-f, 8a)

*Metapteronyssus capensis* Mironov, 2002: 187, fig. 16.

Material examined. – SOUTH AFRICA: male holotype and 1 male, 5 female paratypes ex *Ploceus capensis* (Linnaeus, 1766) (Ploceidae), Cape Province, East London, October 1966, coll. unknown (MRAC 180635); 3 males, 7 female paratypes, same data (MRAC 180618).

Diagnosis
Setae ba of tarsi I, II present. In males, opisthosoma with convex posterior end, setae ps2 anterior to setae h2; terminal lobules short, terminal membranes semicircular, clearly demarked from lobules; adanal shield split into median sclerite and pair of lateral fragments; transvентрal sclerite narrow, without epiandrium tips; setae 3a off transvентрal sclerite; setae c3 narrowly lanceolate, 30-32 in length; tarsus III with curved apex (figs. 5d-f). In females, central sclerite as longitudinal bar extending to level of trochanters IV, greatest width 30-35, its posterior end with long narrow incision, setae e1 on margins of central sclerite, d2 off this
sclerite; external copulatory tube cone-shaped, long, 34-42 in length (fig. 8a).

Remarks
This species is known only from the type host, cape weaver *Ploceus capensis*, in South Africa (table 3).

5. *Metapteronyssus gaudi* Mironov
(figs. 9a-c, 10a)

*Metapteronyssus gaudi* Mironov, 2002: 185, fig. 8, 10.

Material examined. – NIGERIA: Male holotype and 1 female paratype ex *Ploceus aurantiacus aurantiacus* (Vieillot, 1805) (Ploceidae), S. Nigeria, Degema, 14 January 1902, W.J. Ansorge (MRAC 180 639). – CAMEROON: 2 males, 2 females ex *P. bicolor amaurocephalus* (Vieillot, 1819), S. Cameroon, November 1955, coll. unknown (MRAC 180 631, 180 632); 2 males, same host, Yaoundé, July 1955, coll. unknown (MRAC 180 633); 2 males, 2 females ex *P. nigricollis brachypterus* (Swainson, 1834), S. Cameroon, August 1955, coll. unknown (MRAC 180 630).

Diagnosis
Setae *ba* of tarsi I, II present. In males, opisthosoma with convex posterior end, setae *ps2* anterior to setae *h2*, terminal lobules short, terminal membranes semicircular, clearly demarked from lobules; adanal shield split into median sclerite and pair of lateral fragments; transventral sclerite narrow, with short epiandrium tips; setae *3a* off transventral sclerite; setae *c3* narrowly lanceolate, 24-26 in length; tarsus III with curved apex (figs. 9a-c). In females, central sclerite fused with pygidial shields forming fish-shaped shield, anterior end of this shield extending to level of trochanters III, greatest width 55-60, setae *d1, e1* on central sclerite, external copulatory tube cone-shaped, long, 28-30 in length (fig. 10a).

Remarks
*Metapteronyssus gaudi* is known from four species of weavers of the genus *Ploceus* Cuvier, 1816 in west and north of Sub-Saharan Africa (table 3). This species differs from all species of the genus *Metapteronyssus* by the unique shape of the central sclerite in females (fig. 10a).

Fig. 7. *Metapteronyssus hordacei*, male. – a, ventral view of hysterosoma; b, dorsal view of opisthosoma; c, setae *c3*; d, tarsus III, dorsal view.
6. *Metapteronyssus hordacei* sp. n.  
(figs. 7a-c, 8b)

Type material. – CENTRAL AFRICAN REPUBLIC: male holotype and 2 male, 3 female paratypes *ex* *Euplectes hordaceus* (Linnaeus, 1758) (Ploceidae), Bossangoa, July 1951, coll. unknown (MRAC 179 896); 3 male, 4 female paratypes, same data (MRAC 179 996). Holotype and all paratypes – MRAC.

Diagnosis

Setae *bs* of tarsi I, II present. In males, opisthosoma with blunt posterior end, setae *ps2* lateral to setae *h2*, terminal lobules tongue-like, terminal membrane not clearly demarked from lobules; adanal shield T-shaped; transventral sclerite narrow, with short epiandrium tips; setae *3a* off transventral sclerite; setae *c3* setiform, slightly thickened in basal part, 32-35 in length; tarsus III with curved apex (figs. 7a-c). In females, central sclerite as very narrow median bar extending to the level of trochanters III, greatest width 14-18; setae *d1, e1* on central sclerite; external copulatory tube cone-shaped, short, 13-15 in length (fig. 8b).

Description.

Male (holotype). – Idiosoma length × width 294 × 164 (in 5 paratypes 270-295 × 144-158). Length of hysterosoma 179. Prodorsal shield: size 70 × 49, without posterolateral extensions, setae *se* separated by 56. Setae *c3* setiform, slightly thickened in basal part, 33 in length, 1.5 in width.
Hysteronotal shield: anterior margin slightly convex in median part, anterior angles extended, relatively short, size $162 \times 95$. Distance between prodorsal and hysteronotal shields about 70. Opisthosoma with blunt posterior end, setae $ps_2$ lateral to setae $h_2$. Terminal lobules small tongue-like, terminal membrane not clearly demarked from lobules, length of incision between membranes 8. Margins of opisthosoma between setae $h_2$ and $h_3$ with short subterminal membranes. Dorsal measurements: $c_2:d_2 \ 50$, $d_2: e_2 \ 62$, $d_2:gl \ 35$, $e_1:gl \ 3-9$, $e_2:h_3 \ 45$, $e_2:e_2 \ 49$, $h_2:h_2 \ 30$. Transventral sclerite narrow, 6 along midline; tips of epiandrium short, not extending to genital apparatus apex; genital arch $16 \times 9$; setae $g$ at base of genital apparatus. Adanal shield T-shaped, with very weakly sclerotized lateral parts. Diameter of anal discs 11. Ventral measurements: $ps_2:ps_2 \ 40$, $ps_3:ps_3 \ 35$, $ps_3: h_3 \ 38$. Setae $ba$ of tarsi I, II small spiniform. Tarsus III 38 in length, with straight apex; tarsal setae $f$, $w$ setiform, setae $s$ slightly thickened in basal part; setae $r$ longer than segment.

Female (paratype). – Idiosoma length $\times$ width $366 \times 164$ (in 6 paratypes $355-375 \times 150-175$). Length of hysterosoma 250. Prodorsal shield as in
the male, 76×53, setae se separated by 65. Setae c3 narrowly lanceolate, 24 in length. Arrangement of hysteronotal shields: central sclerite, and pair of opisthosomal sclerites and pair of pygidial sclerites. Central sclerite as very narrow median sclerite (fig. 8b) extending by anterior end to level of trochanter III, length 180, greatest width 18 (in other paratypes 170-180×14-18). Lateral sclerites with acute anterior end and narrowed posterior end, with opening gl on inner margin, 92-94 in length. Pygidial sclerites small triangular, encompassing bases of setae h2, h3, ps1. Setae d1 on lateral margins of central sclerite; setae d2, e1, e2 on striated tegument; setae e1 slightly posterior to the level of openings gl. External copulatory tube cone-shaped, slightly curved downward, 13 in length, 12 in width at base. Dorsal measurements: c2:d2 83, d2:e2 112, d2:gl 60, gl:e1 10-12, e2:h3 47, e2:e2 56, h2:h2 59, h3:h3 51. Epigynium semicircular, 40×72.

**Etymology**

The specific epithet derives from the species name of the type host and is a noun in the genitive case.

7. *Metapteronyssus plocei* Mironov
(figs. 9d-f, 10b)


Material examined. – **CENTRAL AFRICAN REPUBLIC**: male holotype and 3 male, 1 female paratypes ex *Ploceus cucullatus* (Statius Müller, 1776) (Ploceidae), Oubangai,
July 1951, coll. unknown (MRAC 180 622); 5 male, 2 female paratypes, same host, Bossangoa, July 1951, coll. unknown (MRAC 180 634); 15 male, 13 female paratypes, same host, Bamako, October 1950, coll. unknown (MRAC 180 623 – 180 625); 14 males, 8 females ex *P. nigricollis brachypterus* (Swainson, 1834), Bobodioulasso, October 1950, coll. unknown (MRAC 180 626 – 180 629). – *South Africa*: 1 female ex *P. xanthops* (Hartlaub, 1862), Transvaal, Haenertsburg, 26-27 November 1961, S.A.I.M.R. (MRAC 180 638).

**Diagnosis**

Setae *ba* of tarsi I, II present. In males, opisthosa with convex posterior end; setae *ps2* antero-lateral to setae *h2*; terminal lobules short; terminal membranes semicircular, clearly demarked from lobules; adanal shield represented by longitudinal median plate, transventral sclerite narrow, with very short epiantrum tips, setae *3a* off transventral sclerite; setae *c3* lanceolate, with thin apex, 30-38 in length; tarsus III with curved apex (figs. 9d-f). In females, central
sclerite as longitudinal bar extending to the level of trochanters III, greatest width 45-52, posterior end of this sclerite with short incision; setae d1, e1 on central sclerite; external copulatory tube cone-shaped, medium-sized, 15-18 in length (fig. 10b).

Remarks

This species is known from three weaver species of the genus *Ploceus* in central and southern Africa (table 3).

8. *Metapteronyssus puylaerti* Mironov
(figs. 11a-c, 12a)

*Metapteronyssus puylaerti* Mironov, 2002: 185, fig. 9, 11.

Material examined. – SOUTH AFRICA: male holotype and 3 male, 3 female paratypes ex *Ploceus velatus* (Vieillot, 1819) (Ploceidae), Transvaal, Potchefstroom, 26 December 1952, S.A.I.M.R. (MRAC 180 045), 4 male, 5 female paratypes, same data (MRAC 180 042, 180 046).

**Diagnosis**

Setae ba of tarsi I, II present. In males, opisthosoma with convex posterior end; setae p2 anterior to setae h2; terminal lobules short, terminal membranes clearly demarked from lobules; adanal shield represented by median part and a pair of lateral fragments; transventral sclerite narrow, with short epandrium tips, setae 3a off transventral sclerite; setae c3 lanceolate with thin apex, 30-35 in length; tarsus III with curved apex (figs. 11a-c). In females, central sclerite split into two fragments (anterior piece of irregular form situated at the level of trochanters III, IV and longitudinal plate in posterior third of opisthosoma), greatest width of posterior fragment 55-60, its posterior end with short incision, setae d1 and e1 on anterior and posterior fragments of the central sclerite, respectively; external copulatory tube cone-shaped, elongated, 34-42 in length (fig. 12a).
Remarks

This species is known only from the type host, southern masked-weaver *Ploceus velatus*, in South Africa (table 3).

Group *plocepasseri*

Diagnosis

Male. – Opisthosoma with strongly convex postero-lateral margin and with trapezoidal median extension between setae *ps2*, the terminal part of this extension between setae *h3* with pair of small terminal lobules bearing short membranes; subapical membranes absent or present. Adanal shield T-shaped or represented by only a transverse bar-like plate. Tarsus III with slightly curved apex.

Female. – Central sclerite ovate, or represented by wide longitudinal bar-like plate extending to sejugal region (*M. pseudonigritae*), or absent (*M. anoplonotus*). Lateral shields band-like or kidney-shaped.

9. *Metapteronyssus anoplonotus* Mironov


Material examined. – ZIMBABWE: 13 males, 15 females ex *Plocepasser mahali* Smith, 1836 (Passeridae), South Rhodesia (sic), Kariba, February 1964, coll. unknown (MRAC 180 615 – 180 619); 12 males, 15 females ex *Quelea quelea* (Linnaeus, 1758) (Ploceidae), South Rhodesia (sic), Kariba, February 1964, coll. unknown (MRAC 180 609 – 180 614).


Diagnosis

Setae *ba* of tarsi I, II present. In males, opisthosoma with convex lateral margins and trapezium-shaped median extension having pair of short terminal lobules; setae *ps2* anterior to setae *h2*; terminal membranes semicircular, short, clearly demarked from lobules; supranal concavity not extending to the level of setae *ps3*; adanal shield represented by transverse plate; transversal sclerite with scarcely expressed epiandrium tips; setae *3a* on transversal sclerite; setae *c3* lanceolate, 24–28 in length, tarsus III with slightly curved apex (figs. 13a-c). In females, central sclerite represented by one large, ovate shield extending to the level of trochanters III, greatest width 80–85, and a pair of small additional sclerites situated near its lateral margins at the level of trochanters IV, setae *d1*, *e1* on central sclerite; copulatory tube cone-shaped, long, 40–46 (fig. 14a).

Remarks

Known only from the type host, red-backed sparrow weaver *Plocepasser rufoscapulatus*, in Zambia (table 3).

10. *Metapteronyssus daberti* Mironov


Material examined. – ZAMBIA: male holotype and female paratype ex *Plocepasser rufoscapulatus* Bürtikofer, 1888 (Passeridae), North Rhodesia (sic), Luanshya, 22 March 1953, E.L. Haydock (UGA 3044 USNM 46038). Holotype and paratype are deposited in USNM.

Diagnosis

Setae *ba* of tarsi I, II present. In males, opisthosoma with convex lateral margins and trapezoidal median extension having pair of short terminal lobules; setae *ps2* anterior to setae *h2*; terminal membranes semicircular, short, clearly demarked from lobules; supranal concavity not extending to the level of setae *ps3*; adanal shield represented by transverse plate; transversal sclerite with scarcely expressed epiandrium tips; setae *3a* on transversal sclerite; setae *c3* lanceolate, 24–28 in length, tarsus III with slightly curved apex (figs. 13a-c). In females, central sclerite represented by one large, ovate shield extending to the level of trochanters III, greatest width 80–85, and a pair of small additional sclerites situated near its lateral margins at the level of trochanters IV, setae *d1*, *e1* on central sclerite; copulatory tube cone-shaped, long, 40–46 (fig. 14a).

Remarks

This species is known from two passeridan hosts of different families in South Africa (Mironov 2002): white-browed sparrow weaver, *Plocepasser mahali* (Passeridae), and red-billed quelea, *Quelea quelea* (Ploceidae). Taking into consideration that all other members of the *plocepasseri* group are associated exclusively with birds of the family Passeridae, we do not exclude that the record of this species on *Q. quelea* could be the result of contamination.
median extension having pair of short terminal lobules; setae ps2 anterior to setae h2, terminal membranes semicircular, short, clearly demarked from lobules; supranal concavity not extending to the level of setae ps3; adanal shield T-shaped, transventral sclerite with well-expressed epiandrium tips not extending to the level of genital arch apex; setae 3a on transventral sclerite; setae c3 narrowly lanceolate, 18-20 in length; tarsus III with slightly curved apex (figs. 13d-f). In females, central sclerite narrowly ovate, scarcely extending to level of trochanters III, greatest width 58-65, setae d1 off central sclerite, e1 on this sclerite; external copulatory tube absent (fig. 14b).

Remarks

Metapteronyssus plocepasseri is known only from the type host, white-browed sparrow weaver Plocepasser mahali, in Zimbabwe. It is interesting to note that one more species, M. anoplonotus (see above), was also recorded from this host in South Africa; however both mite species have not been recorded in samples from the same host specimens (Mironov 2002).
12. Metapteronyssus pseudonigratae sp. n. (figs. 15a-e, 17a)

Type material. – Kenya: male holotype and 1 male, 1 female paratypes ex Pseudonigrita cabanisi (Fischer et Reichenov, 1884) (Passeridae), Waso, 12 June 1923, K. Caldwell (UGA 5914 AMNH 210 302). Holotype, 1 male paratype – AMNH; 1 male paratype – ZISP.

Diagnosis

Setae ba of tarsi I, II absent. In males, opisthosome with convex lateral margins and trapezium-shaped median extension with a pair of short terminal lobules; setae ps2 anterior to setae h2, terminal membranes semicircular, not clearly demarked from lobules; subterminal membranes present; supranal concavity not extending to the level of setae ps3; anal shield T-shaped; transventral sclerite wide, tips of epiandrium thin and acute, not extending to the level of genital arch apex; setae 3a on transventral sclerite; setae c3 narrowly setiform, slightly thickened in basal part, about 24 long; tarsus III with slightly bent apex (figs. 15a-e). In females, central sclerite a wide almost rectangular longitudinal plate extending to the level of setae c2, posterior margin without incision, greatest width about 60, setae d1, e1 on central sclerite; external copulatory tube small, cylindrical in form, about 9 long (fig. 17a).

Description

Male (holotype). – Idiosoma length × width 298 × 172 (in paratype 300 × 180). Length of hysterosoma 174. Prodorsal shield with posterolateral extensions, size 70 × 49, setae se separated by 56. Setae c3 setiform, slightly thickened in basal part, 24 in length, 1.5 in width. Hysteronotal shield:
anterior margin strongly convex in median part, size 162 × 95. Distance between prodorsal and hyster-onotal shields about 50. Postero-lateral margins of opisthosoma greatly convex; setae $ps2$ antero-lateral to setae $h2$, terminal region of opisthosoma between setae $ps2$ with trapezoidal extensions having short lobules ending by terminal membranes; incision between lobules 6 long; terminal membranes semicircular, not clearly demarked from lobules (fig. 15b). Opisthosomal margins between setae $h2$ and $h3$ with semicircular subterminal membranes. Supranal concavity not extending to the level of setae $ps3$. Dor-sal measurements: $c2:d2$ 54, $d2:e2$ 65, $d2:gl$ 30, $e1:gl$ 7-24, $e2:h3$ 32, $e2:e2$ 46, $h2:h2$ 29. Transventral scler-ite thick, 20 in length including median extension on posterior margin; tips of epiandrium acute, not extending to genital apparatus apex; genital arch 18 × 9; setae $g$ at base of genital arch. Adanal shield T-shaped.

Female (paratype). – Idiosoma length × width 374 × 172. Length of hysterosoma 245. Prodorsal shield as in the male, 64 × 73, setae $se$ separated by 64. Setae $c3$ spiculiform, 18 in length, 1.5 in width. Arrangement of hysteronal shields: central sclerite, pair of lateral sclerites and pair of pygidial sclerites. Central sclerite as wide longitudinal bar (fig. 17a) extending by anterior end to level of setae $c2$, length 194, greatest with 62. Lateral sclerites kidney-shaped, 56-60 long, with opening $gl$ on anterior half. Pygidial sclerites small triangular, encompassing bases of setae $h2$, $h3$, $ps1$. Setae $d1$ and $e1$ on central sclerite; setae $d2$, $e2$ on striated tegument; setae $e1$ anterior to

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Fig. 15. *Metapteronyssus pseudonigritae*, male. – a, ventral view of hysterosoma; b, dorsal view of opisthosoma; c, seta $c3$; d, tarsus I, ventral view; e, tarsus III, dorsal view.
level of openings gl. External copulatory tube a small cylindrical process, 9 in length, 5 in width. Dorsal measurements: \(c2:d2 \approx 70, d2:e2 \approx 124, d2:gl \approx 93, e1:gl \approx 17-19, e2:h3 \approx 44, e2:e2 \approx 50, h2:h2 \approx 60, h3:h3 \approx 49\). Epigynium bow-shaped, 22 X 65.

**Etymology**

The specific epithet derives from the generic name of the type host and is a noun in a genitive case.

**Group angolensis**

**Diagnosis**

Male. – Opisthosoma moderately attenuate to posterior end, posterior margin bluntly rounded or with pair of small finger-like lobules between setae \(h3\) (\(M. \ amadinae\)). Posterior margin of opisthosoma bears entire opisthosomal membrane between bases of setae \(ps2\) (with free margin of this membrane slightly convex or bilobate) (figs. 18a, b, f); if opisthosoma with lobules, the opisthosomal membrane is represented by a narrow band along the entire margin of opisthosoma and lobules (figs. 16a, b). Adanal shield T-shaped. Tarsus III straight, cone shaped.

Female. – Central sclerite as median bar-like plate extending to the level of trochanters III (figs. 17a, 19a, b); lateral sclerites as longitudinal plates of irregular form.

13. *Metapteronyssus amadinae* sp. n. (figs. 16a-e, 17b)

Type material. – ETHIOPIA: male holotype and 3 male, 2 female paratypes ex *Amadina fasciata alexanderi* Neumann, 1908 (Estrildididae), SW Ethiopia, Indumunra Mountains, 15 July 1912, E.A. Mearns (UGA 3055 USNM 247 105). Holotype, 2 male and 1 female paratypes – USNM, 1 male, 1 female paratypes – ZISP.

**Diagnosis**

Setae \(ba\) of tarsi I, II absent. In males, opisthosoma with short median extension between setae \(h3\) bearing pair of finger-shaped terminal lobules, setae...
ps2 antero-lateral to setae h2, opisthosomal membrane along entire margin of opisthosoma and lobules narrow, 2-3 in width; adanal shield T-shaped, transventral sclerite wide; tips of epiandrium thin and acute, not extending to the level of genital arch apex; setae 3a on transventral sclerite; setae c3 narrowly lanceolate, 22-24 in length, tarsus III with straight apex (figs. 16a-e). In females, central sclerite as longitudinal parallel-sided plate extending to the level of trochanters III, posterior margin with deep narrow incision, greatest width 40-43; setae d1, e1 on central sclerite; external copulatory tube a small cone rounded apically, 6-8 in length (fig. 17b).

Description
Material examined. – SonMer: male holotype from Lonchura cantans orientalis (Gmelin, 1789) (Estrildidae), Bikendula, 16 March 1919, coll. unknown (MRAC 180 047); female paratype, same data (MRAC 180 048).

Diagnosis

Setae ba of tarsi I, II present. In males, opisthosoma bluntly rounded; setae ps2 lateral to setae h2; opisthosomal membrane on posterior margin of opisthosoma between bases of setae ps2 with slightly convex free margin; adanal shield T-shaped, transventral sclerite wide; tips of epiandrium acute, not extending to the level of genital arch apex; setae 3a on transventral sclerite; setae c3 lanceolate, 24 long; tarsus III with straight apex (figs. 18a-e). In females, central sclerite as a narrow bar slightly attenuated posteriorly, anterior end extending to the level of trochanters III, posterior margin without incision, greatest width 24-27; setae d1, e1 on margins of central sclerite; external copulatory tube small, cylindrical, 6-8 long (fig. 19a).

Remarks

This species was originally described from the blue waxbill (or cordon bleu) Uraeginthus angolensis in South Africa (Mironov & Kopij 2000); in the course of the present study it was also recorded from the red-cheeked blue waxbill U. bengalus ugogoensis in Rwanda. The figures of ’M. glossifer’ given by Faccini & Atyeo (1981: figs. 17-20) in the generic revision of pteronyssids correspond well to specimens of Metapteronyssus angolensis rather than to those of M. glossifer from its type host Euplectes franciscanus, and we suggest that they were probably based on the material of Gaud (1953) from U. bengalus from Sudan (see above, remarks to M. glossifer).

15. Metapteronyssus lonchurae Mironov (figs. 18f-h, 19b)

Metapteronyssus lonchurae Mironov, 2002: 197, fig. 21, 22.

Material examined. – SomM: male holotype from Lonchura cantans orientalis (Gmelin, 1789) (Estrildidae), Bikendula, 16 March 1919, coll. unknown (MRAC 180 047); female paratype, same data (MRAC 180 048).

Diagnosis

Setae ba of tarsi I, II present. In males, opisthosoma bluntly rounded; setae ps2 lateral to setae h2; opisthosomal membrane along its margin between setae ps2 large, with pair of wide and rounded extensions, greatest length of membrane 14-18; adanal shield T-shaped, transventral sclerite wide; tips of epiandrium acute, extending to the level of genital arch apex; setae 3a on transventral sclerite; setae c3 lanceolate, 21-25 in length; tarsus III with straight apex (figs. 18a-e). In females, central sclerite as a narrow bar slightly attenuated posteriorly, anterior end extending to the level of trochanters III, posterior margin without incision, greatest width 24-27; setae d1, e1 on margins of central sclerite; external copulatory tube small, cylindrical, 6-8 long (fig. 19a).

Remarks

This species is known only from the African silverbill Lonchura cantans orientalis in Somali (table 3). Metapteronyssus lonchurae clearly differs from other known species of the genus by having an opisthosomal membrane with a slightly convex free margin in the males.
Fig. 18. *Metapteronyssus* males. – a, *Metapteronyssus angolensis*, ventral view of hysterosoma; b, dorsal view of opisthosoma; c, seta c3; d, tarsus I, ventral view; e, tarsus III, dorsal view; f, *M. lonchurae*, ventral view of hysterosoma; g, seta c3; h, tarsus III, dorsal view. om - opisthosomal membrane.
Discussion

Phylogeny

The branch-and-bound search produced a single shortest tree having length of 47 steps and standard indices, excluding uninformative characters, as follows: $ct=0.8140$, $rt=0.9048$, $rc=0.7508$ (fig. 20). Monophyly of the genus *Metapteronyssus* is supported by eleven unambiguous synapomorphies, four of which are characters for both sexes (see table 1): loss of prodorsal shield in posterior part of prodorsum (character 1.1), fusion of epimerites I as a narrow U (2.1), loss of unpaired vertical seta $vi$ (3.1), reduction of seta $ba$ of tarsi I, II to small spine-like seta (4.1). Three synapomorphies characterizing males represent features of the hysteronotal shield: development of a pair of lateral hysteronotal ridges (6.1) and median ridge (7.1), and placement of hysteronotal gland openings $gl$ at postero-lateral incisions in the hysteronotal shield (9.1). Four synapomorphies are female characters: setae $e2$ moved relatively close to midline of the body (23.1), development of central (24.1) and lateral (30.1) shields due to splitting of entire hysteronotal shield, and development of external copulatory tube (33.1).

The *Metapteronyssus* branch forms three clusters corresponding to our taxonomic concept of three species groups. The first cluster to split off corresponds to the *plocepasseri* group and is supported by three synapomorphies representing structures of the opisthosoma in males: strongly convex posterolateral margins (8.1) and median trapezium-shaped extension between setae $h2$ (10.1), and a pair of short terminal membranous lobules (13.1). The clade bearing
three derived species of this cluster, *M. anaplonotus*, *M. daberti* and *M. plocepasseri*, is characterized by the ovate form of the central sclerite (25.1) and narrow band-like lateral sclerites (31.1) in females.

The branch bearing two other clusters (*angolensis* and *glossifer*) is characterised by two synapomorphies: straight, almost conical form of tarsus III in males (21.1) and relatively narrow band-like central sclerite in females (26.1). The *angolensis* cluster is supported by the development of entire (11.1) and relatively wide (14.1) opisthosomal membrane between setae *ps2* in males. In the basal species of the group, *M. lonchurae*, the margin of membrane is smooth and slightly convex (fig. 18e), while in the two derived species, the membrane forms a pair of rounded extensions as in *M. angolensis* (figs. 18a, b) or it is secondarily narrowed and represented by narrow band along the margin of the opisthosoma and a pair of finger like lobules as in *M. amadinae* (figs. 17a, b).

The *glossifer* cluster is supported by two synapomorphies: the development of membranous terminal lobules between setae *h3* (13.1) and subapical membranes (15.1) in males. The main clade of this cluster, which is the sister to a sole species *M. bubalornis*, is characterized by a narrowed transventral sclerite in males (16.1) and development of a cone-like and relatively long external copulatory tube in females (34.1). The *plocei* clade uniting the five most derived species of the *glossifer* cluster (*M. anaplecti*, *M. capensis*, *M. gaudi*, *M. plocei*, and *M. puylaerti*) is characterised by three apomorphies in males: setae *3a* are situated off the transventral sclerite (17.1), lateral parts of the adanal shield are separated from the median part (20.1), and tarsus III has a curved apex (21.0). In the context of the genus *Metapteronyssus*, a curved tarsus III in the *plocei* clade represents a reversion to a plesiomorphic state of this character. Three relatively primitive species of the *glossifer* cluster (*M. bubalornis*,

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**Fig. 20. Phylogeny of *Metapteronyssus*.** Single most parsimonious tree. 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 italics to the right from nodes are Bremer indices. (*) Species is also recorded from Ploceidae, see detailed remarks in the text.
M. glossifer, and M. hordacei) retain setae 3a on the transventral sclerite and a T-shaped adanal shield, but have a straight tarsus III (figs. 2a, f, 5a, c) which is the derived state of this character.

In mapping the main evolutionary changes in the genus Metapteronyssus (fig. 20) it is possible to note that its three clusters demonstrate some similar trends in morphological modifications. A strong tendency to reduce the central sclerite in females is realized in each lineage independently and in some cases in different ways. In the glossifer and angolensis groups the central sclerite is commonly represented by a narrow longitudinal band, the greatest width of which is less than 1/3 of idiosomal width. In M. angolensis (angolensis group) and M. hordacei (glossifer group) this sclerite is reduced to a narrow, almost rod-shaped sclerite (figs. 8b, 19a). In two species of the glossifer group (M. anaplecti and M. puylaerti), the central sclerite is relatively large but split into anterior and posterior fragments (fig. 12a). In the plocepasseri group, most species have a relatively wide rectangular or oval central sclerite (figs. 14a, b), but in M. anaplonotus this sclerite is completely lost (fig. 12b). In males the most characteristic trend independently realized in different lineages is the extension of the terminal end of the opisthosoma between setae ps2 and development of terminal lobules with membranous margins. This structure of the opisthosoma was apparently developed independently in the glossifer (figs. 2a, b) and plocepasseri groups (figs. 13a, d) and in M. amadinae from the angolensis group (figs. 16a, b).

Host associations
Representatives of the genus Metapteronyssus (table 3) are restricted to three families of the superfamily Passeroidea (parvorder Passerida) distributed in the Old World. Each species group of mites recognized in the course of phylogenetic analysis is restricted to a particular host family: M. angolensis to estrildid finches (Estrildidae), glossifer to weavers (Ploceidae), and plocepasseri to sparrows, (Passeridae). Within all species groups most species are either monoxenous or restricted to a certain bird genus (with the exception of one species from the plocepasseri group). For example, a relatively primitive species of the glossifer group, M. bubalornis, occurs on the buffalo weaver Bubalornis albirostris, and two closely related species M. glossifer and M. hordacei are associated with the bishops Euplectes franciscanus and E. hordaceus, respectively. Members of the derived subgroup

| Table 2. Data matrix of characters states for Metapteronyssus and outgroup taxa. Character states are scored as 0 to 2, inapplicable states as ‘-’. |
|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| 1 1111111112 2222222223 3333 1234567890 1234567890 1234567890 1234567890 |
| Sturnotrogus subtrincatus       | 0000000000 000-0000-- 0000-00-00 0000-00-00 | 0000-00-00 | 000-00-00 | 00-00-00-0-0- |
| Scutulanysus dayritidis         | 0000000000 000-00000 000-00000 000-00000 | 0000-00000 | 0000-00000 | 0000-00000 |
| Pteronyssoides boloplaex        | 0000000000 000-00001 000-00001 000-00001 | 0000-00001 | 0000-00001 | 0000-00001 |
| Metapteronyssus glossifer       | 1111011010 0-1011000 1111010000 1111010000 | 0011010000 | 1111010000 | 1111010000 |
| M. hordacei                     | 1111011010 0-1011000 1111010000 1111010000 | 0011010000 | 1111010000 | 1111010000 |
| M. plocei                       | 1111011010 0-1011000 1111010000 1111010000 | 0011010000 | 1111010000 | 1111010000 |
| M. capensis                     | 1111011010 0-1011110 1111010000 1111010000 | 0011010000 | 1111010000 | 1111010000 |
| M. puylaerti                    | 1111011010 0-1011110 0111011022 0111011022 | 0011011022 | 0011011022 | 0011011022 |
| M. anaplecti                    | 1111011010 0-1011110 1111011022 1111011022 | 0011011022 | 0011011022 | 0011011022 |
| M. gaudi                       | 1111011010 0-1011110 1111011022 1111011022 | 0011011022 | 0011011022 | 0011011022 |
| M. bubalornii                   | 1111011010 0-1010010 1111011022 1111011022 | 0011011022 | 0011011022 | 0011011022 |
| M. plocepasseri                 | 1111011011 0-1000010 0111000002 1001100000 | 0011000002 | 1001100000 | 1001100000 |
| M. anaplonotus                  | 1111011111 0-1000010 0111000002 1001100000 | 0011000002 | 1001100000 | 1001100000 |
| M. dabeti                       | 1111011111 0-1000010 0111000002 1001100000 | 0011000002 | 1001100000 | 1001100000 |
| M. pseudonigratiae              | 1111111111 0-1010010 0111000002 1001100000 | 0011000002 | 1001100000 | 1001100000 |
| M. lonchiae                     | 1111011010 100100010 1111010000 1111010000 | 0011000002 | 1001100000 | 1001100000 |
| M. angolensis                   | 1111011010 110100010 1111020002 1001100000 | 0011000002 | 1001100000 | 1001100000 |
| M. amadinae                     | 1111111100 110100010 1111010002 1011000002 | 0011000002 | 1001100000 | 1001100000 |
Weavers of the genera Ploceus Cuvier, 1816 and Anaplectes Reichenbach, 1863. The records of *M. anoplonotus* (plocepasseri group) on hosts belonging to different families, *Plocepasser mahali* (Passeridae) and *Quelea quelea* (Ploceidae) are exceptions and could be the result of natural or accidental contamination.

Associations with particular host taxa noted at species and species group levels give clear evidence of co-speciation of the genus *Metapteronyssus* with their hosts. We realise that species diversity of this genus is so far incompletely known, because many avian species of the three host families, *Plocepasser mahali* (Passeridae) and *Quelea quelea* (Ploceidae) are unexplored (almost 300 avian species). Nevertheless, based on the phylogenetic relationships within *Metapteronyssus* (fig. 20), currently known host associations (table 3), a current phylogenetic hypothesis for suprageneric taxa of passerine hosts (Sorenson & Payne 2001, Ericson et al. 2002, Ericson & Johanson 2003, Barker et al. 2004), it is possible to propose a very provisional co-phylogenetic hypothesis for *Metapteronyssus* species and their hosts.

We hypothesize that the genus *Metapteronyssus* originated on the common ancestor of the core of Passeroidea and owing to co-speciation has become distributed among three avian families of this vast grouping of sparrow-like passerines. However, taking into consideration its numerous derived features and significant morphological differences from related genera, it is possible that *Metapteronyssus* originated earlier, even on the ancestor of the parvorder Passerida, where it split off from a common ancestor with the genus *Pteronyssoides*. However, in contrast to the closely related genus *Pteronyssoides*, which is distributed on twelve families of Passerida including nine families of Passeroidea (Mironov & Wauthy

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<table>
<thead>
<tr>
<th>Mite species</th>
<th>Host species</th>
<th>Locality</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>glossifer</em> group</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>M. anaplecti</em></td>
<td><em>Anaplectes rubriceps</em></td>
<td>Rwanda</td>
<td>Present study</td>
</tr>
<tr>
<td><em>M. bubalornis</em></td>
<td><em>Bubalornis albirostris</em></td>
<td>Cameroon</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td><em>M. capensis</em></td>
<td><em>Ploceus capensis</em></td>
<td>South Africa</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td><em>M. gaudi</em></td>
<td><em>Ploceus aurantius aurantius</em></td>
<td>Nigeria</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td></td>
<td><em>P. bicolor amaurocephalus</em></td>
<td>Cameroon</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td></td>
<td><em>P. nigerrimus</em></td>
<td>Cameroon</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td></td>
<td><em>P. nigricollis brachypterus</em></td>
<td>Cameroon</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td><em>M. glossifer</em></td>
<td><em>Euplectes frankianus</em></td>
<td>Sudan</td>
<td>Gaud 1953</td>
</tr>
<tr>
<td><em>M. hordacei</em></td>
<td><em>E. hordaceus</em></td>
<td>Central African Republic</td>
<td>Present study</td>
</tr>
<tr>
<td><em>M. plocei</em></td>
<td><em>Ploceus cucullatus</em></td>
<td>Central African Republic</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td></td>
<td><em>P. nigricollis brachypterus</em></td>
<td>Central African Republic</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td></td>
<td><em>P. xanthops</em></td>
<td>South Africa</td>
<td>Mironov 2002</td>
</tr>
<tr>
<td><em>M. pseudolaelerti</em></td>
<td><em>Ploceus velatus</em></td>
<td>South Africa</td>
<td>Mironov 2002</td>
</tr>
</tbody>
</table>

| plocepasseri group | | | |
| *M. anoplonotus* | *Plocepasser mahali* | South Africa, Zimbabwe | Mironov 2002 |
| | *Quelea quelea* | Zimbabwe | Mironov 2002 |
| *M. daberti* | *Plocepasser ruficapulatus* | Zambia | Mironov 2002 |
| *M. plocepasseri* | *Plocepasser mahali* | Zimbabwe | Mironov 2002 |
| *M. pseudonigrata* | *Pseudonigrata cabanisi* | Kenya | Present study |

| angolensis group | | | |
| *M. angolensis* | *Uraeginthus angolensis* | South Africa | Mironov & Kopij 2000 |
| | *U. bengalus* | Sudan | Gaud 1953 |
| | *U. bengalus ugogoensis* | Rwanda | Present study |
| *M. amadinae* | *Amadina fasciata alexanderi* | Ethiopia | Present study |
| *M. lonchurae* | *Lonchura cantans orientalis* | Somali | Mironov 2002 |

The *plocepasseri* group of *Metapteronyssus* probably originated on the ancestors of the larger branch, but was retained only on representatives of Passeridae. The absence of *Metapteronyssus* on other avian families of this major branch of the core Passeroidea has no clear explanation and is open for speculation. One of possible suggestions is that the representatives of *Metapteronyssus* have gone extinct on other familial lineages of this passeroidean branch.

Two other species groups, *angolensis* and *glossifer*, evolved in association with two families of the second major branch of Passeroidea, Estrildidae and Ploceidae respectively. It is interesting to note that representatives of *Metapteronyssus* are not known from the third family of this branch, Viduidae, which is phylogenetically closest to Estrildidae (Sorenson et al. 2003). The biological peculiarity of viduids, which are brood parasites, may give an explanation of that. In viduids, there are no transfers of mites from the biological parents to their chicks in the nest period, i.e., the main pathway used by feathers mites to infest the next generation of hosts is absent. In relation to this it is necessary to stress the curious fact that common hosts of viduids are the estrildid finches (Sorenson & Payne 2001), which do bear *Metapteronyssus* species of the *angolensis* group. The absence of *Metapteronyssus* species on viduids may mean that *Metapteronyssus* species associated with the estrildid finches are too specialised and cannot move to or survive on the whydah or indigobird chicks. For comparison it is interesting to point out that representatives of the related pteryonysiid genus *Pteronyssoides* do occur on hosts of the three families, Estrildidae, Ploceidae and Viduidae (Mironov & Wauthy 2005a). Unfortunately, diversity of *Pteronyssoides* on these avian families is not yet explored enough to find out whether viduids have their own specific representatives of this genus, which are transferred between individuals in the moments of copulation and other close contacts, or whether their chicks accept mites from respective adopt parents of the family Estrildidae.

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