

Revision of the Afrotropical species of *Parapachycerina* (Diptera: Lauxaniidae)

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ABSTRACT

Parapachycerina Stuckenberg, a genus of small, usually yellow-orange sapromyziform lauxaniids (Diptera: Lauxaniidae) restricted to the Old World, is redescribed. The African and Malagasy representatives are revised, with four new species described: *P. bispina* sp. n., *P. infuscata* sp. n., *P. lalitra* sp. n. and *P. talea* sp. n. There are now five Afrotropical *Parapachycerina* species, including the type species, *P. munroi* Stuckenberg, 1971. Further, the paper provides an identification key to the Afrotropical species, a summary of the available biological information, and preliminary remarks on the phylogenetic relationships of the genus.

KEY WORDS: Diptera, Lauxaniidae, *Parapachycerina*, *Neogeomyza*, *Neopachycerina*, *Tanyura*, taxonomy, identification key.

INTRODUCTION

The Afrotropical lauxaniid fauna comprises approximately 28 genera and at least 90 described species (Stuckenberg 1971; Miller 1980). Lauxaniids are generally small acalyprate flies, which can be identified in the vast Afrotropical acalyprate assemblage by, *inter alia*, their (a) lack of vibrissae, (b) two reclinate fronto-orbital bristles, (c) decussate (cruciate) postvertical bristles, (d) complete subcosta, (e) lack of costal breaks and (f) dorsal pre-apical tibial bristles.

The lauxaniid fauna in sub-Saharan Africa, as elsewhere in the world, is found principally in forest (e.g. *Homoneura* van der Wulp, *Cainohomoneura* Stuckenberg, *Prosomyza* Stuckenberg), moist savannah and grassland (e.g. *Chaetolauxania* Kertész, *Diplochasma* Knab), and shows low species richness and diversity in arid regions (e.g. <2% of lauxaniid specimen lots in the Natal Museum Diptera Collection originate from the drier, western provinces of South Africa, viz. Northern Cape, North-West and Free State).

Despite the widespread occurrence and diversity of lauxaniids in sub-Saharan Africa, little research has been published on the Afrotropical representatives in recent years. In this paper we revise *Parapachycerina*. The genus was erected by Stuckenberg (1971: 539) and, to date, only three species are recognized in the published literature (Shewell 1977; Miller 1980; Evenhuis & Okadome 1989): the type species, *P. munroi* Stuckenberg, 1971 and two Oriental species (both originally described as *Lauxania* species), *P. hirsutiseti* (de Meijere, 1910) and *P. cuneifera* (Kertész, 1913).

In his major review of Old World lauxaniids, Stuckenberg (1971: 588) indicated that ‘there are a number of species of *Parapachycerina* in tropical Africa, all undescribed, and these will be dealt with fully in a forthcoming monograph’. Later events precluded the production of this monograph, and it is the task of this paper to describe these new African and Malagasy *Parapachycerina* species.

The four goals of this paper are: (1) the description of new Afrotropical (including Malagasy) species; (2) the provision of an updated dichotomous key to the Afrotropical

species; (3) the description and illustration of the salient morphological features of the genus (except female postabdomen); and (4) a preliminary comparison with putatively related genera.

MATERIAL AND METHODS

Terminology generally follows Stuckenberg (1971) and Kim (1994), including their postabdominal terminology. Departures from their terminology are discussed hereunder. Antennal terminology is according to Stuckenberg (1999). A rather bewildering array of terms has been applied to cuticular processes (chaetation) in dipterology. In this paper, chaetotaxy largely follows Miller (1977a: 153), although the term 'setulae' is used more broadly here also to refer to very short, fine processes with alveoli. Although lauxaniidologists have used the term 'costal spinules' (e.g. Shewell 1987; Kim 1994), these processes are socketed (alveolus-derived) and are thus setulae rather than spinules, which are immovable, socket-less cuticular processes ('microtrichia' in D.K. McAlpine's (1973) terminology). Oddities also emerge when some standard chaetae change their length and shape; for example, in *Parapachycerina*, the anterior fronto-orbital bristle is a tiny, fine process and, structurally speaking, is not a bristle, which is defined in Miller (1977a) as a distinctly long, larger, more robust seta. *Pro tempore*, we continue to use such terms despite the inherent contradictions. Proboscidal terminology follows Broadhead (1984); specifically she identified remarkable serrated lamella-like modifications of the pseudotracheal canals as 'scoops' and 'prongs', and a hamate 'beak' at 'the anterior tip of the labial gutter' (Broadhead 1984: 646). *Contra* most dipterological papers, the 'face' is here termed the 'prefrons', a well-known synonym (e.g. D.K. McAlpine 1973: 17; J.F. McAlpine 1981: 10). The term face, although traditionally and widely-used in dipterology, is too general and open to misunderstanding by non-dipterists; its use in the discipline should be discontinued. The area usually called the 'frons' in dipterology (i.e. the area above the antennal sockets and below the vertex) is here termed the 'postfrons'. Following the arguments of D.K. McAlpine (2007: 32), the bristles usually termed 'postocellar bristles' (e.g. by most lauxaniid researchers) are here called 'postvertical bristles'. Following Stuckenberg (1971: figs 1, 2) the term 'sapromyziform costa' is used to indicate that the stubby costal setulae (as opposed to the fine costal setae) diminish in size and terminate before reaching R_{4+5} (vein 3), in contrast to the 'homoneuriform costa' (where the costal setulae reach R_{4+5}). Measurements are in millimetres (mm) and averages are cited with ranges in parentheses (except where there is no variability in measurements). Standard abbreviations for abdominal sclerites are used (e.g. T3 for tergite 3, S3 for sternite 3). Scanning electron microscope/microscopy is abbreviated as SEM. Male terminalia were removed from relaxed specimens, and treated for approximately 12–24 hours in KOH, before being transferred to acetic acid for approximately 30 minutes and finally water for another 30 minutes. Cleared terminalia were mounted in glycerine on microscope slides.

At times in this paper we indulge in some speculative narrative, an approach considered a scientific solecism by most researchers; see Sand-Jensen (2007) for rebuttal on this issue.

Material originated from the following institutions:

BMNH – Natural History Museum, London, UK;

CASC – California Academy of Sciences, San Francisco, USA;

- HNHM – Hungarian Natural History Museum, Budapest, Hungary;
 MHNB – Muséum d'Histoire Naturelle de Bâle (Basel), Basel, Switzerland;
 MNHN – Muséum National d'Histoire Naturelle, Paris, France;
 MRAC – Musée Royal de l'Afrique centrale, Tervuren, Belgium;
 NMSA – Natal Museum, Pietermaritzburg, South Africa;
 NMWC – National Museum and Gallery of Wales, Cardiff, UK;
 UZMD – Zoological Museum, Copenhagen, Denmark;
 ZMLU – Zoological Museum, Lund University, Sweden.

The type series of both *Parapachycerina munroi* Stuckenberg, 1971 (NMSA) and *Neogeomyza* (= *Micropachycerina*) *stenoptera* (Stuckenberg, 1971) (NMSA), and two specimens from the type series of *Neopachycerina aristata* Malloch, 1933 (BMNH), were all examined for this study.

TAXONOMY

Parapachycerina Stuckenberg, 1971

Parapachycerina Stuckenberg, 1971: 539. Type species: *Parapachycerina munroi* Stuckenberg, by original designation.

Diagnosis:

Small (ca 2.5–5 mm), compact, usually yellow-orange sapromyziform lauxaniids with two reclinate fronto-orbital bristles placed far forwards and close together on postfrons; anterior fronto-orbital bristle small (Fig. 1). Postfrons devoid of setulae (at 50×). Arista plumose; proximal rays longer than height of postpedicel. Postpedicel longer than high, slightly elongated. Ocellar triangle demarcated by dark brown or black spot. Ocellar bristles long, proclinate and subparallel. Prefrons (face) not bulging, without maculations. 0+3 dorsocentral bristles on scutum. No intra-alar bristle. Ctenidium present in some species on profemur. Two ventral mesotibial spurs. Wings hyaline or slightly infuscated. Surstylus unusual; tiny, displaced medially as narrow lamella or flat blade. Immature stages unknown.

In the Afrotropics, *Parapachycerina* most resembles *Neogeomyza* Séguéy, 1938 (= *Micropachycerina* Stuckenberg, 1971) of East Africa and Madagascar (Miller 1980: 606; see also McAlpine & de Keyser 1994: 307). *Neogeomyza* differs from *Parapachycerina* in having an even smaller anterior fronto-orbital (<0.2× length of posterior fronto-orbital bristle), a larger black ocellar spot, a mildly tumid and translucent prefrons (face), 0+2 dorsocentral bristles, fewer setal rows on scutum, no acrostichal bristles, and an anal lobe in the wing (see Stuckenberg 1971: figs 33, 34). As a generalization, *Neogeomyza* is also a more gracile and delicate-looking fly than *Parapachycerina*.

Description:

Colour and pruinescence: Head and thorax usually rich yellow-orange with orange medial mesonotal vitta/e, but dorsal surface of thorax and parts of head strongly infuscated in *P. infuscata*. Dark brown or black ocellar spot always present. *P. infuscata* with occiput mostly black, other species have occiput yellow-orange. Pruinescence weak (when viewed at 50×), some silver pruinescence usually visible on anterolateral corner of postfrons, parafacial, and dorsal surface of thorax (oblique lighting sometimes necessary to see pruinosity). Aside from fronto-orbital bristles, postfrons devoid of pruinosity and vestiture (when viewed at 50×), but when viewed with SEM (ca 500–

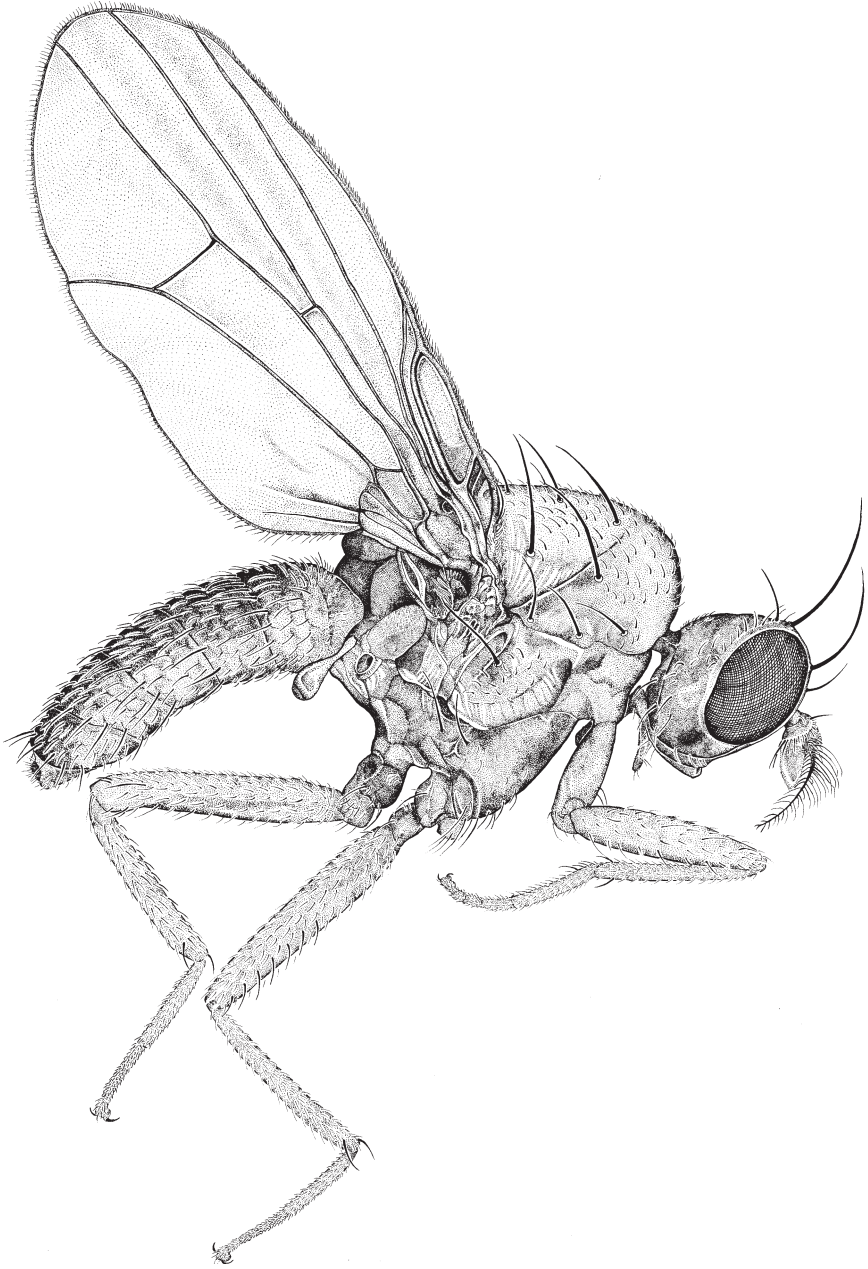
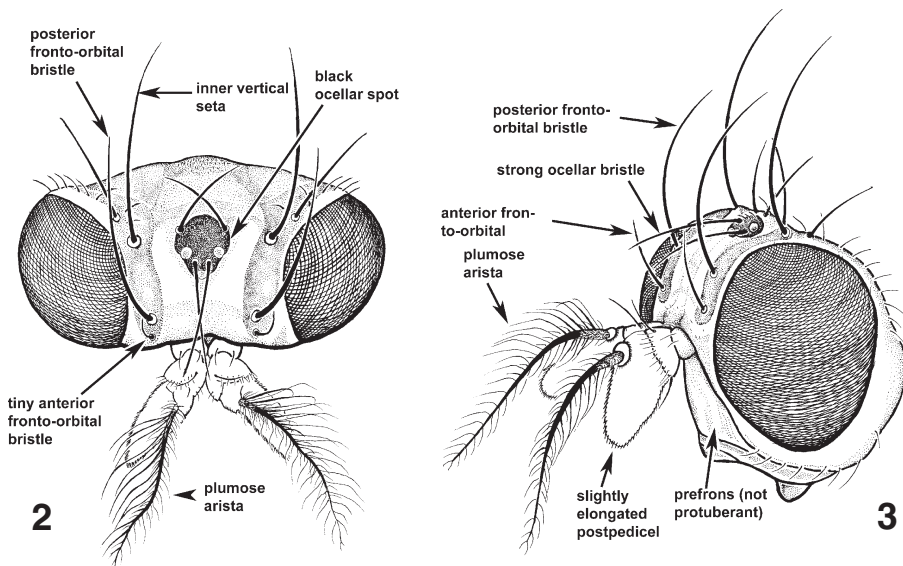


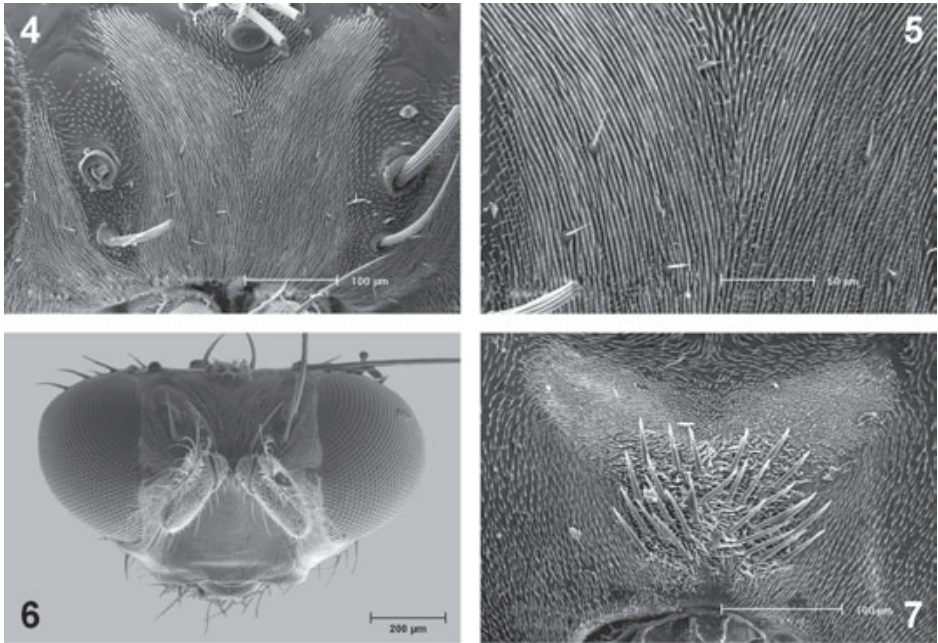
Fig. 1. *Parapachycerina munroi* Stuckenberg, type species of genus in lateral view. Length approximately 5 mm.



Figs 2, 3. (2) Dorsal view of head of *Parapachycerina munroi* Stuckenberg, (3) oblique lateral view of head of *P. lalitra* sp. n. Note small anterior fronto-orbital bristles (relative to posterior fronto-orbital bristles), short distance separating fronto-orbital bristles, plumose aristae and long ocellar bristles.

2000 \times) postfrons with abundant closely-appressed carinae bearing spicules on medial postfrontal surface, and prefrons with abundant spinules in irregular rows which are not borne on carinae. Eye red or greyish; sparse, simple ommatrichia between facets (only visible with SEM). Maxillary palpus yellow to black. Supracervical area with dusting of silver pruinescence. Haltere yellow or light orange. Legs yellow. Abdomen orange-brown to black, depending on species. Teneral specimens are lightly sclerotized and weakly pigmented, often with collapsed legs and heads.

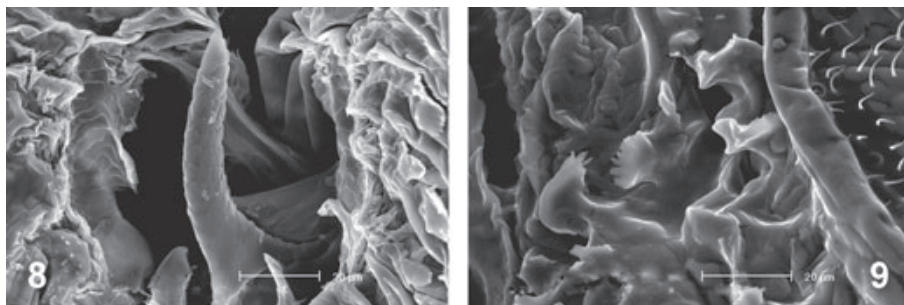
Head (Figs 2–9): Head higher than long, height:longitudinal length ratio 1.25:1. Head broader than long, transverse width:longitudinal length ratio 1.6:1. Head broader than high, transverse width:height ratio 1.5:1. Two reclinate fronto-orbital bristles, anterior bristle much shorter (*ca* 0.4 \times length) than posterior bristle and not as recurved. Fronto-orbital bristles placed far forward on frons, and close together (distance between fronto-orbital bristles is shorter than distance from posterior fronto-orbital to inner vertical seta). Posterior fronto-orbital bristle strong, only slightly shorter than inner vertical seta (*ca* 0.8 \times length). Antenna positioned high on head relative to eye (opposite upper third of eye). Arista plumose, rays longer on dorsal surface and progressively shorter distally. Proximal rays of arista are longer than the height of the postpedicel. Postpedicel longer than high (1.6:0.9), tapering gently to moderately pointed apex, shape differing subtly amongst species (most pointed in *P. munroi*). Pedicel *ca* 1/3 length of postpedicel, fan of *ca* 10 short, proclinate setulae distolaterally, single erect, latero-clinate seta dorsally, and two long, subparallel setae distoventrally (*ca* 0.7 \times length of postpedicel). Postfrons broader than high (3:2), gently to moderately curved in lateral profile (not straight); prefrontal (facial)-postfrontal angle obtuse. Prefrons not bulging; prefrontal (facial) carina weak. Orbital plates usually concolorous with remainder of frons and not easily differentiated, except in *P. infuscata*, where orbital plates usually easily discerned. Inner



Figs 4–7. (4) Postfrons of *Parapachycerina munroi* Stuckenberg showing abundant carinae medially, (5) medial section of *P. munroi* postfrons showing spiculate carinae, (6) anterior view of *P. munroi* head, (7) supracervical setulae on occiput of *P. munroi*.

vertical seta reclinate, and much longer than outer vertical seta (o.v.s. *ca* 0.4 \times length of i.v.s.); o.v.s. latero-clinate. Ocellar triangle variable, sides may be equal (e.g. *P. bispina*), sides may be longer than base (e.g. *P. infuscata*) or base may be longer than sides (e.g. *P. munroi*). Ocellar setae strong, semi-erect, proclinate, subparallel and extending to overhang pedicel; ocellar triangle with *ca* 3 inconspicuous, fugitive setulae behind ocellar setae. Postvertical bristles decussate; intersection of bristles about half-way up the bristles. Postocular setulae in a single row of *ca* 10 setulae, beginning between o.v.s. and i.v.s.; first 2 or 3 setulae separate from others, slightly longer, inclinate and resembling paravertical setulae. Occiput with 25–35 supracervical setulae. Occipital setulae sparse, restricted to ventrolateral corner of occiput, but extending up towards postocular setulae in some species (e.g. *P. bispina*), where forming weak second row behind postocular setulae. Postgena with sparse, scattered setulae. Gena moderately expanded. Proboscis with labellar ‘beak’, and pseudotracheael ‘scoops’ and ‘prongs’ (but preparations crude and further observations needed).

Thorax: 1 pair of acrostichal bristles (setae); 1 humeral (*ca* 10 weak setulae encircling bristle on callus); 2 notopleurals; 1 presutural; 1 supra-alar; 2 postalars (1 or 2 setulae between bristles), ventral postalar bristle (i.e. bristle closest to the pleurotergite) is considerably (*ca* 2 \times) longer than the upper postalar; no intra-alar bristle; 0+3 dorsocentral bristles; setulae rows fairly numerous and rather irregular in pattern, *ca* 6 longitudinal rows between dorsocentral bristles, *ca* 8–10 transverse rows behind transverse suture; 1 mesopleural bristle, placed near posterior margin, attended closely by *ca* 10 short setulae; 1 or 2 sternopleural bristles (if present, anterior bristle weaker and *ca* 0.7 \times



Figs 8, 9. (8) Falcate labellar 'beak' of *Parapachycerina munroi* Stuckenberg, (9) labellar 'scoops' and 'prongs' of *P. munroi*.

length of posterior one). Prosternum bare (at 50 \times). Propleural bristle present, but small and inconspicuous. Posterior pair of bristles on scutellum decussate.

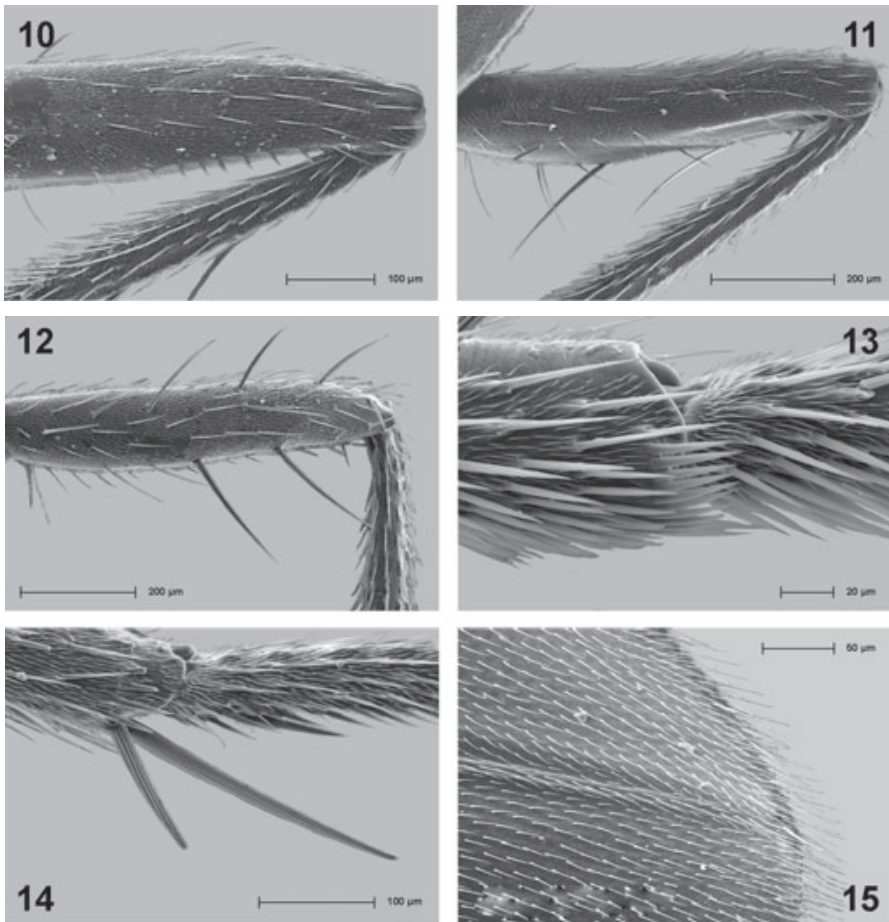
Legs (Figs 10–15): Procoxa has row of 4–6 setae (and a few scattered setulae) on anteroventral margin. Ctenidium on profemur variably present in some species; when present, 4–9 short, stout setulae (rather resembling teeth on a saw). Profemur with posteroventral row of 2 or 3 long setae and posterodorsal row of *ca* 4 setae. Distoposterior edge of protibia with 2 short spurs, anterior spur *ca* 2 \times length of posterior spur. Small (grooming?) comb of *ca* 10 stout setulae on inner apex of protibia and metatibia (absent on mesotibia). All tibia with dorsal, pre-apical dorsal seta (most robust on mesotibia). Mesocoxa has fan of *ca* 6 setae (no setulae). Mesofemur with anteromedial row of *ca* 5 stout, proclinate setae; mesofemur posteriorly largely bare. Mesotibia with 2 short, divergent, distoventral spurs (posterior spur 0.5 \times length of anterior spur). Metafemur with anterodorsal, preapical, stout, semi-erect seta. Two flattened spurs on inner face of metatibia, anterior one is longer.

Wing: Hyaline or weakly infuscated (in two species). Costa sapromyziform (stout costal setulae terminating 3/4 way between R_{2+3} and R_{4+5}). Costal chaetotaxy Type B2 *sensu* Hackman & Väisänen (1985: 171). Subcosta and R_1 (Vein 1) closely associated, but diverging somewhat when terminating on costal margin. Veins A_2 and A_1+CuA_2 parallel, A_2 extending much further towards hind margin of wing (but still falling well short), A_1+CuA_2 shorter than A_2 .

Abdomen: Chaetation pattern conservative: row of *ca* 10–15 flat, black setae on posterior margins of syntergite 1+2, T3 and T4, on T5 and T6 these posterior rows become erect. T2 with lateral tufts of short setae. Abdomen tapering posteriorly, T6 slightly less than half (transverse) width of syntergite 1+2.

Male terminalia (e.g. Figs 20–22 of type species; Stuckenberg 1971: figs 91, 92; Sasakawa 2003: fig. 2): Protandrium saddle-shaped (i.e. broad dorsally and narrowing laterally), asetulose and continued ventrally as narrow band (i.e. protandrium is entire). Epandrium displays interspecific variation, but broader laterally than dorsally (cf. protandrium), usually elongated posteriorly as epandrial process (especially in *P. bispina* and *P. lalitra*); sparse cover of scattered vestiture (*ca* 15 setulae laterally and *ca* 4 strong setae on medio-posterior edge dorsally). Surstylus small, narrow, laterally compressed, posteriorly hooked lamella or dorsoventrally flattened, blade-like process, fused to inner margin of epandrium; inconspicuous in lateral view, usually resembling small finger projecting posteroventrally. Cerci separate, heavily setulose and partially

exposed in lateral view. Inner genitalia small, lightly sclerotised, tightly associated and composed of two ‘systems’: hypandrium + gonopods and aedeagal apodeme + aedeagus; minor additional sclerites include ejaculatory apodeme and subepandrial sclerite. In repose, genitalia point posteriorly, parallel to protandrium and epandrium. No setulae visible on any of genitalic sclerites (at 50×). Hypandrium ventral-most sclerite lying beneath aedeagal apodeme and anterior part of aedeagus; U- or H-shaped, consisting of thin ‘transverse band’ and narrow, lateral arms; hypandrium lacks any medioanterior process. Width of transverse band varies, as does length of lateral arms. Lateral hypandrial arms rise obliquely upwards and posteriorly towards gonopods. At apex of lateral hypandrial arms, hypandrium extends dorsally and anteriorly as thin, weakly sclerotized ‘filaments’ (here termed the ‘dorsal loop’) articulating weakly on anterolateral or anterodorsal edge of aedeagus. Hypandrium can be visualized as square frame of thin sides



Figs 10–15. (10) Profemur of *Parapachycerina infuscata* sp. n. with ctenidium (comb) of short, stout setulae on anteroventral edge, (11) profemur of *P. munroi* Stuckenberg without ctenidium, (12) posterior view of *P. munroi* profemur showing dorsal and ventral rows of setae, (13) presumed grooming comb on distal edge of *P. munroi* protibia, (14) distoventral mesotibial spurs of *P. munroi*, (15) saporomyziform costa of *P. infuscata* sp. n.

that has partially folded back on itself. Articulating with posterior apices of lateral hypandrial arms are sheath-like, ensiculate or gently rounded gonopods. Gonopods usually closely ensheath apical part of aedeagus. Aedeagus best visualized as tubular structure ('aedeagal tube') comprising two blade-like halves or 'wings' joined anteriorly in narrow 'dorsal arch' (dorsal-most part of genitalia, cf. hypandrial transverse band); the two halves taper to pointed apices posteriorly where ensheathed by gonopods. Medially, aedeagus is membranous, but this section may be dissolved by strong KOH treatment. Anteriorly, two halves of aedeagus may bulge out in anterolateral flanges. Aedeagal apodeme articulates posteriorly with aedeagus, and is fairly narrow, laterally compressed, Y-shaped, ribbon- or rod-like sclerite, with two short posterior arms. Depending on species, aedeagal apodeme may be longer than aedeagus, approximately equal in length, or slightly shorter. Ejaculatory apodeme is tiny sigmoidal or T-shaped sclerite lying dorsally above bifurcation of aedeagal apodeme. Above posterior sections of aedeagus is subepandrial sclerite, a subrectangular sclerite attached by membranous tissue to posteroventral edge of cercus.

Female terminalia: Unexceptional, short and blunt (not elongated); S9 subrectangular with straight posterior edge and lightly setulose; subanal and supra-anal plates roughly semi-circular; cerci dorsoventrally flattened. Inner genitalia not investigated. Stuckenberg (1971: 590) reported three subspherical spermathecae.

Key to Afrotropical *Parapachy cerina*

- 1 Ctenidium (comb) present on anteroventral edge of profemur; ocellar spot brown or black 2
- Ctenidium (comb) absent on anteroventral edge of profemur; ocellar spot black 6
- 2 With upper parts of occiput black 3
- Without black markings on occiput 4
- 3 Dorsal surface of thorax dark chestnut brown to black, mesonotum with silver pruinosity; mesopleuron yellow to orangish brown, no black mark [widespread in sub-Saharan Africa] **P. infuscata** sp. n.
- Dorsal surface of thorax orange with three black stripes, silver pruinosity weakly developed; mesopleuron with large black patch, orange-yellow colouration restricted to margins of mesopleuron [Comoros] Undescribed taxon C
- 4 Part of brown ocellar spot posteriorly with a short medial extension (rod); apex of postpedicel darkened, wings anteriorly fumose [Madagascar] **P. talea** sp. n.
- Brown ocellar spot confined to ocellar triangle, apex of postpedicel not darkened; wings hyaline 5
- 5 Gonopods long, as long as aedeagus; ventrolateral edge of aedeagus with mucro and small notches [Madagascar] **P. lalitra** sp. n.
- Gonopods short, only half as long as aedeagus; ventrolateral edge of aedeagus without mucro, and largely smooth [Madagascar] Undescribed taxon A
- 6 Black ocellar spot extends backwards to clearly touch inner margins of postvertical setal sockets; wing hyaline [southern and western Africa] **P. munroi** Stuckenberg
- Black ocellar spot confined to ocellar triangle; wing infuscated anteriorly 7

- 7 Cross-veins of wing infuscated; ocellar triangle large and ocellar spot deep black [widespread in sub-Saharan Africa] **P. bispina** sp. n.
 – Cross-veins of wing not infuscated; ocellar triangle small and ocellar spot dark brown [Madagascar] Undescribed taxon B

Parapachycerina bispina sp. n.

Figs 17, 23

Etymology: From Latin *bis* (twice) and *spina* (thorn, spine, spike); refers to the two stout setulae on the apex of the surstylus, which are characteristic of the species.

Diagnosis:

P. bispina is broadly sympatric over much of Africa with *P. munroi*, and can be separated from that species by: (1) the black ocellar spot not extending back to touch the postvertical setae; (2) wing with light brown infuscations, shading the outer 3/4 of the costal cell, most of the marginal cell and anterior portion of the submarginal cell, anterior and posterior cross-veins (r–m; m–m) and also M_{3+4} (vein 5) (*P. bispina* is the only Afrotropical species in the genus with marked wings, apart from the Malagasy *P. talea*); (3) the paired, black spines on apex of epandrial process; and (4) pale orange-yellow cerci (dark brown in *P. munroi*). *P. bispina* is also sympatric in areas with *P. infuscata*, but the deep yellow-orange coloration, gently rounded vertex, black ocellar spot and absence of a ctenidium distinguish *P. bispina*.

The wing illustration purportedly of *P. munroi* in Stuckenberg (1971: fig. 42) is in fact *P. bispina* (as it shows infuscation of the cross-veins and anterior portions of the wing). This specimen is noted as a *P. munroi* paratype in the legend, but no specimen bearing these wing characteristics can be found in the *P. munroi* paratype series (NMSA), and evidently there was some mix up in the preparation of that figure.

Description:

Colour: Viewed with naked eye and under low magnification, impression is of uniformly rich yellow-orange fly. Occiput yellow. Ocellar spot deep black. Scape, pedicel and postpedicel all yellow, slight darkening at base of arista; pedicel may have orange tinge. Maxillary palpus yellow-orange. Thorax yellow-orange with two orange longitudinal stripes (vittae) on scutum (faint in some specimens), stripes are placed slightly mesad of dorsocentral bristles. Scutum sometimes shows darkening on humeral callus and along border of notopleuron and mesopleuron. Postnotum and postscutellum yellow-orange. Scutellum yellow with broad orange medial stripe. Mesopleuron, pteropleuron, sternopleuron, pleurotergite and meropleuron all yellow-orange. Haltere pale yellow. Legs yellowish. Abdomen yellow-orange to dark brown (generally the former).

Head: Postfrons fairly strongly sloping, wider than long (3:2). Orbital plates weakly differentiated from surrounding postfrons. Postfrons ending in narrow lip over proximal portion of scape. Prefrons very weakly tumid. Ocellar triangle large and expanded (relative to other Afrotropical *Parapachycerina* species), anterior ocellus nearly reaching level of posterior fronto-orbital bristle; ocellar spot encloses all three ocelli.

Thorax: Five or six longitudinal, rather irregular rows of setulae between dorsocentral bristle rows. Posterior pair of acrostichals *ca* 0.5× length of posterior dorsocentral bristles. Anterior dorsocentral bristle *ca* 0.5× length of posterior dorsocentral; middle

dorsocentral intermediate in length. Weak, barely visible pruinosity on scutum. Two sternopleural bristles, posterior bristle more robust and longer (area around bristles generally bare of setulae; ventrally usually a patch of *ca* 20 setulae). Pteropleuron, meropleuron, pleurotergite and prosternum bare of bristles and setulae.

Legs: No ctenidium on profemur, in that area *ca* 8 widely-spaced, weak setulae. Profemur posteriorly with ventral row of *ca* 3 strong, widely-spaced setae and dorsal row of *ca* 6 equally strong setae. 2 short spurs on posterior, distal edge of protibia, outer spur is *ca* 2× length of inner spur. Procoxa has ventral row of *ca* 4 or 5 setae and few scattered setulae. Mesocoxa has fan of *ca* 6 setae (no setulae visible). Mesofemur strong, anteromedial row of 5 robust, proclinate setae, posteriorly largely bare. Metacoxa largely bare, but 2 strong setae on opposite margins of coxa. Metafemur with unexceptional vestiture of *ca* 6 irregular rows of setulae on anterior face.

Wings: Mostly hyaline, but distal 3/4 of costal cell, most of marginal cell and anterior section of submarginal cell, anterior and posterior cross-veins (r–m, m–m) and M_{3+4} (vein 5) light infuscated (in some specimens infuscation very pale and requiring careful discrimination).

Male terminalia (Figs 17, 23): Protandrium roughly ring-shaped in transverse view, having small ventral processes, in lateral view fairly narrow dorsally and tapering laterally (slightly less so than in type species, *P. munroi*). Epandrium moderately broad dorsally, expanding posterolaterally, before tapering to small, rounded epandrial extension, at apex of epandrial extension characteristic stout, paired, black setae, in extracted genitalia inclinate, interdigitate with opposing pair, lower seta of each pair is longer than upper seta (upper seta is *ca* 0.8× length of lower seta). Surstylus hidden in lateral view, fused to inner medial margin of epandrium. Surstylus relatively large (in relation to aedeagus), flattened dorsoventrally, blade-like, tapering posteriorly to acute point and with mediolateral mucro. Surstyli closely associated with aedeagal complex (could on initial examination be considered to be gonopods). Cerci pale yellow. Hypandrium composed of broad ‘transverse band’, short, weakly latero-clinate anterior arms and longer, inclinate posterior arms that curve upward to terminate near base of gonopods and lateral edges of aedeagus (in ventral view, hypandrium resembles a ‘wobbly’ H). Hypandrial ‘transverse band’ broader than ‘aedeagal tube’. Aedeagal apodeme approximately same length as aedeagus, bifurcating beneath ‘dorsal arch’ of aedeagus. Aedeagus composed of two halves (‘wings’) that taper posteriorly, halves meet anteriorly in ‘dorsal arch’; posteriorly each ‘wing’ is bifurcate, subapically each half (wing) has ventrolateral mucro. Medially, aedeagus is membranous. Gonopods are blade-like, lightly sclerotised, broad basally, emarginate subbasally, widening medially and tapering to acute apex.

Measurements: total length – ♀ (n=7) 3.6 (3.2–4.1), ♂ (n=2) 3.2 (2.9–3.5); head height – ♀ (n=7) 0.7 (0.6–0.8), ♂ (n=2) 0.7; head width – ♀ (n=5) 1.1, ♂ (n=1) 1; head length – ♀ (n=7) 0.5 (0.5–0.7), ♂ (n=2) 0.6, thorax length – ♀ (n=7) 1.4 (1.3–1.5), ♂ (n=2) 1.4, wing length – ♀ (n=5) 3.3 (3.0–3.7), ♂ (n=2) 3.0; abdomen length – ♀ (n=7) 1.7 (1.3–2.1), ♂ (n=2) 1.3.

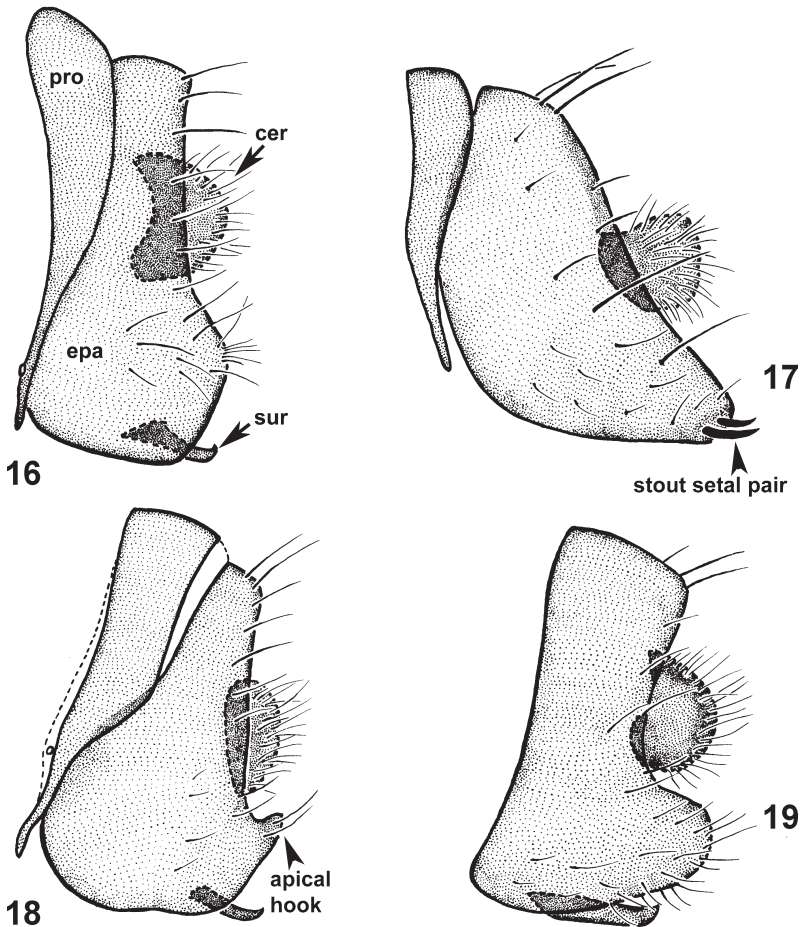
Holotype: ♂ SOUTH AFRICA: *Limpopo*: Kruger National Park, Pafuri, near Luvuvhu R., 22–23.iv.1981, R.M. Miller & P. Stabbin (NMSA).

Other material examined: CAMEROON: 2♀ Baigom, Bamoun, no date (MNHN); 1♂ Lake Barombi (near Kumba), 1939 (MNHN). DEMOCRATIC REPUBLIC OF CONGO: 1♀ Walikale (39 km S of), 25.xii.1957, E. Ross & R. Leech (CASC). GUINEA: 1♂ Mount Nimba, M. Lamotte and R. Roy, vii–xii.1951 (MNHN).

IVORY COAST: 1 ♀ Lamto, Bandana, 22.xii.1971, D. Lachaise (MNHN). KENYA: 1 ♂ Kakamega Forest, Isecheno Station, 22.vi.1995, Earthwatch Team (NMSA). NIGERIA: 1 ♂ 1 ♀ Bauchi State, nr Tilden Fulani, Kogin Salla, 9.iii.1997, J.C. Deeming (NMWC). SOUTH AFRICA: *Limpopo*: 1 ♂ 2 ♀ same data as holotype (NMSA). *Mpumalanga*: 2 ♂ 1 ♀ Nelspruit (20.5 km S of), Noordkaap R., 1–2.xii.1976, R.M. Miller & P. Stabbins (NMSA). *KwaZulu-Natal*: 1 ♀ Pietermaritzburg, Ukulinga Research Farm, 13.viii.2007, R.M. Miller (NMSA); 1 ♂ 1 ♀ same data except 22.viii.2007 (NMSA); 1 ♀ Pietermaritzburg, 10.x.1985, R.M. Miller (NMSA); 1 ♀ Ndumo Game Reserve, 1–10.xii.1963, B. & P. Stuckenberg (NMSA). TANZANIA: 1 ♂ 1 ♀ Matengo Highlands, WSW of Songea, xii.1935–i.1936, Zerny (NMSA). UGANDA: 1 ♀ Budongo Forest, 14.xi.1972, H. Gønget (UZMD); 1 ♀ Kampala, Tank Hill, 22.xii.1970, H. Gønget (UZMD); 4 ♂ 1 ♀ Semliki Forest, 27.viii–3.xi.1952, Fletcher (BMNH); 1 ♀ Ankole, Kalinzu Forest, 6–15.ii.1973, H. Gønget (UZMD); 1 (sex unknown) Segibwa Falls, 29.iii.1935, E.G. Gibbins (BMNH); 2 ♀ Mujenje, viii–ix.1913, K. Kittenberger (HNHM).

Distribution: Throughout much of sub-Saharan Africa. From KwaZulu-Natal (South Africa) in the south, northwards to Guinea in West Africa and Uganda in East Africa.

Remarks: 1 ♂ 3 ♀ Amani, East Usambara Mts, 27.i.1977, H. Enghoff *et al.* (UZMD) are notable for their expanded ocellar triangles and may potentially represent a new species.



Figs 16–19. Lateral views of outer ♂ terminalia: (16) *P. munroi* Stuckenberg, (17) *P. bispina* sp. n., (18) *P. infuscata* sp. n., (19) *P. lalitra* sp. n. (protandrium of *P. lalitra* not illustrated). Abbreviations: cer – cercus, epa – epandrium, pro – protandrium, sur – surstylus.

***Parapachy cerina infuscata* sp. n.**

Figs 10, 15, 18, 24

Etymology: From Latin *infuscus* (dusky, dark or blackish); refers to the black coloration on head and thorax, immediately setting the species apart from congeners.

Diagnosis:

Small (*ca* 2.8–3.5 mm) flies notable for the darkened scapes and pedicels (but some variation, with certain individuals having yellow scapes and pedicels), black orbital plates, blackish mesonotum and scutellum, black roughly triangular patches on the occiput, and dark triangular patches on anterolateral corners of postfrons (covered in silver pollinosity; from certain angles giving the impression of reflective ‘head-lights’). Prefrons may also be partially infuscated. This strong melanin deposition is unusual in the genus, and facilitates identification of the species. Teneral specimens are pale, and may be confused with *P. munroi* and *P. bispina*, which are, however, rich yellow-orange and lack a profemoral ctenidium.

Description:

Colour: Occiput with dark brown or black triangular markings on upper half; lower half yellowish; silvery pruinescence above supracervical setulae. Ocellar spot black. Scape and pedicel may vary from yellowish to dark brown or black. Individuals from one locality may show complete variation. Postpedicel yellow, base around arista rather tumid and brown. Maxillary palpi yellow to dark brown. Proboscis orange-yellow. Mesonotum and scutellum dark chestnut-brown to blackish, edges yellow to orange, dorsum covered in conspicuous silver pruinescence. Propleuron, mesopleuron, sternopleuron, meropleuron and pteropleuron yellow to orangish brown. Postscutellum and postnotum dark brown. Knob of haltere yellow to orange-brown. Abdomen dark brown or black.

Head: Ocellar plates vary from weakly differentiated from remainder of postfrons (i.e. mildly shiny, yellow portions of postfrons) to strongly differentiated, black, shiny longitudinal plates (individuals from same population can show this variation). Ocellar triangle small and sides approximately equal in length. Vertex/occiput boundary abrupt. Eye somewhat emarginate ventrally, slightly pointed.

Thorax: Two sternopleural bristles. Approximately 6 irregular, transverse rows of setulae behind suture.

Legs: Profemoral ctenidium with 4–8 setulae. Profemur posteriorly with ventral row of 2 setae and dorsally with row of 3 setae. Mesofemur with distal medio-anterior row of 4 setae.

Wings: Hyaline.

Male terminalia (Figs 18, 24): Protandrium saddle-shaped, narrowing sharply laterally. Epandrium fairly narrow dorsally, bulging antero- and posterolaterally; posterior epandrial process short, dorsally hooked. Surstylus thin, laterally compressed lamella with hamate tip, fused to inner edge of epandrium. Cerci dark brown. Hyandrium U-shaped, ‘transverse band’ fairly broad (slightly exceeding width of ‘aedeagal tube’), lateral posterior arms very short, ‘dorsal loop’ of hyandrium articulated on anterolateral margin of aedeagus. Gonopods blade-like, tapering unevenly posteriorly to pointed apices, closely ensheathing aedeagus. Aedeagal apodeme short (slightly shorter than aedeagus).

Ejaculatory apodeme lying above aedeagal apodeme, tiny, T-shaped sclerite. Subepandrial sclerite of irregular outline, lying below cercus.

Measurements: total length – ♀ (n=4) 3.2 (2.8–3.7), ♂ (n=2) 3; head length – ♀ (n=4) 0.5 (0.5–0.6), ♂ (n=2) 0.5; head height – ♀ (n=4) 0.6 (0.6–0.7), ♂ (n=2) 0.6; head width – ♀ (n=4) 1.0 (0.8–1.1), ♂ (n=2) 0.9; thorax length – ♀ (n=4) 1.4 (1.2–1.6), ♂ (n=2) 1.4; abdomen length – ♀ (n=4) 1.3 (1–1.5), ♂ (n=2) 1.2; wing length – ♀ (n=4) 2.8 (2.5–3.1), ♂ (n=2) 2.7.

Holotype: ♂ SOUTH AFRICA: *KwaZulu-Natal*: Enseleni N.R., near Empangeni, 26.vii.1980, R. M. Miller (NMSA).

Other material examined: DEMOCRATIC REPUBLIC OF CONGO: 1 ♀ Virunga National Park, Rwindi, 20–24.xi.1934, G.F. de Witte Mission (MRAC); 1 ♀ Virunga National Park, Kanyabayongo (Kabasha), 7.xii.1934, G. de Witte (MRAC); 1 ♂ Virunga National Park, Kabasha Escarpment, 12.xii.1934, G. de Witte Mission (MRAC); 1 (sex unknown) Kivu, Rutshuru, Rutshuru R., 3.vii.1935, de Witte Mission (MRAC); 2 ♂ ♀ Garamba National Park, 13.ii.1952, 8.iv.1952, 31.iii.1952 (MRAC); 3 ♀ Garamba National Park, de Saeger Mission, 2.iv.1952 (♀), 8.v.1951 (2 ♀) (MRAC); 1 ♂ 1 ♀ Garamba, 2.v.1952, 3.i.1952 (MRAC). KENYA: 2 ♂ Matembur, 26–27.v.1980, Malaise trap, B. Lamoral (NMSA). NIGERIA: 1 ♀ North West State, Mokwa IAR, viii.1970, P. Ward (BMNH); 1 ♀ Zaria, Samaru, 5.ix.1964 (BMNH) and 1 (sex unknown) from same locality, x.1979, J. Deeming (NMWC). SOUTH AFRICA: *Mpumalanga*: 6 ♀ Nelspruit (20 km S of), Noordkaap R., 1–2.xii.1976, R.M. Miller (NMSA); 2 ♀ Ofcolaco, Selati R., 7–8.xii.1976, R.M. Miller (NMSA). *KwaZulu-Natal*: 3 ♂ 16 ♀ Enseleni Nat. Res., 26.vii.1980, R.M. Miller (NMSA); 1 ♂ 8 ♀ same locality, 14.ii.1981, R.M. Miller (NMSA); 2 ♀ Dukuduku Forest (between St Lucia and Mtubatuba), 7–8.iv.1960, B. & P. Stuckenberg (NMSA); 1 ♂ 2 ♀ Umtentweni R., vii.1951, A.L. Capener (NMSA); 1 ♀ Krantzkloof Nat. Res., nr Durban, 18.xii.1990, A. Whittington (NMSA); 1 ♀ same locality, 24.xi.1999, S. James (NMSA). UGANDA: 1 ♀ Mujenje, viii.1913, K. Kittenberger (HNHM). ZIMBABWE: 1 ♀ North Vumba, 27.ii.1965, D. Cookson (NMSA).

Distribution: South Africa (coastal KwaZulu-Natal, escarpment of Mpumalanga), eastern Zimbabwe (Vumba mountains), Democratic Republic of the Congo, Kenya, Uganda, Nigeria.

***Parapachycerina lalitra* sp. n.**

Figs 3, 19, 25–27

Etymology: From Malagasy *lalitra* (a fly) (Anonymous 1999).

Diagnosis:

Diminutive (*ca* 2.5 mm) Malagasy species with yellow-orange head and thorax, and dark brown abdomen. Ocellar triangle small and dark brown, with sides and base of triangle equal. Postpedicel all yellow with no dark patches or infuscation. Profemoral ctenidium with *ca* 4 setulae. Wings hyaline. *P. talea* (which can be sympatric, e.g. at Andasibe), is larger (*ca* 3.7 mm), darker orange in colour, and has fumose wings and darkened apices to postpedicels. An undescribed *Parapachycerina* taxon A, represented by a single male from the east coast is extremely similar, and can only be separated by dissection of the male genitalia (see below and Figs 25–28). Another undescribed Malagasy taxon (B) from Amber Mt in the far north of the island, is larger and lacks a profemoral ctenidium (see below).

Description:

Colour: Head yellow, ocellar spot dark brown and confined to ocellar triangle, scape, pedicel and postpedicel yellow (no darkening, not even at arisal base). Maxillary palpi yellow. Thorax yellow, medial orange-brown stripe on scutum (between dorsocentral bristles) and scutellum, stripe more pronounced on scutellum. Brown wedge on noto-

pleuron (may be faint). Haltere pale yellow. Legs all yellow. Abdomen dark brown, first two segments slightly paler. Protandrium, epandrium and genitalia yellow.

Head: Largely as per genus. Orbital plates shining, but not easily differentiated from surrounding postfrons at low magnification (6–25×). Ocellar triangle small, all sides approximately equal in length, *ca* 4 ‘fugitive’ setulae between posterior ocelli; vertex/occiput boundary rounded (not abrupt). Prefrons very weakly tumid, slightly translucent.

Thorax: Largely as per genus. Acrostichal bristles very short, only *ca* 0.2× length of posterad dorsocentral bristles.

Legs: Profemoral ctenidium with *ca* 4 setulae. Profemur posteriorly with ventral row of *ca* 2 setae and dorsal row of *ca* 4 setae.

Wings: Hyaline.

Male terminalia (Figs 19, 25–27): Protandrium saddle-shaped. Epandrium narrow dorsally and laterally, slight protuberance in posterior lateral margin; epandrium expands posteriorly in broadly rounded, hirsute epandrial process. Surstylus long thin lamella fused to inner edge of epandrium, dorsally with weakly hamate tip. Cerci dark brown, hirsute. Hypandrium rather complex relative to other species in genus, transversely broad but longitudinally narrow ‘transverse band’ (broader than ‘aedeagal tube’), fairly short lateral posterior arms that rise dorsally at oblique angle then curve back anteriorly and continue as ‘dorsal loop’ terminating on anterodorsal (not lateral) corner of aedeagus; below ‘transverse band’ is unique (within genus), lightly sclerotised extension or ‘apron’. Aedeagal apodeme stem long (exceeding aedeagus in length), posterior arms very short. Aedeagus composed of two halves (‘wings’) and membranous medial section; aedeagal halves of unusual shape, externally with noticeable mucro on ventrolateral margin, deep incision subapically and recurved, falcate apices (resembling claws); small spinules (teeth) on posterior subapical margin of aedeagal halves. Gonopods long, unexceptional, broadly tapering to rounded apices; unlike other species in genus, gonopods do not tightly ensheath aedeagus. Subepandrial sclerite rather lunate in shape and lying ventrad of cercus. Ejaculatory apodeme not evident (probably lost during dissection).

Measurements: ♂ (n=1) ♀ (n=1): total length – ♀ = 2.5, ♂ = 2.5; head height – ♀ = 0.7, ♂ = 0.5; head width – ♀ = 0.8, ♂ = 0.8; head length – ♀ = 0.4, ♂ = 0.4; thorax length – ♀ = 1.2, ♂ = 1.1; wing length – ♀ = 1.4, ♂ = 1.3; abdomen length – ♀ = 0.9, ♂ = 1.1.

Holotype: ♂ MADAGASCAR: Andasibe (= Périnet), xii.1955, B. Stuckenberg (NMSA).

Other material examined: MADAGASCAR: 1 ♀ same datum as holotype (NMSA); 2 ♀ Ranohira, 26.i–4.ii.1958, B. Stuckenberg (NMSA).

Distribution: Restricted to Madagascar. Recorded from eastern escarpment (Andasibe), and western edge of Horombe escarpment in south-central portion of the island (Ranohira).

Parapachycerina munroi Stuckenberg, 1971

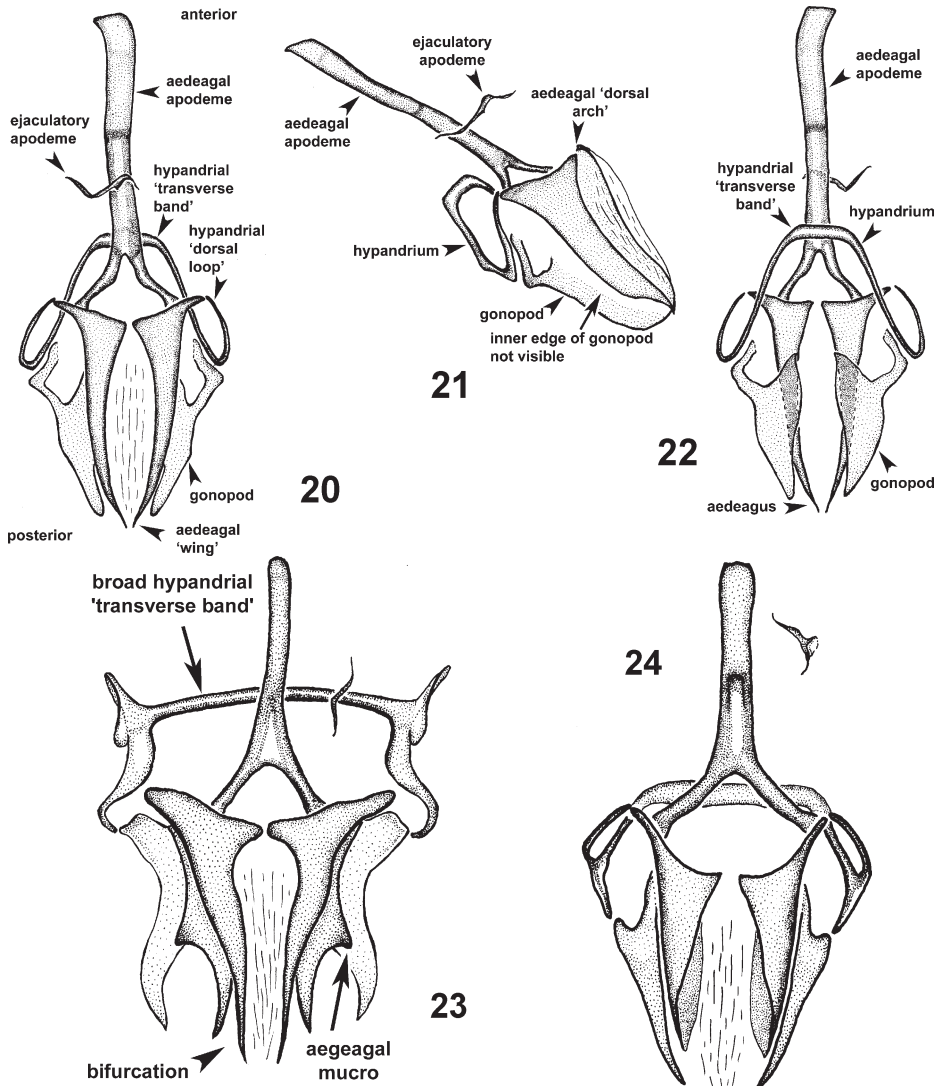
Figs 1, 2, 4–9, 11–14, 16, 20–22

Parapachycerina munroi Stuckenberg, 1971: 588. Type locality: Nangweshi, Zambesi River, Zambia.

Stuckenberg’s (1971: 588–590, figs 35 (head), 89–92 (male terminalia)) description was thorough, and does not need to be revisited. However, as mentioned above, the photograph of the wing purportedly of *P. munroi* (Stuckenberg 1971: fig. 42) is that of

P. bispina (as it shows infuscation of the anterior portion of the wing and cross-veins). Furthermore, all eight specimens mentioned in Stuckenberg's description originated from Nangweshi (16°26'S:23°20'E) in western Zambia. This gives an incomplete impression of the distribution of the species. *P. munroi* is in fact broadly distributed throughout much of southern and western Africa, as the following records show.

Material examined: ANGOLA: 1 ♀ Villa Luso, Moxico, 25.ix.1949, B. Malkin (CASC); 1 ♂ Dundo, ii.1960, B. Machado (NMSA). DEMOCRATIC REPUBLIC OF CONGO: 1 ♂ Lumbumbashi, Sabenahouse, 1280 m, 23.i.1958, E.S. Ross & R.E. Leech (CASC). GAMBIA: 1 ♀ at road junction to Situ Sinjang, 1.iii.1977, Cederholm *et al.* (ZMLU). IVORY COAST: 1 ♀ Lamto, 8.v.1971, Q. Flauch (MNHN); 1 ♀ Lamto, 3.iv.1971, Q. Flauch (MNHN). NIGERIA: 1 (sex unknown) Ibadan, 16.i.1966, J. Deeming (BMNH); 1, Zungeru, xi.1910, J.W.



Figs 20–24. Inner ♂ genitalia: (20–22) *P. munroi* Stuckenberg in dorsal (20), oblique dorsal (21), and ventral (22) views; (23) *P. bispina* sp. n. and (24) *P. infuscata* sp. n. in dorsal view.

Scott-Macfie (BMNH); 1♂ North West State, Mokwa, 14.viii.1970, P. Ward (BMNH); 1♂ Kogin Sirikin Aawa, 1911, J.W. Scott-Macfie (BMNH); 1♀ Zaria, Samaru, ix.1979, J.C. Deeming (NMWC). SENEGAL: 1♂ 1♀ Djibélor (1.5 km NE of), 8.iii.1977, Cederholm *et al.* (ZMLU). SOUTH AFRICA: *Mpumalanga*: 18♂ 3♀ Nelspruit (20 km south of), Noordkaap R., 23.ix.1980 and 18.iv.1981, R.M. Miller (NMSA); 1♂ Nelspruit (20.5 km south of), 1–2.xii.1976, R. Miller (NMSA); 4♂ 1♀ Barbeton, Stentor, 22.viii.1924, H.K. Munro (NMSA); 5♂ 8♀ Montrose, 20.ix.1980, R.M. Miller (NMSA). ZIMBABWE: 1♂ 4♀ Umfuli R., Hartley, 8.v.1956, C.N. Smithers (NMSA); 1♂ half way between Lupane and Hwange, 8.viii.1929, G. van Son (NMSA); 1♂ Hunyani R., 10.vii.1956, C.N. Smithers (NMSA); 1♂ North Vumba, 23.vii.1964, D. Cookson (NMSA).

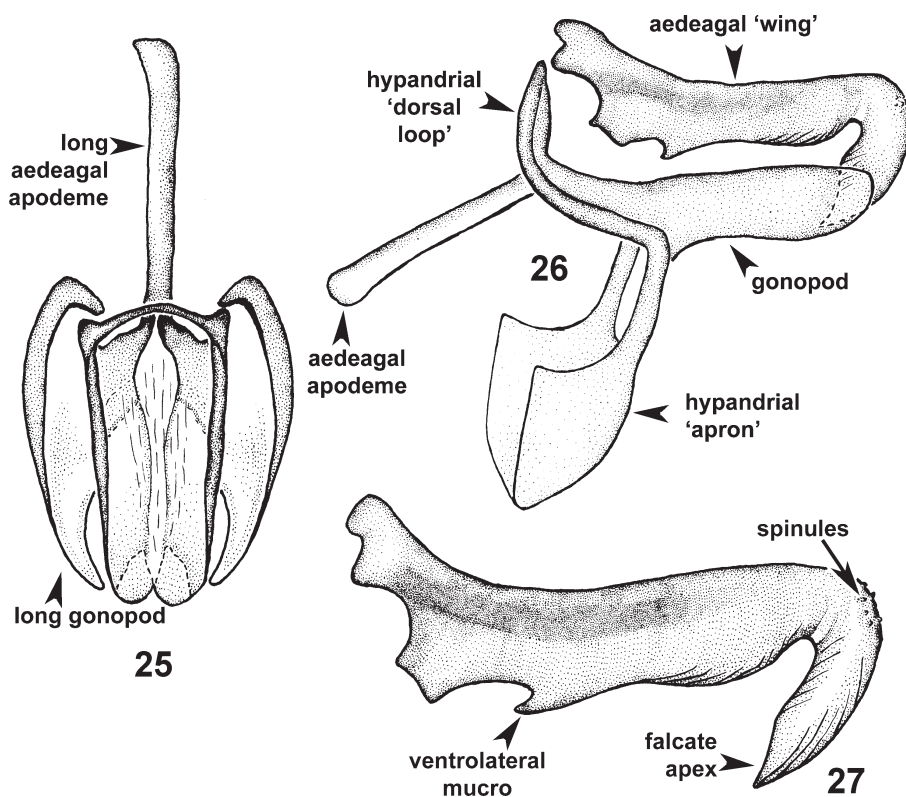
There appear to be no records from East Africa (i.e. Kenya, Tanzania, Uganda).

Parapachycerina talea sp. n.

Etymology: From Latin *talea* (small rod), referring to posterior extension of ocellar spot that reaches onto the occiput.

Diagnosis:

Robust Malagasy species only known from female specimens. Ocellar triangle small and compact. Ocellar spot brown (not black) with narrow extension (“prong”) posteriad. Postpedicel with darkened apical end. Thick brownish edge to scutum/notopleuron. One sternopleural bristle. Profemoral ctenidium present. Anterior edge of wing fumose (specifically costal cell, marginal cell and anterior part of submarginal cell; no brownish



Figs 25–27. Inner ♂ genitalia of *P. lalitra* sp. n.: (25, 26) dorsal and lateral views, (27) aedeagus ‘wing’.

smudges on anterior and posterior cross-veins). Undescribed taxon B closely resembles *P. talea*, see below for further details.

Description:

Colour: Mainly yellow-orange. Scape and pedicel yellow. Distal half of postpedicel and area at arisal tumidity brown, rest of postpedicel yellow. Ocellar spot brown with characteristic brown medial prong extending posteriorly. Maxillary palpi yellow. Thorax yellow with rather faint orange-brown medial stripe on mesonotum; edges of notopleuron infuscated orange-brown. Abdomen brownish orange.

Head: Orbital plates weakly differentiated. Basal half of scape recessed under anterior lip of postfrons. Vertex rounded. Ocellar triangle small, sides slightly longer than base.

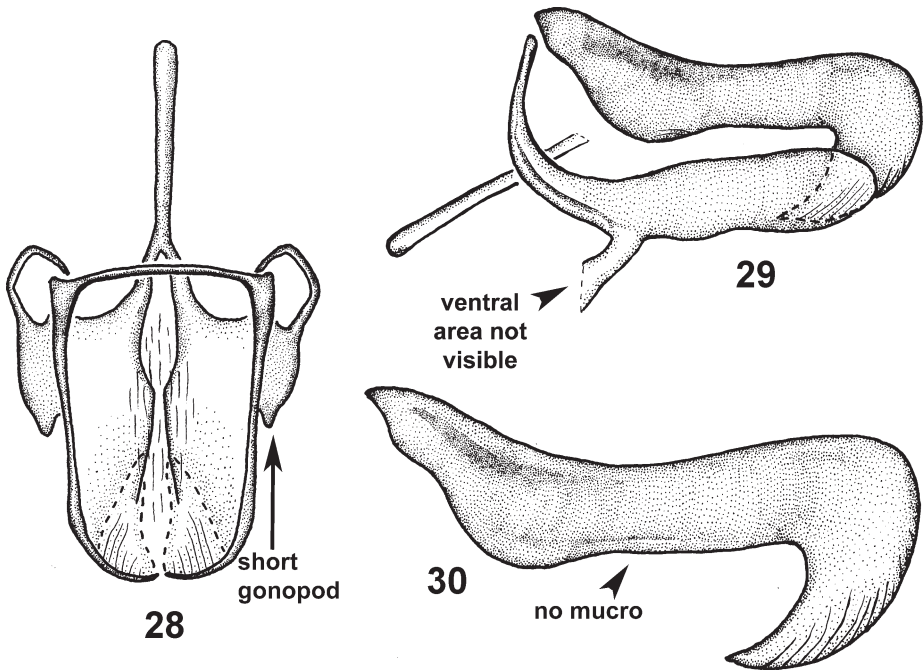
Thorax: Chaetation largely as per genus. One sternopleural bristle.

Legs: Ctenidium present on profemur, *ca* 9 setulae. Profemora posteriorly with ventral row of *ca* 2 setae and dorsal row of *ca* 4 setae. Mesofemur with medioanterior row of 5 setae.

Wings: Costal cell, marginal cell and anterior section of submarginal lightly infuscated.

Abdomen: Male terminalia unknown.

Measurements: ♀ (n=3): total length – 3.8 (3.6–4.1); head length – 0.5; head height – 0.8; head width – 1.1; thorax length – 1.8 (1.7–1.9); abdomen length – 1.5 (1.3–1.7); wing length – 3.5 (3.3–3.8).



Figs 28–30. Inner ♂ genitalia of undescribed taxon A, Ivondro, Madagascar: (28, 29) dorsal and lateral views, (30) aedeagus ‘wing’. Note that the ventral area of the hypandrial ‘apron’ is not illustrated due to the extreme transparency of the sclerite following over-treatment in KOH.

Holotype: ♀ MADAGASCAR: Andasibe (= Périnet), 5.xii.1957, F. Keiser (MHNB).

Other material examined: MADAGASCAR: 1 ♀ Vohiparara, 13.ix.1958, F. Keiser (MHNB); 1 ♀ Ambalamananakana, 18.i.1958, F. Keiser (MHNB).

Distribution: Restricted to Madagascar. Known only from forested areas along eastern versant.

Undescribed taxon A

A male from east coast of Madagascar (Ivondro, i.1900, C. Alluaud, MNHN) is extremely similar to *P. lalitra* externally, but differs in genitalic features in having shorter gonopods, a weaker hypandrial 'apron' and lacking the mucro on the ventrolateral margin of the aedeagus (Figs 28–30). The single specimen available is in rather poor condition, and the genitalia were left too long in KOH during extractive treatment, resulting in the genitalic sclerites becoming largely translucent and difficult to view. Consequently, this taxon is left undescribed until further material becomes available.

Undescribed taxon B

A single female from the lush forest on Montagne d'Ambre, Antsiranana (Diego-Suarez; 23.xi–4.xii.1958, B. Stuckenberg, NMSA) appears to represent a new species. For want of more material, it is left undescribed. It resembles *P. talea* in being a robust, deep orange *Parapachycerina* with very lightly infuscated wings. It differs, however, in lacking the posterior extension from the ocellar spot, and in lacking a profemoral ctenidium (a feature which also separates it from the smaller *P. lalitra*). Other salient features of this specimen are: small ocellar triangle (with sides approximately equal); blackish ocellar spot; postpedicel mostly yellow but darkened apically; sides of notopleuron strongly infuscated; dark orange medial stripe on mesonotum; and 2 sternopleural bristles. The isolated Amber Mt (a forest-clad late Tertiary volcano) is well-known as a site of local endemism in Madagascar.

Undescribed taxon C

The late Loïc Matile collected a distinctive female specimen from Grande Comore, the largest island in the Comoros archipelago (Grande Comore, La Grille (Guiri), 850–900 m, 15.xi.1973, L. Matile, MNHN). Immediately notable about this specimen are the large black spot on the mesopleuron, the weakly fumose anterior part of the wings, three broad, black mesoscutal vittae, and the black marks on the lateral sides of the occiput. The profemoral ctenidium is present. The arrangement, size and orientation of cephalic setation are as per the genus.

This specimen definitely seems to represent a new species, but until further specimens are procured, in particular males, it is left undescribed. The presence of *Parapachycerina* on Grande Comore hints at the possibility that the genus may yet be found on the Seychelles. Based on superficial colouration similarity and the presence of a profemoral ctenidium, this taxon may be the sister-species of *P. infuscata*. Interestingly, the three species with profemoral ctenidia are the two Malagasy species and *P. infuscata* of the African mainland. Taxon C is a geographical annectant step joining these ctenidia-bearing *Parapachycerina* taxa. Whether this is a coincidence, or represents cognate phylogenetic affinity, is still to be determined.

DISCUSSION

Cladogenesis in Parapachycerina

The low number of species in the genus (seven in total, five in the Afrotropics) is immediately apparent and appears to reflect a limited degree of cladogenesis ('speciation'), but possibly collecting biases or recent extinctions are involved. Although there remains considerable taxonomic work in the Afrotropical lauxaniid fauna, a total of five Afrotropical species is a circumscribed number when compared to genera such as *Cestrotus* Loew and *Homoneura*, which have diversified extravagantly in Africa. Other African lauxaniid genera have a similarly limited degree of 'speciation', including presumed near-relatives of *Parapachycerina* such as *Neogeomyza*. Why *Parapachycerina* should have diversified so weakly is unknown.

Cladogenesis within *Parapachycerina* has involved rather modest morphological and colour pattern changes in: (1) intensity and extent of the dark ocellar spot; (2) shape of ocellar triangle; (3) presence/absence of profemoral ctenidium; (4) wing colour; (5) body size; (6) general coloration; and (7) male terminalia.

Some of the differences enumerated above are possibly the result of sexual selection, e.g. differences in male terminalia and variation in the intensity, size and shape of the ocellar spot (a signalling feature?). The inconsistency in the presence of the profemoral ctenidium is, at first glance, perplexing. Profemoral ctenidia are found only in the two Malagasy species (*P. lalitra* and *P. talea*) and *P. infuscata* of Africa, and are absent in *P. munroi*, *P. bispina* and *P. hirsutiseta* (of Asia and northern Australia). The function of the ctenidium is unknown, and we are unaware of any serious functional consideration of this morphological feature in the dipterological literature. Profemoral ctenidia are present in other acalyprate fly families such as Campichoetidae (e.g. J.F. McAlpine 1962: figs 1, 2), Diastatidae (e.g. Chandler 1987: 4; J.F. McAlpine 1987: fig. 4), Curtonotidae (e.g. J.F. McAlpine 1987: 1008) and Canacidae (e.g. Mathis 1989: figs 11, 12), but their function in these acalyprate flies is also obscure. The ctenidium is modified in *Parapachycerina* from a ventral row of ca 10–15 downward-pointing fine setulae. Perhaps it functions to clean the plumose arista, but there appears to be no unambiguous relationship between the plumosity of the arista and the presence of profemoral ctenidia. Perhaps of significance, the profemora of sepsids bear armature (Meier 1995: 435–436; Eberhard 2001), which are considered to be adaptations for gripping the females' wings during copulation, but this explanation is unlikely to apply to *Parapachycerina* as the ctenidium is found in both sexes. Although this paragraph is speculative, we must not lose sight of these functional considerations because features such as the profemoral ctenidium have been given high classificatory and phylogenetic 'weight' by some lauxaniidologists (e.g. Shewell 1987: 953; Yarom 1995). Critical interrogation of the value of presumptive apomorphies is essential to avoid phylogeneticists being misled by uncomplex characters that easily result from convergence.

Constructing a phylogeny for *Parapachycerina* will not be formally attempted here. Reticence is needed because the differences between species are subtle, the characters themselves are of low complexity, their distribution amongst the members of the genus is not congruent, and the full diversity of taxa in Asia and Australia is as yet unknown. Evidence from the male terminalia suggests that *P. munroi*, *P. infuscata*, *P. lalitra* and

the Oriental *P. hirsutiseta* (see Sasakawa 2003: fig. 2) form a clade to the exclusion of *P. bispina* (*P. talea* and the Oriental *P. cuneifera* are ignored here because the male terminalia are unknown). *P. bispina* is distinctive by having the two robust setae at the apex of the epandrial process, a unique condition in the genus. *P. bispina* also has a distinctive surstylus, which is not visible in lateral view. The surstyli in other *Parapachycerina* species are narrow, laterally-compressed lamellae with hamate apices, whereas in *P. bispina* the surstylus is a dorsoventrally flattened blade that lacks the dorsal apical hook. It is unfortunate that the male terminalia of *P. talea* are unknown, because this species, like *P. bispina*, has the anterior part of the wing slightly smoky and also resembles *P. bispina* in general size, shape and colour. In contrast to the postabdominal evidence, the presence of the profemoral ctenidia would suggest a clade consisting of *P. lalitra*, *P. infuscata* and *P. talea* to the exclusion of *P. bispina*, *P. hirsutiseta*, and *P. munroi* (we are unaware of the condition of the profemora in the Oriental *P. cuneifera*).

Phylogenetic considerations

Is *Parapachycerina* a monophylum? Unambiguous apomorphies for the genus are elusive, but the surstylus has an unusual, distinctive shape, arising on the inner margin of the epandrium and resembling a tiny, laterally compressed finger; it is possibly a synapomorphy. For the present, the notion of *Parapachycerina* as a monophylum appears a defensible position, given its unique combination of characters.

Accepting, *pro tempore*, *Parapachycerina* as a monophyletic entity, the next question is: what is its sister-clade? The senior author was initially strongly impressed by the similarity of the genus to the Neotropical *Neopachycerina*. This South American genus was described by Malloch (1933: 357, fig. 67c) on the basis of six specimens from Montevideo, Uruguay (with the single species, *N. aristata*). *Neopachycerina* looks a lot like *Parapachycerina*—both are small, orangish lauxaniids with black ocellar spots, plumose aristae, small anterior fronto-orbital bristles, generally hyaline wings and sapromyziform costae. The two genera also key out in the same couplet in Stuckenberg's (1971) generic key (couplet 32), although Stuckenberg warned that the resemblance was possibly 'a case of convergence'.

Differences shown by *Neopachycerina* include: a more protuberant ocellar hump; dense ocellar setulae (lacking in *Parapachycerina*); the presence of tiny setulae on the anterolateral portions of the postfrons (absent in *Parapachycerina*); a conspicuous lunule; a very weak anterior sternopleural bristle; stout, costal setulae terminating well short of R_{4+5} (approximately half way); and densely plumose arista (loosely plumose arista in *Parapachycerina*). Compared to *Parapachycerina*, the male terminalia of *Neopachycerina* (Fig. 31) show noteworthy differences in the shape of the protandria and aedeagal complexes. The protandrium of *Neopachycerina* is bonnet-like, lengthened longitudinally and shortened laterally in comparison to *Parapachycerina* species. The protandrium is also incomplete ventrally in *Neopachycerina*, in contrast to *Parapachycerina*. The epandria are generally similar in both genera (broader laterally than dorsally). What are interpreted to be the surstyli in *Neopachycerina* are broadly rounded processes, which are not articulated or fused to the inner surfaces of the epandria, but meet below the cerci. The aedeagus is a navicular (boat-shaped) sclerite with spinules (teeth) posteriorly on the inner subapical surfaces. The aedeagal apodeme is very short (<0.5× length of

aedeagus), having an anterior disc and posterior stem (vaguely recalling a ping-pong bat in lateral view), tapering strongly posteriorly to short posterior arms. The hypandrial 'transverse band' is broad with a small 'apron' projecting downwards at an oblique angle; the lateral hypandrial arms are long, and the 'dorsal loop' found in *Parapachycerina* does not occur in *Neopachycerina*—instead, the lateral arms curve upwards and inwards forming an irregularly shaped convolution bearing a tiny lappet that, rather unusually for internal genitalic sclerites, has 2 or 3 setulae; the inner edge of this convolution then fuses with the base of the gonopods. These differences suggest convergence between the two genera. Shewell (1986) had also pointed out convergent similarities in unrelated Old and New World lauxaniid genera.

It was also interesting to note a third row of setulae along the costal margin from between subcosta and vein 1 to ca 60% of the way down the marginal cell in *Neopachycerina*, a condition not found in *Parapachycerina*. This extra row of setulae is a strange condition in lauxaniids, judging from Hackman and Väisänen (1985), who found two rows to be uniform throughout the lauxaniids they examined, but the extra row in *Neopachycerina* was noted in two co-types examined (part of the type series lodged at the BMNH).

An anonymous referee kindly pointed out to us the genus *Tanyura* described by Kim (1994: 313–315) from Australia and the Phillipines, which we had overlooked. We have not examined *Tanyura*, but judging from Kim's description, figures of the terminalia and comparison with *Parapachycerina* (Kim 1994: 314–315), this genus emerges as a good candidate for sistership. Kim (1994) gave a list of 11 morphological differences between the two genera. With increased knowledge of *Parapachycerina* some of the differences cited by Kim (1994) are now known to be incorrect; for example, he states that *Parapachycerina* lacks the profemoral ctenidium, whereas it is present in certain Afrotropical species. Differences that continue to hold include: (a) one mesotibial spur in *Tanyura* (two in *Parapachycerina*); (b) *Tanyura* lacking shorter setulae in plumose arista (these shorter macrotrichia present in *Parapachycerina*); (c) homoneuriform costa (sapromyziform in *Parapachycerina*); and (d) elongated, ventrally pointing male cerci (rounded, non-elongated male cerci in *Parapachycerina*). A potential sister-relationship with an Oriental and Australasian genus also makes far more sense biogeographically than sistership with a South American genus. The senior author must, therefore, concede that he was mistaken in pursuing *Neopachycerina* as the potential sister-clade to *Parapachycerina*.

Comprehension of the high-level phylogenetics of the Lauxaniidae is still in a nascent stage, although it has become customary to recognise two subfamilies, the Homoneurinae and Lauxaniinae (e.g. Shewell 1977, 1987; Miller 1980; Evenhuis & Okadome 1989). Stuckenberg (1971) and Miller (1980) did not include *Parapachycerina* in the Homoneurinae owing to its sapromyziform costa. Shewell (1977) transferred it to the Homoneurinae. He did not provide explanation in the Oriental Catalogue for this move, but in a letter to Miller (11 December 1978) explained that 'the [*Parapachycerina*] genitalia seem to me typically oriental homoneurine' and referred to a manuscript on Nepalese lauxaniids, in which he intended to discuss the matter further. This paper, based on the Coe collection of Nepalese lauxaniids, regrettably was never published (see Shewell's bibliography in Arnaud 2001).

In an investigation of Homoneurinae monophyly based on parsimony-derived cladograms, Yarom (1995) also found that *Parapachycerina* grouped within a monophyletic

Homoneurinae, specifically with what he termed the ‘*Katalauxania* genus-group lineage’. The latter clade was founded on five synapomorphies. Several of these are, subjectively-speaking, not convincing (e.g. ‘eye not round, posterior margin slanting’, ‘face not prominently inflated’) because they are simple characters and appear in other lauxaniids; furthermore, one of the synapomorphies ‘surstylus freely articulated’ is not correct for *Parapachycerina*. Returning to higher-level divisions, Yarom’s analysis identified several ‘highly supportive’ synapomorphies for the Homoneurinae: (a) homoneuriform wing; (b) profemoral ctenidium present; and (c) two mesotibial spurs (Yarom 1995: 46–49). These characters had previously been identified as diagnostic for the homoneurines by Stuckenberg (1971: 516–517) and Shewell (1987: 953).

Parapachycerina does not have a typical homoneuriform wing and the profemoral ctenidium is variably present (absent in the type species). The two mesotibial spurs are, however, always present. Although *Parapachycerina* does not have a typical homoneurine wing (the original definition by Stuckenberg (1971: 501) is ‘spinules reach or very nearly reach the apex of R_{4+5} where they stop abruptly without marked prior diminution in size’), the setulae do extend *ca* 75% of the way to R_{4+5} . Other sapromyziform lauxaniids have the setulae terminating well before that (*ca* 50% of the way between the two vein apices), as mentioned above with regard to *Neopachycerina*. It is possible that the recognition of only two costal setulae categories (sapromyziform and homoneuriform) is an artificial one, and rather than two distinct states, a messy series of intermediates reflects reality better. This is also suggested by Kim’s (1994: 19) comment that ‘in this study numerous species of *Trypetisoma* with both forms of costa have been identified, and they show different end points of costal spinules between the apices of veins 2 (R_{2+3}) and 3 (R_{4+5})’. Conversely, there are some *Homoneura* species where the stout, costal setulae end before R_{4+5} , notably, *H. citreifrons* (Malloch, 1920) of the Nearctic (Miller 1977a: 159, fig. 11b) and *H. kaszabi* Shewell, 1971 and *H. amphibola* Shatalkin, 1992 of the Palearctic (Shatalkin 2000).

Likewise, the profemoral ctenidium shows variation being absent in homoneurines like *Homoneura tenera* (Loew, 1846) (Shatalkin 2000), but present in the sapromyziform *Lyciella rorida* complex in the Palearctic (Shatalkin 2000).

Inconsistency in these ‘strong’ homoneurine synapomorphies reinforces the view expressed that lauxaniids display pronounced morphological plasticity (Stuckenberg 1971: 500; J.F. McAlpine 1989: 1445). We would also note that these ‘strong’ synapomorphies comprise morphologically simple characters, respectively: (1) extension by very short distances of costal setulae and slight diminution in length of these setulae (the homoneuriform/sapromyziform dichotomy); (2) strengthening of the row of fine anteroventral setae of the profemur into shorter, stouter setulae (the profemoral ctenidium); and (3) development of one of the mesotibial setula into a robust but short spur (two mesotibial spurs). Although the genetic and selective processes underlying these changes are unknown, it is a legitimate inference that the changes required are not complex. As insightful phylogeneticists have warned (e.g. Bechly 2000: 5–6; Wägele 2004, 2005), erecting phylogenies on the basis of simple characters is a risky enterprise (irrespective of whether the cladograms are arrived at by putative ‘objective’, parsimony-aided ‘analysis’). As mentioned above, the senior author burnt his fingers badly in contemplating *Neopachycerina* as the sister-clade to *Parapachycerina*, an example where conver-

gence also can mislead taxonomists, and a phenomenon which Stuckenberg (1971) and Shewell (1986) had warned of.

The phylogeny of lauxaniids will remain a considerable challenge to dipterists in the future until new character systems (e.g. terminalia) can be adequately assessed across the family (Remm and Elberg's (1979) pioneering efforts aside). For now, the drift of consensus is to place *Parapachycerina* amongst the homoneurines. In the absence of better data, we cannot offer any conclusive opinion, but note either the absence or variability in *Parapachycerina* of the characters deemed definitive homoneurine synapomorphies by lauxaniidologists.

Historical biogeographical considerations

Parapachycerina displays a distribution pattern typical of innumerable invertebrate and vertebrate clades in being restricted to the Old World tropics, specifically in Africa, South-East Asia and weakly in northern Australia (Shewell 1977; Miller 1980; Evenhuis & Okadome 1989). *Parapachycerina* is also represented on Madagascar and the Comoros, but not from the Seychelles and Mascarene Islands; possibly future collecting will reveal endemic species on these islands.

The aridity of North Africa and Arabia is (on a geological time-scale) a recent event, beginning in the late Miocene (Pickford 1999, 2000; Pickford *et al.* 2006) and intensifying through the Pliocene and Quaternary (with some brief fluctuations). Compelling palaeontological evidence also points to extensive interchange between Africa and

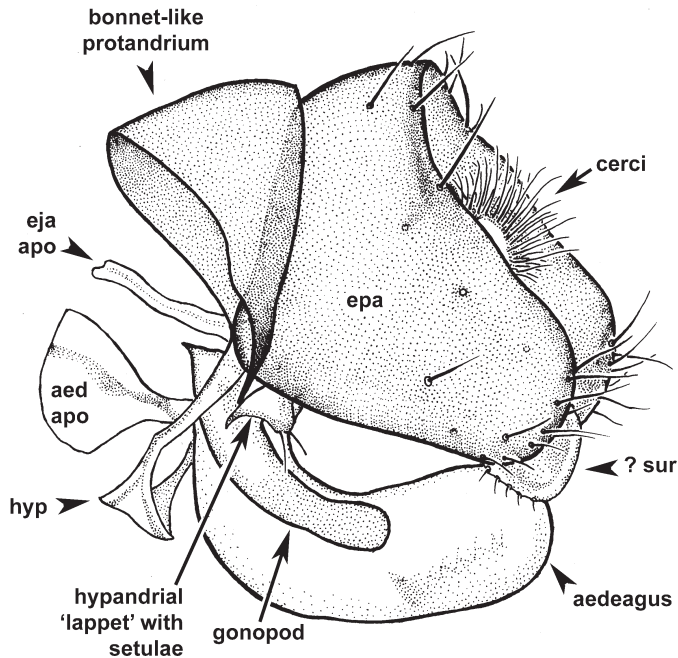


Fig. 31. Lateral view of ♂ terminalia of *Neopachycerina aristata* Malloch. Note differences from *Parapachycerina* in protandrium shape and inner genitalia. Abbreviations: aed apo – aedeagal apodeme; eja apo – ejaculatory apodeme; epa – epandrium; hyp – hypandrium; ? sur – probable surstylus.

Eurasian faunae in the Neogene (e.g. Thomas 1985; Pickford 2002). Doubtless proto-*Parapachy cerina* was involved in this mixing of Afrotropical and Eurasian fauna, explaining its presence in much of the paleotropics.

As for Madagascar, geological data show that there has been no terrestrial connection between Africa and Madagascar since the Jurassic (de Wit 2003). The Comoros are volcanic Cenozoic islands and the presence there of *Parapachy cerina* taxon C, indicates that the Comoros may have been used as 'stepping-stones' to reach Madagascar.

Acalyprate flies only began their explosive diversification in the Palaeogene (Hennig 1965; Grimaldi & Engel 2005: fig. 12.78), the oldest putative lauxaniids being from the Eocene and Oligocene (Evenhuis 1994: 433–434). Given the age of the separation of Madagascar from Africa, and the constrained dates of acalyprate diversification, we must turn to aerial dispersal to explain the occurrence of *Parapachy cerina* on Madagascar.

The circumstantial case for a dispersalist scenario is strong. For example, Chapman *et al.* (2003: 503, 507) observed that 'millions of metric tons of insects are aloft in Earth's atmosphere at any given moment', and that 'a conservative estimate of the total bioflow over a 1 km stretch of the southern English countryside is an astounding 3 billion insects per month'. These data underline the potency of aerial dispersal in transporting volant insects far and wide, as was borne out from the earlier empirical studies of Holzapfel and Harrell (1968) and Wise (1983), among others. Further, in investigations of the biotic recolonisation of the volcanic island Krakatau (Indonesia), Lauxaniidae were one of the fly families to successfully recolonise the island (Thornton *et al.* 1990: fig. 13).

In sum, considering these disparate strands of evidence (geological history of Madagascar, potency of aerial dispersal of insects, and rapid colonization of the 'real-life biogeographical experiment' of Krakatau by lauxaniids), the most parsimonious view is that ancestral *Parapachy cerina* reached Madagascar by aerial dispersal. It also appears more plausible to posit colonization of Madagascar from Africa, rather than reverse.

Within Africa itself, *Parapachy cerina* is closely associated with the distribution of tropical and subtropical savannah and moist escarpment grasslands. Current evidence shows that it is absent from the lowland Guineo-Congo rainforest, although occurring at its edges. The genus is largely tropical and subtropical, its range terminating at about 30°S, and at a similar latitude in the north.

Biology of Parapachy cerina

Biological information on *Parapachy cerina* is sparse. Most adult specimens have been caught in grassland and at forest/grassland ecotones by sweeping. Only two specimens examined were captured in a Malaise trap (both *P. infusata* males from Kenya). The adults are possibly fungivorous, as indicated by the presence of a labellar beak and some pseudotracheal scoops and prongs, which Broadhead (1984, 1989) showed were adaptations for feeding on phylloplane fungi. We did not notice any fungal hyphae or spores in proboscides dissected, but our preparations were crude. Consequently, confirmation of a fungivorous habit by *Parapachy cerina* calls for further investigation. Perhaps unusually, an adult of *P. bispina* from Segibwa Falls, Uganda (BMNH) was 'attracted to human faeces' (label datum). Specimens of *P. bispina* collected by Deeming in northern Nigeria (Tilden Fulani) were taken 'on tomatoes' at a mixed vegetable farm.

The larvae are unknown, but, it is likely that *Parapachycerina* larvae feed on dead and decaying grass and other vegetable matter, as is the case with grassland-dwelling lauxaniids in general (Miller 1977b), and phylogenetically-related flies in the Celyphidae (Miller 1986) and Natalimyziidae (Miller 1984; Barraclough & D.K. McAlpine 2006).

Parapachycerina adults have been collected alongside other small, mostly yellow lauxaniid species of *Diplochasma* Knab and *Chaetolauxania* Kertész in South African grasslands. *Parapachycerina* is usually not as commonly encountered as these other yellowish lauxaniid genera, and the larger, darker grass-inhabiting *Calliopum* Strand, *Lauxania* Latrielle and *Mycterella* Kertész. Being small flies, *Parapachycerina* are easily overlooked by collectors, and possibly are more abundant and widespread than reflected in the rather small number of specimens in collections (<200).

Most specimens have been collected at low altitudes (<1000 m), but the genus is known from mid-altitude escarpments in South Africa (e.g. the Mpumalanga Drakensberg) and mountain ranges in Zimbabwe (e.g. the Vumba Mts) and Tanzania (e.g. the Songea highlands).

Interestingly, several species may be found in sympatry, for example all three African species (*P. bispina*, *P. infuscata* and *P. munroi*) have been collected in the Noordkaap River area (Mpumalanga province) by Miller in lush, damp grassy drainage lines, and the two Malagasy species (*P. lalitra* and *P. talea*) have both been collected at Andasibe (Périnet).

The phenology of the species with sufficient specimens (*P. bispina*, *P. infuscata*, *P. munroi*) shows that there is no seasonality to their flight period, and specimens of all of these species have been collected throughout the year, even at the height of the austral winter.

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