Picicola Clay and Meinertzhagen (Phthiraptera: Philopteridae) from jacamars and puffbirds (Piciformes: Galbulidae, Bucconidae), with descriptions of five new species

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Abstract

The three species of previously named Picicola Clay and Meinertzhagen from jacamars and puffbirds are redescribed and five new species are described and illustrated. These new species and their type hosts are: Picicola valquii ex Notharchus tectus (Boddaert), P. naokii ex Bucco capensis Linnaeus, P. osheai ex Malacoptila fusca (J.F. Gmelin), P. faucetti ex Chelidoptera tenebrosa (Pallas), and P. oneilli ex Notharchus macrorhynchos (J.F. Gmelin). We collected partial cytochrome oxidase I (COI) sequences for all of the species in this group, and these data support the genetic distinctiveness of these new species. A key is provided for the identification of all eight species of Picicola from jacamars and puffbirds.

Key words: chewing lice, phylogeny, taxonomy

Introduction

The status of the currently recognized species of the philopterid chewing louse genus Picicola Clay and Meinertzhagen has been reviewed by Valim and Linardi (2006) and two molecular data sets strongly support Picicola found on the Jacamar (Galbulidae) and Puffbird (Bucconidae) families as a monophyletic group (Johnson et al. 2002, Weckstein 2003). The description of two new species of this genus, respectively from a puffbird and a jacamar (Valim and Linardi 2006), coupled with the earlier description of a new species from a puffbird by Oniki and Emerson (1981), brings the total Picicola now known from these two host families to three. Here, we redescribe the three known species and describe and illustrate five additional new species in this clade of Picicola following the collection of additional specimens by the junior author and his colleagues.

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We collected partial mitochondrial Cytochrome Oxidase I (COI) sequences (379 base pairs) for all of the species, from as many hosts as were available, to assess their genetic distinctiveness and reconstruct their phylogenetic relationships. Laboratory methods followed the protocols outlined in Weckstein (2003, 2004). DNA sequences analyzed for this study are deposited in GenBank (Accession numbers AF444846, AF444848, AF444872, EF101565-EF101577).

In the following descriptions, all measurements are in millimeters. Abbreviations are TW, temple width; HL, head length at midline; CI, cephalic index (HL/TW); PW, prothorax width; MW, metathorax width; AWV, abdomen width at segment V; GL, male genitalia length; PL, male penis length; and TL, total length. Subordinal host classification follows Dickinson (2003).

We examined some of the DNA vouchers from Johnson et al. (2002), which are deposited at the Price Institute for Phthirapteran Research at the University of Utah (PIPeR), Salt Lake City, Utah, USA. All other DNA vouchers and holotypes of the new species described here are deposited in the collection of The Field Museum, Chicago, Illinois, USA. Paratypes, as numbers allow, are divided between there and the collection at the Illinois Natural History Survey, Champaign, Illinois, USA.

Where known, we have used the following abbreviations in the “Material” sections to identify the collectors of the lice and/or their hosts: AA (A. Aleixo), DHC (D.H. Clayton), DW (D. Willard), JLK (J.L. Koederitz, now J.K. Armenta), AWK (A.W. Kratter), DFL (D.F. Lane), JPO (J.P. O’Neill), TV (T. Valqui), BJO (B.J. O’Shea), KB (K. Balta), JDW (J.D. Weckstein), DGC (D.G. Christian) and CCW (C.C. Witt). Where known, abbreviations for the museums housing the host voucher specimens are listed prior to the collector abbreviations. These museums include The Field Museum (FMNH), Louisiana State University Museum of Natural Science (LSUMZ), Baton Rouge, Louisiana, USA, and Museu Paraense Emilio Goeldi (MPEG), Belém, Pará, Brazil.

Genus Picicola Clay and Meinertzhagen

Picicola Clay and Meinertzhagen 1938:74. Type species: Picicola praeposterus Clay and Meinertzhagen by original designation. Now recognized as P. snodgrassi (Kellogg).

A thorough characterization of this genus may be found in the works cited by Valim and Linardi (2006). We provide here only the diagnostic characters that are pertinent to define the genus as it pertains to the jacamar and puffbird lice and serve to distinguish them as a unit from Picicola species found on various families of the suboscine Passeriformes and on the woodpeckers (Piciformes: Picidae).

General morphology as in Figs. 1 and 2. Head evenly rounded anteriorly, longer than wide, with temple slightly wider than preantennal portion; with conspicuous transverse dorsal preantennal suture; with well-developed complete marginal carina; each side of
temple with two long marginal setae. Thorax with small quadrangular pronotum bearing single seta at each posterior corner; metanotum with four very long setae on each side; thoracic sternal plate large, with setae as shown. Abdomen slender, much longer than wide; tergites II–IX undivided medially; postspiracular setae very long on III–VII, shorter on VIII. Tergite II with medioanterior pair of setae in addition to medioposterior tergocentral setae. Female and male subgenital plates of fused sternites VII–IX. Male genitalia with prominent inwardly-curved parameres, a median slender penis, and complex of endomeral structures.

There is only slight sexual dimorphism, which is limited to males having somewhat smaller dimensions and differences associated with the posterior abdomen. Characters cited above for the genus will not be repeated in the species descriptions.

**Picicola striata** Oniki and Emerson
(Figs. 1–6)

*Picicola striata* Oniki and Emerson 1981:511. Type host: *Malacoptila striata* (Spix), the Crescent-chested Puffbird.

**Redescription.** Male as in Fig. 1; female posterior abdomen as in Fig. 2. Head shaped as in Fig. 4, with marginal carina thin, having irregular inner border, and becoming thinnest at point of juncture with preantennal suture. Tergites II–VI each with 2 tergocentral setae; VII–VIII, usually 4–5, less often 3 or 6. Male tergite IX as in Fig. 3, with margin having only single very long inner seta on each side. Abdominal segments with prominent pleural thickening and reentrant head. Female subgenital plate as in Fig. 5; vulval margin with row of 15–16 short setae, with slight medial concavity, and with short seta displaced on each side lateroposterior to this row. Male subgenital plate as in Fig. 6; genitalia similar to Fig. 8; with 3 sensilla on each endomeral arm. Female dimensions: TW, 0.38–0.42; HL, 0.46–0.51; CI, 1.21–1.24; PW, 0.23–0.25; MW, 0.33–0.36; AVW, 0.50–0.58; TL, 1.77–2.01. Male dimensions: TW, 0.35–0.38; HL, 0.42–0.46; CI, 1.20–1.24; PW, 0.21–0.23; MW, 0.30–0.32; AVW, 0.43–0.51; GL, 0.28–0.31; PL, 0.035–0.040; TL, 1.47–1.67.

FIGURES 1–13. 1–6, Picicola striata. 1, Entire dorsoventral male. 2, Dorsoventral female terminal segments. 3, Male tergites VIII–IX. 4, Female head outline. 5, Female subgenital plate and vulval margin. 6, Male subgenital plate. 7–8, P. galbulica. 7, Female head outline. 8, Male genitalia. 9–11, P. valqui. 9, Female head outline. 10, Male subgenital plate. 11, Male genitalia. 12–13, P. naokii. 12, Female head outline. 13, Male subgenital plate.
Remarks. This is the first species of *Picicola* described from the puffbird family Bucconidae. The principal features for its recognition involve the head shape, a cephalic index of at least 1.20, and an irregular marginal carina, narrowest at the level of the preantennal suture (Fig. 4).

*Picicola galbulica* Valim and Linardi
(Figs. 7–8)


Redescription. Head shaped as in Fig.7, with marginal carina of equal thickness and having even inner border. Tergites II–V each with 2 tergocentral setae; VI with 2–4; VII–VIII, usually 4–5, less often 3 or 6. Pleural thickenings and male tergite IX as for *P. striata*. Female subgenital plate much as in Fig. 5; vulval margin with row of 16–18 short setae, with slight medial concavity, and with short seta displaced on each side lateroposterior to this row. Male subgenital plate as in Fig. 6; genitals as in Fig. 8, with 3 sensilla on each endomeral arm. Female dimensions: TW, 0.37–0.40; HL, 0.44–0.47; CI, 1.15–1.21; PW, 0.21–0.24; MW, 0.31–0.35; AWV, 0.42–0.52; TL, 1.59–1.86. Male dimensions: TW, 0.35–0.36; HL, 0.41–0.43; CI, 1.17–1.20; PW, 0.20–0.21; MW, 0.29–0.32; AWV, 0.38–0.43; GL, 0.25–0.31; PL, 0.035; TL, 1.45–1.53.


Remarks. We agree with Valim and Linardi (2006), who note the morphological closeness of *P. galbulica* to *P. striata*. However, they give the male of *P. galbulica* as differing by having four tergocentral setae on segment VII; this does not hold true, as *P. striata* males also have these setae, although Oniki and Emerson (1981) neglected to illustrate the presence of these setae in their Fig. 1. The few other features given for separation are nebulous and of dubious value. We have found the most reliable feature to be the thicker marginal head carina with its even inner border (Fig. 4 vs Fig. 7).

After having studied material from five species of *Galbula*, we have been unable to
discern any reliable morphological differences among them. This leads us to conclude that likely all ten of the *Galbula* species recognized by Dickinson (2003) share the same louse species.

**Picicola valquii** Price and Weckstein, *new species*  
(Figs. 9–11)

**Type host.** *Notharchus tectus* (Boddaert), the Pied Puffbird.

**Description.** Head shaped as in Fig. 9, with broadly rounded preantennal portion and thick marginal carina having irregular inner border. Tergites II–V each with 2 tergocentral setae; VI, 2–4; VII–VIII, usually 4, less often 5. Pleural thickenings and male tergite IX as for *P. striata*. Female subgenital plate much as in Fig. 5; vulval margin with row of 14–15 short setae, indented slightly medially, and with short seta displaced on each side lateroposterior to this row. Male subgenital plate as in Fig. 10; genitalia as in Fig. 11, with 3 sensilla on each endomeral arm. Female dimensions: TW, 0.41–0.42; HL, 0.47–0.48; CI, 1.14–1.15; PW, 0.23–0.25; MW, 0.32–0.33; AWV, 0.49–0.51; TL, 1.63–1.71. Male dimensions: TW, 0.38–0.39; HL, 0.44; CI, 1.13–1.16; PW, 0.22; MW, 0.31–0.32; AWV, 0.43–0.45; GL, 0.26–0.29; PL, 0.025–0.030; TL, 1.41–1.50.

**Type material.** Ex *N. tectus*, holotype male, PERU: Dpto. Loreto, 7 km SW Jeberos, 5° 18' 48" S, 76° 56' 1" W (LSUMZ, TV-308, 6 June 2001); 1 male, 3 females (including DNA voucher 1.13.2003.20), paratypes, same data as holotype.

**Remarks.** This new species is best recognized from the previous two species by both sexes with the irregular inner margin of the head carina and a slightly different head shape with its smaller cephalic index, and the male by its shorter penis.

**Etymology.** This species is named for Thomas Valqui for his interest in lice and in recognition of his valuable assistance in collecting specimens vital to this and other louse studies.

**Picicola naokii** Price and Weckstein, *new species*  
(Figs. 12–14)

**Type host.** *Bucco capensis* Linnaeus, the Collared Puffbird.

**Description.** Head shaped as in Fig.12, with wide rounded preantennal portion and marginal carina uniformly thick with even inner border. Tergites II–V each with 2 tergocentral setae; VI, 2–4; VII–VIII, usually 4–5, less often 3 or 6. Pleural thickenings and male tergite IX as for *P. striata*. Female subgenital plate close to Fig. 5; vulval margin with row of 12–16 short setae, indented slightly medially, and with short seta displaced on each side lateroposterior to this row. Male subgenital plate as in Fig. 13; genitalia as in Fig. 14, with slightly bent penis having indistinct tip; with 3 sensilla on each endomeral arm.
Female dimensions: TW, 0.41–0.44; HL, 0.48–0.49; CI, 1.09–1.17; PW, 0.27–0.28; MW, 0.35–0.38; AWV, 0.53–0.58; TL, 1.69–1.82. Male dimensions: TW, 0.39; HL, 0.44; CI, 1.13; PW, 0.23; MW, 0.31–0.33; AWV, 0.48–0.49; GL, 0.28–0.30; PL, 0.030; TL, 1.47–1.52.

**Type material.** Ex *B. capensis*, holotype male, PERU: Dpto. Loreto, ca. 86 km SE Juanjui, on E bank upper Rio Pauya, 7° 35' 40” S, 75° 54’ 58” W (LSUMZ, TV-173, 23 July 2000); 1 male, 3 females (including DNA voucher 1.13.2003.22), paratypes, same data as holotype.

**Other material.** Ex *B. macrodactylus* (Spix), 6 females, PERU: Dpto. Madre de Dios, Hda. Amazonia near Atalaya (FMNH, DHC 85-1000, 2 November 1985).

**Remarks.** The head shape of both sexes and the unusual structure of the male penis afford the best features for separation from the other species.

**Etymology.** This species is named for Kazuya Naoki in recognition of his help in collecting louse specimens vital to the research of the junior author.

**Picicola osheai** Price and Weckstein, new species
(Figs. 15–18)

**Type host.** *Malacoptila fusca* (J.F. Gmelin), the White-chested Puffbird.

**Description.** Head shaped as in Fig.15, with marginal carina narrowed anteriorly in region of preantennal suture, but having even inner border. Tergites II–VI each with 2 tergocentral setae; VII–VIII, usually 2–4. Male tergite IX (Fig. 16) with medium fine seta on each side mediad of very long marginal seta. With well developed pleural thickenings. Female subgenital plate as in Fig. 17; vulval margin evenly rounded, with row of 13–17 short setae, and lacking short seta displaced lateroposterior to it. Male subgenital plate much as in Fig. 6; genitalia as in Fig. 18. Female dimensions: TW, 0.41–0.46; HL, 0.48–0.53; CI, 1.13–1.19; PW, 0.24–0.28; MW, 0.34–0.38; AWV, 0.51–0.58; TL, 1.83–2.02. Male dimensions: TW, 0.38–0.41; HL, 0.42–0.48; CI, 1.11–1.21; PW, 0.22–0.24; MW, 0.30–0.34; AWV, 0.42–0.48; GL, 0.25–0.29; PL, 0.025–0.030; TL, 1.56–1.67.

**Type material.** Ex *M. fusca*, holotype female, SURINAME: District Sipaliwini, Lely Gebergte, 4° 16.459’ N, 54° 44.323’ W (LSUMZ, BJO 1000, 8 June 2003); 4 males, 3 females, paratypes, same data as holotype.

**Other material.** Ex *M. semicincta* Todd, 1 male, PERU: Dpto. Cuzco, Tono, 870 m (FMNH 321029, DW-3418, 27 November 1985); 1 male, 1 female, same locality as DW-3418 (FMNH 321025, DHC 1190, 28 November 1985); 1 male, 3 females, PERU: Dpto. Madre de Dios, Rio Palotoa, left bank, 12 km from mouth, 490 m (FMNH 321022, DHC 85-229, 21 August 1985); 2 females, same locality as DHC 85-229 (FMNH, DHC no field number given, 21 August 1985).
FIGURES 14–27. 14, Picicola naokii, male genitalia. 15–18, P. osheai. 15, Female head outline. 16, Male tergites VIII–IX. 17, Female subgenital plate and vulval margin. 18, Male genitalia. 19–21, P. faucetti. 19, Male tergites VIII–IX. 20, Female subgenital plate and vulval margin. 21, Male genitalia. 22–24, P. oneilli. 22, Male tergites VIII–IX. 23, Male subgenital plate. 24, Male genitalia. 25–27, P. serrafreirei. 25, Female head outline. 26, Female subgenital plate and vulval margin. 27, Dorsal female abdomen.
Remarks. This new species is readily separated from all of the others from these hosts by the female having a distinctive vulval setal alignment (Fig. 17) and the male with its unique chaetotaxy of tergite IX (Fig. 16).

Etymology. This species is named for Brian J. O’Shea in recognition of his valuable assistance in collecting critical specimens for this and other studies of lice.

*Picicola faucetti* Price and Weckstein, new species
(Figs. 19–21)

**Type host.** *Chelidoptera tenebrosa* (Pallas), the Swallow-wing Puffbird.

**Description.** Head shaped much as in Fig. 7, with marginal carina having even inner border. Tergites II–VI each with 2 tergocentral setae; VII–VIII, 3–4. Male tergite IX (Fig. 19) with very long heavy seta at each lateroposterior corner in addition to usual very long more median seta. Female subgenital plate as in Fig. 20, with broad blunt posterior portion; vulval margin with row of 14–15 short setae, indented slightly medially, and with short seta displaced on each side lateroposterior to this row. Male subgenital plate close to Fig. 6; genitalia as in Fig. 21. Female dimensions: TW, 0.37–0.40; HL, 0.47; CI, 1.18–1.27; PW, 0.22–0.24; MW, 0.33–0.36; AWV, 0.48–0.49; TL, 1.85–1.91. Male dimensions: TW, 0.36; HL, 0.44; CI, 1.22; PW, 0.21; MW, 0.32; AWV, 0.43; GL, 0.30; PL, 0.035; TL, 1.65.

**Type material.** Ex *C. tenebrosa*, holotype male, PERU: Dpto. Loreto, 7 km SW Jeberos, 5° 18’ 48” S, 76° 16’ 32” W (LSUMZ, KB065, 13 June 2001); 1 female, paratype, same data as holotype; 1 male, 1 female (DNA vouchers 1.13.2003.18 and PIPeR 1.17.2000.12), paratypes, BRAZIL: Mato Grosso, S bank Rio Cristalino, 1.3 km upriver from the confluence with Rio Teles Pires, 34 km NE Alta Floresta, 9° 37’ 25” S, 55° 55’ 40” W, (MPEG, JDW-281, 1 August 1999).

Remarks. The unique chaetotaxy of the male tergite IX (Fig. 19), coupled with the male genitalic structure (Fig. 21) and the even inner boarder of the marginal head carina, affords the best means for separating this new species from other species in the group. The female subgenital plate is broader posteriorly (Fig. 20), but this feature is rather plastic and may not be consistent in additional material.

Etymology. This species is named for Robert C. Faucett in recognition of his valuable assistance collecting specimens vital to this and other studies of lice.

*Picicola oneilli* Price and Weckstein, new species
(Figs. 22–24)

**Type host.** *Notharchus macrorhynchos* (J.F. Gmelin), the White-necked Puffbird.

**Description.** Head shaped much as in Fig. 9, with marginal carina having irregular
inner border. Tergites II–IV each with 2 tergocentral setae; V, 3; VI–VIII, 4. Male tergite IX (Fig. 22) with very long heavy seta at each lateroposterior corner in addition to usual very long more median seta; both tergites VIII and IX medially narrowed. Male subgenital plate as in Fig. 23; genitalia as in Fig. 24, with an extremely short penis. Male dimensions: TW, 0.37; HL, 0.42; CI, 1.14; PW, 0.22; MW, 0.33; AWV, 0.44; GL, 0.25; PL, 0.015; TL, 1.43.

**Type material.** Ex *N. macrorhynchos*, holotype male (DNA voucher 1.13.2003.19), PERU: Dpto. Loreto, 86 km SE Juanjui on upper Rio Pauya, 7° 35’ 10” S, 75° 56’ 1” W, (LSUMZ, JPO-8121, 8 August 2000).

**Remarks.** Although this new species is based only on a single male louse, the unique small penis structure and the details of the posterior tergal sclerites make us confident of its distinctness. The chaetotaxy of tergite IX is similar to that of *P. faucetti* (Fig. 19), but the differences in penis size and the shape of the inner border of the marginal head carina enable easy separation.

**Etymology.** This species is named for John P. O’Neill in recognition of his generous assistance to students of Neotropical Ornithology and his collecting specimens vital to this and other studies of lice.

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**Picicola serrafreirei** Valim and Linardi
(Figs. 25–27)


**Redescription.** Head shaped as in Fig. 25, with broadly rounded preantennal portion and marginal carina having irregular inner border. Tergites II–VIII (Fig. 27) each with 5–8 tergocentral setae. Inconspicuous pleural thickenings without reentrant heads. Female subgenital plate close to Fig. 5; vulval margin with 6–9 short setae on each side, indented slightly medially, and with short seta displaced on each side lateroposterior to this row. Male subgenital plate as in Valim and Linardi (2006: Fig. 7); genitalia as in Valim and Linardi (2006: Figs. 5–6), with only 2 sensilla on each endomeral arm. Female dimensions: TW, 0.43–0.45; HL, 0.48; CI, 1.07–1.12; PW, 0.26–0.27; MW, 0.39–0.41; AWV, 0.49–0.58; TL, 1.66–1.81. Male dimensions (from Valim and Linardi 2006): TW, 0.33–0.44; HL, 0.43–0.47; CI, 1.07–1.30 (mean=1.13); PW, 0.23–0.26; MW, 0.33–0.38; AWV, 0.37–0.56; GL, 0.22–0.30; TL, 1.30–1.63.


**Remarks.** This species is unique among the *Picicola* found on the jacamars and
Discussion

The *Picicola* of the jacamars and puffbirds represent a morphologically very tight assemblage of species, distinct from the *Picicola* of the Picidae and suboscine Passeriformes, but with only relatively minor morphological differentiation among them. For example, *Picicola galbulica*, the only species known from the jacamars, is morphologically similar to *P. striata* from the puffbird genus *Malacoptila*. Our examination of morphological characters suggests that the irregular wavy shape of the inner margin of the head carina, with a narrowing at the level of the preantennal suture, differentiates all of the *P. striata* specimens examined from the morphologically similar *P. galbulica*. However, mtDNA COI sequences are nearly identical between DNA voucher specimens identified as *P. striata* and *P. galbulica* using morphological characters (Fig. 28). Uncorrected percent sequence divergence within and between *P. striata* and *P. galbulica* samples averaged 2.43% and ranged from 0.53–4.48%. These results may suggest that *P. galbulica* is inseparable from *P. striata*. However, we do not have molecular data from *P. striata* from the type host, *Malacoptila striata*, which would be critical to assess this potential synonymy.

The most distinctive louse of this group is *P. serrafreirei*, which is unique from the others by its possession of more tergocentral setae on all of the abdominal tergites. Species differentiation of most of the other *Picicola* species described here relies on details of the male genitalia, the chaetotaxy of male tergite IX, the chaetotaxy and shape of the female subgenital plate and associated vulval setae, and subtle differences in head shape. Mitochondrial COI sequences are consistent with these characters (Fig. 28) with uncorrected percent sequence divergence between all species, excluding comparisons between *P. striata* and *P. galbulica*, averaging 17.14% and ranging from 13.19% (between *P. faucetti* and *P. galbulica/P. striata*) to 23.48% (between *P. osheai* and *P. faucetti/P. valquii*).

At present only four out of eighteen species of Galbulidae and twelve out of thirty-three species of Bucconidae have *Picicola* described from them. No *Picicola* are described from four out of the five genera in the host family Galbulidae, including *Galbalcyrhynchus, Brachygalba, Jacamaralcyon, and Jacamerops*. Three out of ten genera from the host family Bucconidae, including *Hypnelus, Micromonacha*, and *Nonnula*, do not have *Picicola* described from them. Additional collecting from these host genera lacking *Picicola* records will likely yield new host associations and perhaps new species of *Picicola*. Furthermore, most puffbird and jacamar species are polytypic and, therefore, more detailed collecting could elucidate whether the parasites have patterns of geographic variation that match those of their hosts.
FIGURE 28. Phylogram based on maximum likelihood analysis of 379 base pairs of DNA sequence from the mitochondrial COI gene. Maximum likelihood tree searches involved 10 random addition replicates using the HKY + I + G model (parameters A=0.2761, C=0.1313, G=0.2063, T=0.3862; Ti/Tv Ratio = 4.5023; I=0.5086; α=0.6366). Numbers above or below branches are support from 100 likelihood bootstrap replicates (only values >50% are shown). Branch lengths are proportional to substitutions per site as indicated by the scale bar. Inset shows bootstrap values within the *P. galbulica/striata* clade. Phylogram is rooted on *Austrophilopterus andigenae* (DNA voucher 1.17.2000.8) and *A. thysii* (DNA voucher 1.17.2000.7) (not shown). Taxon labels include louse name, DNA voucher numbers, and host name. Host voucher specimen information is deposited in Genbank. *P. = Picicola*.

### Key to the Species of *Picicola* from the Jacamars and Puffbirds

1. Abdominal tergites II–IV each with 5 or more tergocentral setae (Fig. 27) .................. *P. serrafrei* Valim and Linardi
   - At least tergites II–IV each with only 2 tergocentral setae (Fig. 1) .................. 2
2. Head marginal carina with irregular inner border (Figs. 4, 9) .......................... 3
   - Head marginal carina with even inner border (Figs. 7, 12, 15) .................. 5
3. Cephalic index >1.18 (Fig. 4); penis length 0.035–0.040 (Fig. 8) .................. *P. striata* Oniki and Emerson
   - Cephalic index <1.17 (Fig. 9); penis length not over 0.030 (Fig. 11, 24) ................. 4
4. Male tergite IX with chaetotaxy as in Fig. 22; penis extremely short, 0.015 long (Fig.
Male tergite IX with chaetotaxy as in Fig. 3; penis longer, 0.025–0.030 long (Fig. 11)

- Male tergite IX with chaetotaxy as in Fig. 3; penis longer, 0.025–0.030 long (Fig. 11)

- Female vulval margin as in Fig. 17; chaetotaxy of male tergite IX as in Fig. 16

5 Female vulval margin as in Fig. 17; chaetotaxy of male tergite IX as in Fig. 16

- Female vulval margin as in Fig. 20; chaetotaxy of male tergite IX as in Fig. 3 or 19

6 Chaetotaxy of male tergite IX as in Fig. 19; male genitalia as in Fig. 21; female subgenital plate as in Fig. 20

- Chaetotaxy of male tergite IX as in Fig. 19; male genitalia as in Fig. 8 or 14; female subgenital plate as in Fig. 5

7 Penis as in Fig. 14; head shape as in Fig. 12

- Penis as in Fig. 8; head shape as in Fig. 7

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