



*Zootaxa* 2964: 1–60 (2011)  
www.mapress.com/zootaxa/

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Monograph

ISSN 1175-5326 (print edition)

**ZOOTAXA**

ISSN 1175-5334 (online edition)

# ZOOTAXA

2964

**A review of the monophyly and composition of the Bengaliinae  
with the description of a new genus and species, and new evidence  
for the presence of Melanomyiinae in the Afrotropical Region  
(Diptera, Calliphoridae)**

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Magnolia Press  
Auckland, New Zealand

*Accepted by J. O'Hara: 21 Jun. 2011; published: 13 Jul. 2011*

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(*Zootaxa* 2964)

60 pp.; 30 cm.

13 July 2011

ISBN 978-1-86977-773-9 (paperback)

ISBN 978-1-86977-774-6 (Online edition)

FIRST PUBLISHED IN 2011 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: [zootaxa@mapress.com](mailto:zootaxa@mapress.com)

<http://www.mapress.com/zootaxa/>

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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## Abstract

*Mafikengia ciliata* **gen. nov.**, **sp. nov.** is described from South Africa and assigned to the subfamily Bengaliinae of the Calliphoridae. It is recognisable by its small size (4 mm), mostly yellow body, and a number of peculiar characteristics. The upper end of the bacilliform sclerite is attached to the medial side of the posterior portion of the surstylus on each side, a very unusual feature among calliphorids. This medial connection in *Mafikengia* is found in all genera of Bengaliinae, but is not present in any other calliphorid subfamily. The monophyly of the Bengaliinae is discussed, the subfamily is diagnosed, the component genera are listed, and a key to the world Bengaliinae is presented. The Bengaliinae are a very well circumscribed group within the Oestroidea, and it is suggested that the status of the subfamily might be raised to the rank of family. A cladistic analysis using NONA shows that *Mafikengia* is more closely related to the Oriental genus *Termitoloemus* Baranov, 1936 than to any other genus, and that the tribes Auchmeromyiini and Bengaliini may still be upheld

as separate monophyletic groups, but with very low support. The Afrotropical nominal genus *Neocordylobia* Villeneuve, 1929 is reduced to a synonym of *Cordylobia* Grünberg, 1903, **syn. nov.** The nominal species *Neocordylobia tauffliebi* Zumpt, 1958 is transferred to the genus *Tricyclea* Wulp, 1885, as *Tricyclea tauffliebi* (Zumpt), **comb. nov.** A new interpretation of the male genitalia of *Termitoloemus marshalli* Baranov is presented. The male genitalia of the Afrotropical species *Tricycleala maculipennis* Villeneuve as well as the male and female genitalia of the Afrotropical genera *Adichosina* Villeneuve, *Ochromelinda* Villeneuve and *Onesihoplisa* Villeneuve are figured. The uterine first instar larva of the female of *Ochromelinda thoracica* Villeneuve is described and illustrated. The genera *Adichosina*, *Ochromelinda*, *Onesihoplisa* and *Zernyiella* Zumpt are assigned to the calliphorid subfamily Melanomyiinae on the basis of the morphology of the female ovipositor, male aedeagus and first instar larva. The occurrence of this subfamily in the Afrotropical Region is established for the first time. A lectotype is designated for *Zernyiella dubia* Zumpt, 1956 to fix the interpretation of the name. *Auchmeromyia kurahashi* Lehrer, 2005 is established as a junior synonym of *Auchmeromyia senegalensis* Macquart, 1851, **syn. nov.** *Auchmeromyia pattoniella* Lehrer, 2005 is an unavailable name [no type designation] in the synonymy of *Auchmeromyia bequaerti* Roubaud, 1913. *Cordylobia ebadiana* Lehrer & Goergen, 2006 is established as a junior synonym of *Cordylobia rodhaini* Gedoelst, 1910, **syn. nov.** *Pachychoeromyia kanemia* Lehrer, 2011 is reduced to a synonym of *Pachychoeromyia praegrans* Austen, 1910, **syn. nov.** The family-group name Coganomyiinae of Peris & González-Mora, 2004 is established as a synonym of Bengaliinae Brauer & Bergenstamm, 1889, **syn. nov.**

**Key words:** Diptera, Calliphoridae, Bengaliinae, Melanomyiinae, new genus, new species, genitalia, phylogeny

## Introduction

In July 2007 Thomas Pape of the Zoological Museum of Copenhagen sent me a specimen of a small yellow bengaliine fly that one of his students had captured on the “chimney” of a termite nest (*Odontotermes* sp.) in South Africa. It had a number of peculiar characteristics and he suggested it belonged to a new species. He kindly left it to me to describe it. After close study I found it justified to assign the material to a new genus. Certain discoveries subsequently led me to widen the scope of the investigation to a full-scale review of the monophyly and composition of the Bengaliinae. The purpose of the present paper is thus

- (1) to describe and diagnose the new genus and species;
- (2) to diagnose and confirm the monophyly of the subfamily Bengaliinae;
- (3) to describe the distribution among bengaliine genera of two setae with fixed position known only among the Bengaliinae: Hough's postsutural seta and the Y seta;
- (4) to describe the cerci, the surstyli and the connection between the surstylus and the upper end of the bacilliform sclerite in representatives of all genera of the Bengaliinae, and in all subfamilies of the Calliphoridae;
- (5) to present a key to the World genera of Bengaliinae;
- (6) to list and analyse the phylogenetic relationships of the genera making up the subfamily Bengaliinae;
- (7) to list all family-group and genus-group names associated with Bengaliinae;
- (8) to summarise briefly what is known about the biology of the Bengaliinae; and
- (9) to discuss the systematic position of the genera *Adichosina* Villeneuve, 1934, *Ochromelinda* Villeneuve, 1915, *Onesihoplisa* Villeneuve, 1926 and *Zernyiella* Zumpt, 1956.

## Material and methods

**Material examined.** Material and depositories are listed in Appendix 3. Author of the names of the examined species can also be found there.

### Acronyms for collections.

BMNH Natural History Museum, London, UK

BMSA Department of Entomology, National Museum, Bloemfontein, South Africa

BPBM Bishop Museum, Honolulu, Hawaii, USA

CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada

KR Private collection of Knut Rognes

MNHN Muséum national d'Histoire naturelle, Paris, France  
MRAC Musée Royal de l'Afrique Centrale, Tervuren, Belgium  
MSNM Museo Civico di Storia Naturale, Milano, Italy  
MZLU Museum of Zoology, Lund University, Lund, Sweden  
NMSA KwaZulu-Natal Museum, Pietermaritzburg, South Africa  
NMW Naturhistorisches Museum Wien, Vienna, Austria  
TAU Department of Zoology, Tel Aviv University, Tel Aviv, Israel  
ZMUC Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark  
ZMUN Natural History Museum, Zoological Museum, University of Oslo, Oslo, Norway

**Condition of *Mafikengia ciliata* specimen.** The specimen had been kept for some time in 96% ethanol and then pinned and dried before I received it. Some parts of the body (especially the lateral parts of thorax) were slightly crumpled, likely an effect of drying after the stay in alcohol. Some setae and some sclerites, especially on thorax, were covered with a white residue sometimes difficult to distinguish from true microtrichosity. The genital capsule together with a separate ST5 was kept in glycerol in a big plastic vial, but the capsule was not macerated when I received it. ST4 appears to be lost. I treated the genital capsule further in hot KOH to macerate all soft tissue. Due to fragility of the sclerotised parts, it was not possible to remove the narrow TST7+8 completely from the epandrium as I usually do. Neither did I find it safe to separate completely the ventral epandrial process on each side from their attachment points at the base of the hypandrial arms, although these connections had already been partly and asymmetrically severed upon reception of the specimen. Similarly, for fear of destroying important structures, the lower end of the bacilliform sclerites was not loosened from its attachment point at the distal end of the hypandrial arms. Since the hypandrium with its associated structures (pre- and postgonites, aedeagus, phallapodeme) for these reasons could not be dissected completely free, it was impossible to rotate the aedeagus backwards relative to the hypandrium away from its normal position between the pre- and postgonites. Therefore, these latter sclerites and especially the basiphallus could not be studied freely from all directions of view. This also made it awkward to image many genital parts, partly because they were more or less hidden and partly because they were impossible to balance in the desired angle due to asymmetry of the whole complex.

Numerous phoretic mites were present in various body crevices: between the calypters, behind the hind coxae, between the fore coxae etc.

**Uterine larvae of *Ochromelinda thoracica* Villeneuve.** In a dissected female of *Ochromelinda thoracica* Villeneuve, 1915 from Uganda (in CNC) I found 10 uterine larvae partly emerged from their eggshells. Unfortunately the abdomen had already been boiled in KOH for ovipositor extraction and dissection which made the larvae not very well suited for scanning electron microscopy. They were subsequently transferred to 70% alcohol and sent to Krzysztof Szpila, Toruń, Poland, for examination. He mounted one larva in Euparal and two larvae in Hoyer's semipermanent medium. Other larval specimens were subjected to scanning electron microscopy. He kindly provided the photomicrographs in Figs. 116–119, the scanning electron micrographs in Figs. 120–123, in addition to the description of the larvae given in Appendix 4.

#### Abbreviations used in text for setae and abdominal sclerites.

<i>acr</i>	acrostichal setae
<i>dc</i>	dorsocentral setae
<i>h</i>	humeral setae
<i>ia</i>	intra-alar setae
<i>kepst</i>	katapisternal setae
<i>npl</i>	notopleural setae
<i>pa</i>	postalar setae
<i>ph</i>	posthumeral setae
<i>pra</i>	prealar seta
<i>prst</i>	presutural seta
<i>sa</i>	supra-alar setae

<i>scut</i>	marginal scutellar setae
<i>a</i>	anterior
<i>ad</i>	anterodorsal
<i>av</i>	anteroventral
<i>d</i>	dorsal
<i>p</i>	posterior
<i>pd</i>	posterodorsal
<i>pv</i>	posteroventral
<i>v</i>	ventral
ST	abdominal sternite
T	abdominal tergite
TST	tergosternite

**Abbreviations used on figures of genitalia and external adult features.**

<i>b.scl.</i>	bacilliform sclerite (“ninth coxite, proximal segment” of Patton 1935, 1936; “processus longus”)
<i>cerc.</i>	cercus
<i>d.sur.</i>	distal part of surstylus (“ninth coxite, distal segment” of Patton 1935, 1936);
<i>e.</i>	external hypophallic lobe
<i>ej.o.</i>	opening of ejaculatory duct
<i>ejac.scl.</i>	ejaculatory sclerite
<i>ep.</i>	epandrium (“tenth tergum” of Patton 1935, 1936)
<i>eph.</i>	epiphallus
<i>ep.cerc.art.</i>	articulation between epandrium and posterior part of cercus
<i>Hough seta</i>	“postsutural seta” of Hough (1898)
<i>i.</i>	internal hypophallic lobe
<i>junction</i>	junction of upper end of bacilliform sclerite with surstylus
<i>m.h.</i>	mesohypophallus (“median shaft” of Patton 1935, 1936)
<i>p.sur.</i>	proximal part of surstylus (“ninth coxite, posterior prolongation” of Patton 1935, 1936)
<i>pg.</i>	postgonite
<i>T8+epiproct</i>	sclerite formed by fusion of T8 and epiproct in ovipositor
<i>Y seta</i>	explained in text

**Abbreviations used on figures of first instar larva of *Ochromelinda thoracica*.**

The abbreviations used have been taken from Szpila (2010).

<i>I, II, III</i>	thoracic segments 1–3
<i>A1</i>	abdominal segment 1
<i>ant</i>	antenna
<i>dc</i>	dorsal cornua
<i>is</i>	intermediate sclerite
<i>lb</i>	labrum
<i>mh</i>	mouthhook
<i>mp</i>	maxillary palpus
<i>pb</i>	parastomal bar
<i>vc</i>	ventral cornua
<i>vo</i>	ventral organ
<i>vp</i>	vertical plate

**Photography.** Photographic methods are described in Rognes (2009b). None of the images herein were taken with the macro lens mentioned there. Due to the small size of the holotype of *Mafikengia ciliata* and the incomplete dissection it was very difficult to obtain high quality images of the genitalia.

The images of the slide of the *Termitoloemus marshalli* genitalia in BMNH, which served as the basis for Figs. 69–71, were prepared as follows. I made a total of 48 exposures of the genital slide at various focal levels in a step-wise fashion with equal manual turns of the focus knob of the microscope. The first exposure was of the uppermost (leftmost) part of the genital capsule, the subsequent exposures had their focus deeper and deeper into the slide-mount and the last exposure had its focus on the deepest level of the slide. Fig. 69 was made from an exposure (#9492) at the tenth focusing step below the first, thus from the left part of the genital capsule. It is slightly medial to that part of the epandrium that articulates with the hypandrium. Fig. 70 was fused from six exposures (#9506–#9511, focus step numbers 24–29 from the top) very near the middle of the focus range. Fig. 71 is from an exposure (#9523, focus step 41) seven focusing steps above the deepest focusing level, thus from the right part of the genital capsule.

**Phylogenetic analysis.** Thirteen taxa of the Bengaliinae plus *Calliphora*, *Lucilia* and *Pollenia* as outgroups for rooting the tree were coded for 28 characters, of which five were multistate. The three selected outgroup taxa provided variability in the outgroup for the characters involving setosity of the propleuron, prosternum and lower calypter (characters 9, 10, 18, respectively). The data matrix, characters and character states are given in Appendix 1 (filename: *mafip.ss*). The matrix was analysed with the parsimony program NONA (Goloboff 1993). All characters were treated as unordered, and only unambiguous support for clades was considered (option *amb-*). An exact search was performed in NONA (*whennig; mswap+;*) and 11 most parsimonious trees were found, all of length 56 steps, each with an ensemble consistency index of 0.62, and an ensemble retention index of 0.67. The strict consensus is shown in Fig. 138. The support of the clades (Bremer support) was calculated in NONA (*hold 100 000; bsupport 5;*) and the values entered above the branches in Fig. 138. The consensus tree was output through WinClada (Nixon 2002) as an *.emf* file. This was opened in Adobe Illustrator, and exported as a *.tif* file. The latter was treated further in Photoshop Elements.

To examine whether the hypothetical group (*Auchmeromyia* + *Pachychoeromyia* + *Coganomyia*) occurred in any of the 11 most parsimonious trees, the following command sequence was used after having read all the 11 trees into memory: *force (0 1 2 3 4 5 6 7 8 9 (10 11 12) 13 14 15); mono\**; (the taxon numbers refer to the genera in the sequence they are listed in the matrix).

I also ran a constrained tree search in NONA by using the command sequence: *proc mafip.ss; hold 1000 000; force (0 1 2 3 4 5 6 7 8 9 (10 11 12) 13 14 15); tread (0 1 2 3 4 5 6 7 8 9 (10 11 12) 13 14 15); max /;* to find the length of the shortest tree where this group was monophyletic.

## Family Calliphoridae Brauer & Bergenstamm, 1889

Calliphorinae Brauer & Bergenstamm, 1889: 85. Type genus *Calliphora* Robineau-Desvoidy, 1830: 433. Without description or definition, but available “by an indication” i.e., by being formed before 1931 “from an available generic name” (ICZN 1999; Code Articles 12.1 and 12.2.4).

## Subfamily Bengaliinae Brauer & Bergenstamm, 1889

Bengaliinae Brauer & Bergenstamm, 1889: 85. Type genus: *Bengalia* Robineau-Desvoidy, 1830: 425. Without description or definition, but available “by an indication” i.e., by being formed before 1931 “from an available generic name” (ICZN 1999; Code Articles 12.1 and 12.2.4).

[Eucalliphorinae Villeneuve, 1920: 225. No standing in nomenclature since not based on the name of a genus (ICZN 1999; Code Article 11.7). Villeneuve did not base the name on the genus *Eucalliphora* Townsend, 1908 as one might think. For more details, see Sabrosky (1999: 131, 337, 359).]

[Xantochocalliphorinae Villeneuve, 1920: 225. No standing in nomenclature since not based on the name of a genus (ICZN 1999; Code Article 11.7) (cf. Sabrosky 1999: 359).]

Auchmeromyiinae Patton, 1935: 228 (as Auchmeromyiinae). Type genus: *Auchmeromyia* Brauer & Bergenstamm 1891: 87.

Cordylobiini Lehrer, 1970: 23. *Nomen nudum*. No description or definition (ICZN 1999; Code Article 13.1).

Pachychoeromyiini Lehrer, 1970: 23. *Nomen nudum*. No description or definition (ICZN 1999; Code Article 13.1).

Tricycleinae Lehrer, 1970: 22. Type genus: *Tricyclea* Wulp 1885: ccxciii.

Booponini Fan, 1992: 461. Type genus: *Booponus* Aldrich 1923: 141.

Coganomyiinae Peris & González-Mora, 2004: 117. Type genus *Coganomyia* Dear 1977: 21. **Syn. nov.**

Afridigaliinae Lehrer, 2005a: 21. Type genus: *Afridigalia* Lehrer 2005a: 22.

Gangelomyiinae Lehrer, 2005a: 108 (as Gangelomyiinae). Type genus: *Gangelomyia* Lehrer 2005a: 111.

Maraviolinae Lehrer, 2005a: 154. Type genus: *Maraviola* Lehrer 2005a: 154.

**Diagnosis.** See section “Monophyly and diagnosis of the Bengaliinae” below.

**Generic composition.** The genera I consider to belong to this subfamily are listed in Appendix 2 together with their synonyms. In this appendix the authors of all the genus-group and most of the species-group names belonging to the subfamily (except those belonging in the genera *Bengalia*, *Hemigymnochaeta* and *Tricyclea*) are included. The authors of these names are usually not mentioned in the running text to follow.

**Genus *Mafikengia* gen. nov.**

Type species: *Mafikengia ciliata* sp. nov.

**Etymology.** The name of the new genus is a feminine noun formed after the type locality, the city of Mafikeng in the North West province of South Africa, close to the border with Botswana.

**Diagnosis.** See diagnosis of the type species below.

The genus *Mafikengia* gen. nov. has a single species, *Mafikengia ciliata* sp. nov., known only from the male sex.

**Distribution.** South Africa.



**FIGURE 1.** *Mafikengia ciliata* sp. nov., male holotype. Fly habitus, right lateral view. Inset: original label.



***Mafikengia ciliata* sp. nov.**

Figs. 1–37.

Holotype male, Mafikeng, North West Province, South Africa (ZMUC), here designated. For details, see Type material below.

**Etymology.** The specific epithet *ciliata* is a latinised adjective, gender feminine, in the nominative singular. It is derived from *cilium* (Latin, meaning eyelid, carrying eyelashes) and is referring to the fine setulae (cilia) along the vein  $R_{4+5}$  on both surfaces of the wing extending all the way to the costal margin, as well as to the very long dorsal preapical setae on the hind tibia.

**Diagnosis.** *Mafikengia ciliata* is recognisable on the following combination of characters which is unique among oestroid flies: Ground colour yellow, except much of thoracic dorsum, all of the mediotergite, anatergite, katatergite and meron, and narrow hind bands on the abdominal tergites which are blackish. Eye very small. Frons at narrowest point 0.53x head width. Fronto-orbital plate with two laterocline orbital setae. Genal dilation 0.9x eye height. Palpus dorsoventrally flattened and projecting far beyond lower facial margin. Hind tibia with a very long dorsal preapical seta, longer than first tarsomere. Vein  $R_{4+5}$  ciliate on both surfaces of the wing all the way to the wing margin. Anal vein reaching the wing margin. Vein M gently curved at bend. Cell  $r_{4+5}$  opening at the wing tip. Cerci fused in the midline, except for a narrow slit at the tip. Surstylus undivided, posterior part flat, broad and bare, separated from the epandrium by unsclerotised membrane. Distiphallus with a narrow ring-like ventral plate, a distinct rather broad mesohypophallic sclerotisation proceeding distally from its ventralmost point narrowing to a ridge below the ejaculatory opening and for much of its course situated in a deep groove in the ventral surface of the distiphallus. Lateral wall of distiphallus strongly sclerotised and almost a circular structure with serrated margin distally and ventrally. A short, strongly serrated hypophallic lobe on each side. The hypophallic lobes and the ventral part of the sclerotised lateral wall of the distiphallus form two dentate ridges ventrally on each side converging towards the midline in ventral view.

**Description.**

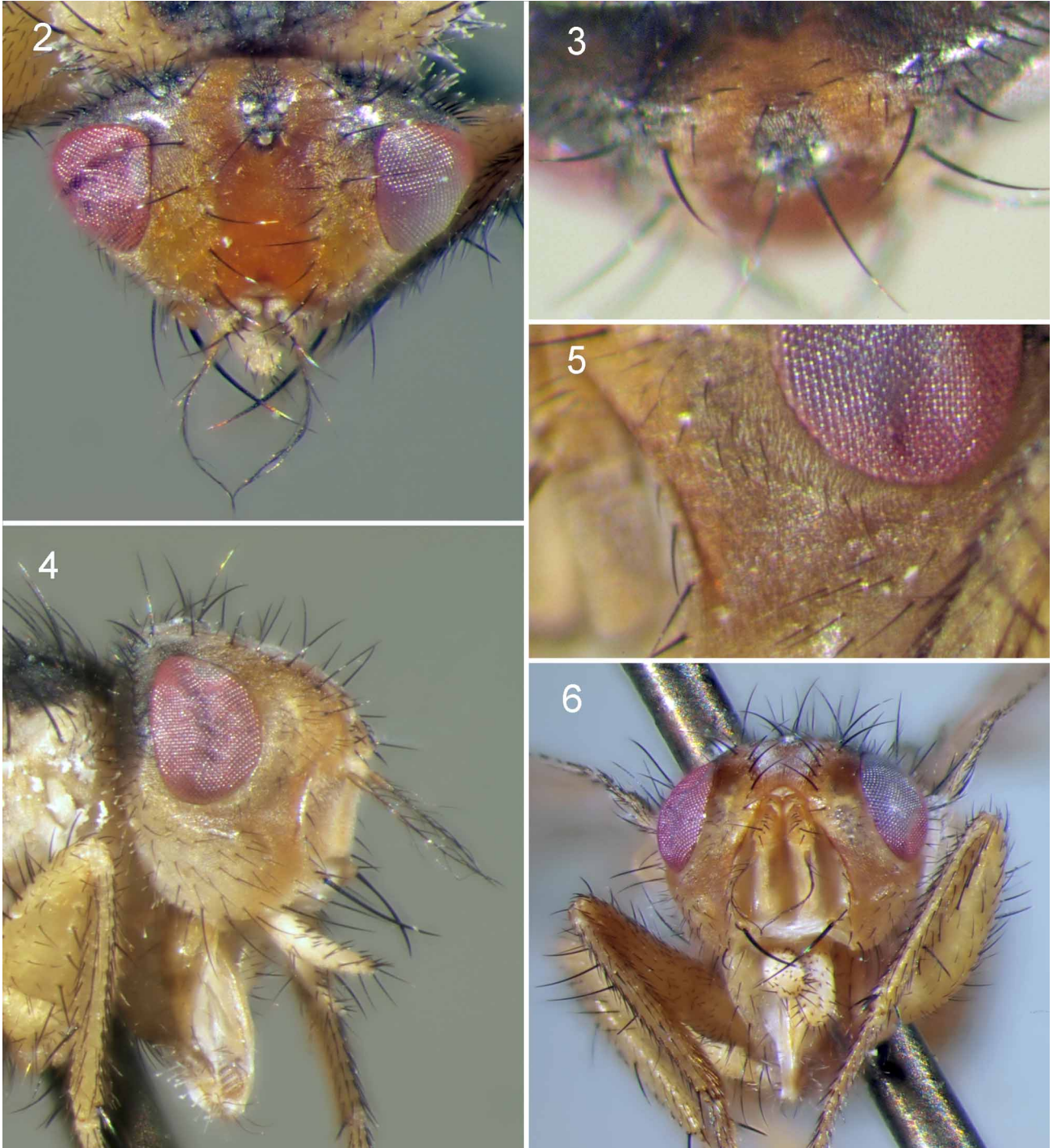
**Male.** Body length: 4 mm. **Ground colour.** Yellow, sometimes with various shades of light brown or reddish yellow, with the following major exceptions. The basal thickening of the arista yellow, but the distal 5/6 of the stalk and all the arisal hairs black. Head black at the upper third or half of the occiput, except for a yellow semicircular area in the middle of the upper occiput; this area being a backward continuation of the yellow frontal vitta (Figs. 2, 3). Ocellar triangle black. The black area of the occiput reaching forward to the hind edge of the eye and to the hindmost part of the fronto-orbital plates, enclosing the outer vertical seta and reaching forward to the hindmost laterocline orbital seta. The latter seta and the inner vertical seta both standing on the border between the yellow and black area. Scutum black, except for the following sclerites which are yellow (Fig. 7): the postpronotal lobe (“humeral callus”) and the area immediately behind it; the notopleuron; the narrow lateral area above the wing carrying the supra-alar setae; the postalar callus and the scutellum. In addition a small wedge-shaped yellow area on each side of the suture. The anterior two-thirds of the postalar wall dark. The mediotergite, anatergite, katatergite and meron black or very dark. The abdominal segments T1+2, T3, T4 and T5 with very narrow brownish black posterior bands; on T3 and T4 with triangular forward brownish projections, reaching at most the middle of each tergite; on T5 the posterior band interrupted in the middle (Figs. 15, 16).

**Pollinosity.** Most of the body covered with a very thin layer of white pollinosity. Parafacial waxy and almost without pollinosity. The abdominal segments also almost without pollinosity except for very narrow areas laterally on the extreme anterior parts of T3–5, visible in a very low angle of view.

**Setae.** Black, except when noted otherwise.

**Head** (Figs. 1–6). Rather globose, with small eyes. Frons width at vertex / head width ratio 0.53. Frontal vitta reddish yellow, contrasting slightly with yellow fronto-orbital plates, narrowing slightly towards lunula, bare, at level of anterior ocellus twice as wide as fronto-orbital plate. 4 frontal seta on right side, 6 on left (2 of the latter weak). 2 strong laterocline orbital setae on each side, anteriormost seta at level with posteriormost frontal seta. Outer and inner verticals strong. Ocellar setae strong. Lunula bare. Fronto-orbital plate with scattered setulae continuing down for the whole length of the parafacial, and also invading the area below the eye. Parafacial broad, in broadest aspect 0.6x width of fore femur. Vibrissal corner slightly projecting, but situated well in front of lower facial margin, which is not projecting. Vibrissa large, distance between vibrissae greater than length of first flagellomere. Face broad, hollow, and without a keel. Facial ridge with 5 small supravibrissal setulae ascending

almost halfway to lunula. Buccal cavity wider than long. 2 subvibrissal setulae and 3 setulae along sides of buccal cavity. Genal height 0.9x height of eye in lateral view. Genal dilation short and high, clothed with scattered setulae. Area between posterior eye margin and postocular row of setae bare. The single postocular row of setae proceeding medially behind the outer and inner verticals as several rows of small setulae to a level slightly medial to the inner vertical, very few setulae invading the yellow occipital area. Occiput convex with black setulae all over, some pale ones below in middle.



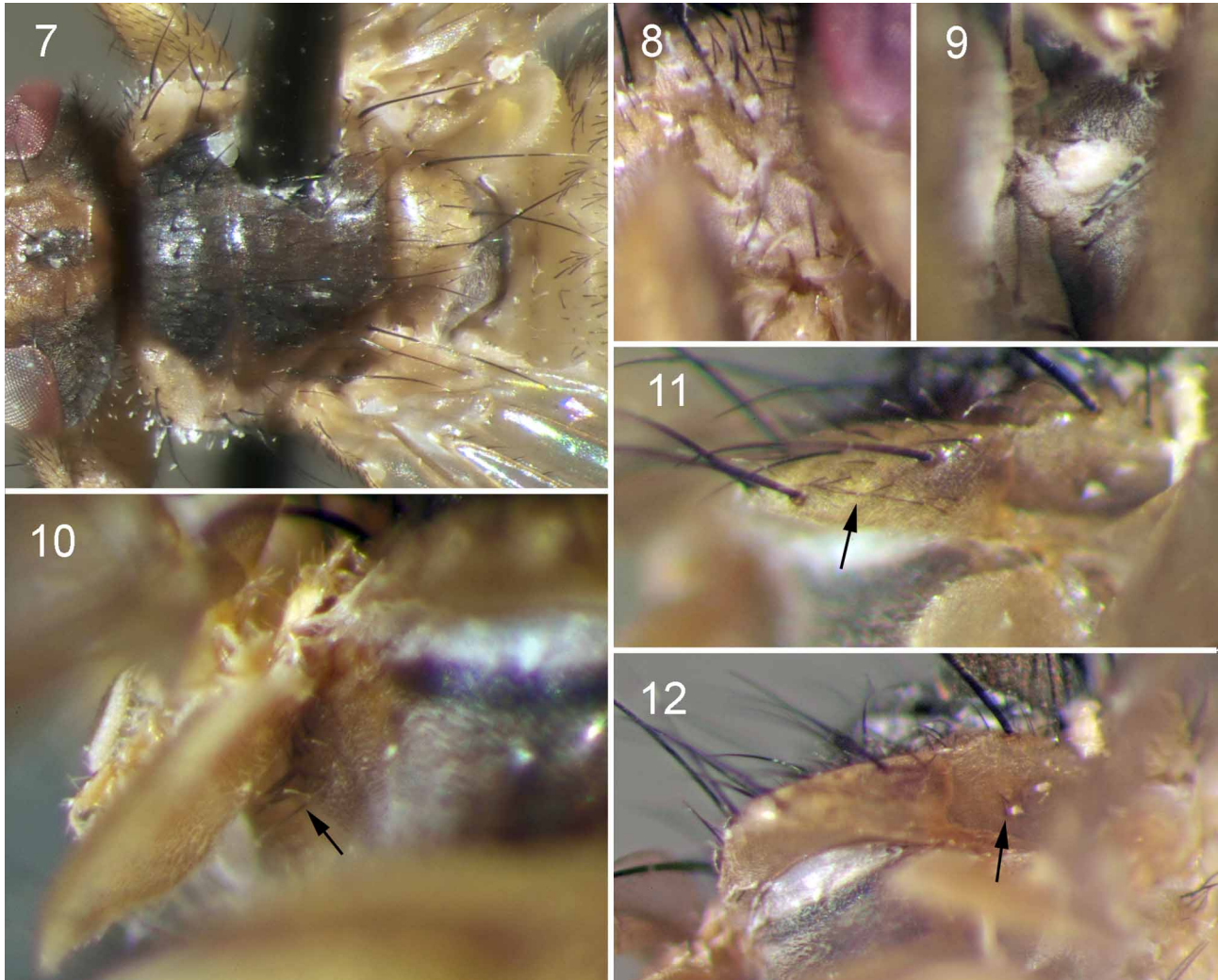
**FIGURES 2–6.** *Mafikengia ciliata* sp. nov., male holotype, head. **2.** Dorsal view. **3.** Detail of upper occipital region, posterodorsal view. **4.** Right lateral view. **5.** Detail of left parafacial. **6.** Anterior view.

Scape with a few very short setulae, scapes touching in midline. Pedicel with a long seta and scattered small setulae. First flagellomere (“third antennal segment” = postpedicel) 3x as long as wide, lower end separated from

lower facial margin by twice the width of the basal part of the arista. Arista very long, almost 2x length of first flagellomere (Figs. 2, 4), moderately long plumose almost to the tip; its basal 1/6 conspicuously thickened.

Palpus white, long, broad distally, longer than antenna, strongly flattened dorsoventrally and projecting far beyond lower facial margin. On upper side with numerous short setae all over, longer setae along margin. On underside palpus almost bare.

Prementum long and broad, boat-shaped, labellum half as long.

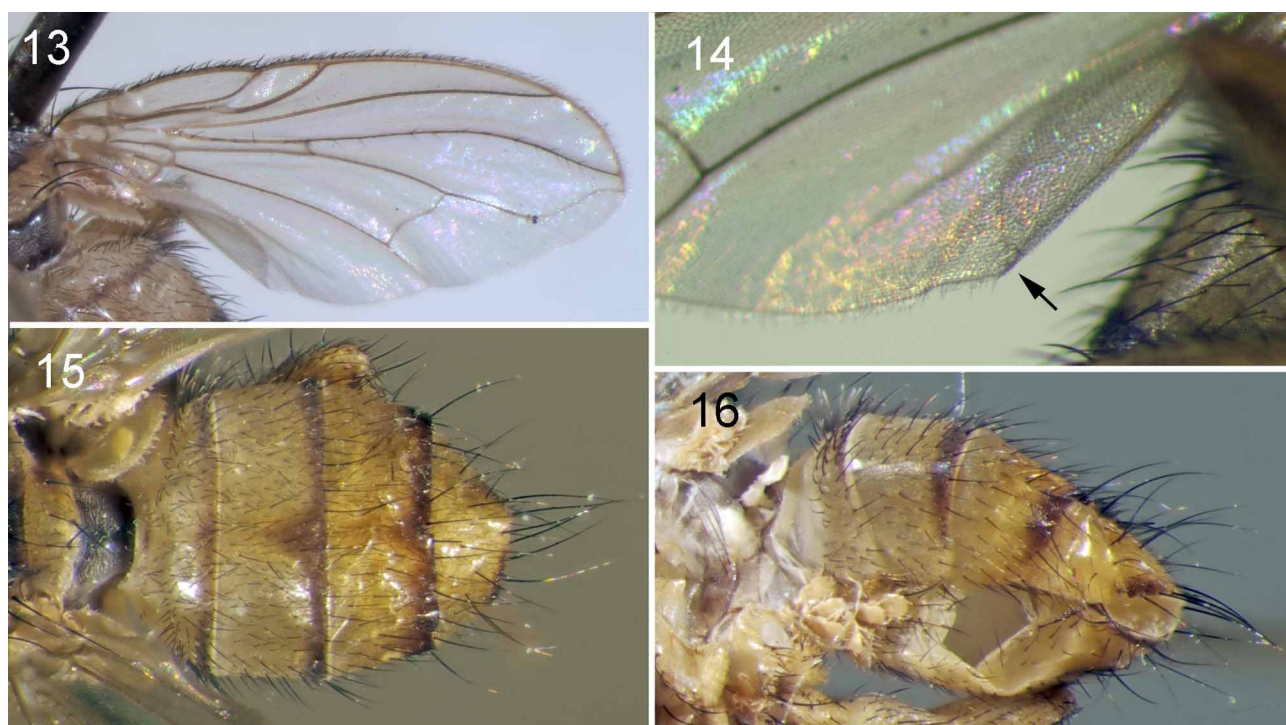


**FIGURES 7–12.** *Mafikengia ciliata* sp. nov., male holotype, thorax. **7.** Scutum, dorsal view. **8.** Anterior spiracle and proepisternal depression, right lateral view. **9.** Posterior spiracle and parts of meron, right lateral view. **10.** Mediotergite, anatergite and lower calypter, posterior view. Arrow points to pale and black setulae on anatergite below lower calypter. **11.** Lateral scutellar declivity, right lateral view. Arrow points to regular row of setulae. **12.** Postalar wall, right lateral view. Arrow points to group of minute black setulae.

**Thorax** (Figs. 7–12). Scutum with sparse microtomentum behind suture. In front of suture more conspicuous white microtomentum, reaching suture in medial part, but widely separated from suture laterally. A dark vitta in midline from the presutural *acr* to the suture, which can be followed in some lights also on the postsutural part of scutum; another much longer vitta between *acr* and *dc* rows. Ground setulae sparse.

Postpronotal lobe (“humeral callus”) with 2 strong *h* on the lateral part, the outermost seta the strongest one; with short stubby setae medial to and between the *h*, and on the anterior and lateral slopes. No setulae on the surface directly behind the *h*. Notopleuron, apart from 2 *npl*, bare (right side) or with 1–2 minute ground setulae (left side). Anterior *npl* 1.5x as long as posterior *npl*. 1 + 3 *acr*, equally strong, the first pair well in front of suture. 2 + 3 *dc*, becoming slightly stronger posteriorly. Rows of *acr* slightly closer to each other than to the row of *dc*. 1 *ph* only present (the inner). *prst* strong. No further setae in the area between the inner *ph* and the *prst*. 0 + 2 *ia*. 3 *sa*: the first

(*pra*) weak, shorter than posterior *npl* and a little longer than ground setulae, the second strong and long, the third weak; all on one line; no distinct Hough seta (discussed below) to the inside of the area between the first and second postsutural *sa* (Rognes 1997: 52, fig. 11), although a few setulae are present closer to the suture. 2 *pa* (both strong and long). Scutellum with two equally strong marginal *scut*, of which the apical reaches a little farther back than the basal, and a discal pair of weaker setae. A regular row of small setulae following lower edge of the lateral scutellar declivity forwards (Fig. 11, arrow). No setulae on the underside of the scutellum. Postalar wall with 2–3 minute setulae on right side (Fig. 12, arrow), the left side could not be examined. Lateral surface of thorax with thin layer of white microtomentum on all sclerites. One strong and upturned proepisternal and one proepimeral seta present, each accompanied by a much smaller supplemental seta just below each of them curving in the same direction. Proepisternal depression bare (Fig. 8). Anterior (prothoracic) spiracle small and white. The suture running from fore coxa to the lower end of prothoracic spiracle is a conspicuous brown and shining line (Fig. 8). Anepisternum (Fig. 1) with 3 marginal setae in upper half, the second from top the largest and of about the same size as the fore *npl*, and one strong marginal seta in lowermost half. Area between the 3 upper and the single lower seta with an irregular group of 3–5 small thin marginal setae. A few setulae in front of marginal row. Upper anterior part of anepisternum with a group of black setulae (covered with white residues from stay in ethanol). Anepimeron bare in anterior half; posterior half below lesser ampulla with a bundle of 4–5 short black setulae, no strong seta among them; behind and below this bundle with some thin pale setulae. Mediotergite bare. No swollen or protruding subscutellum, just a narrow flat sclerotisation below a broader unsclerotised membrane and above the mediotergite (Figs. 10, 12). Anatergite with a few small black and pale setulae below underside of base of lower calypter (Fig. 10, arrow). Katatergite (supraspiracular convexity) bare. Katepisternum with a few long black setulae in upper part and 1+1 *kepst*. Anterior *kepst* weak, posterior strong. Lower part with rows of long strong setae in front of mid coxa. Meron with a row of 4–5 strong black meral setae (Fig. 9). Katepimeron bare with white microtomentum. Coxopleural streak absent. Metathoracic spiracle twice as long as broad, lappets white, and posterior lappet much smaller than anterior one (Fig. 9). Metakatepisternum (area above hind coxa) bare. Metasternal area (in front of hind coxae) bare. Prosternum bare.



**FIGURES 13–16.** *Mafikengia ciliata* sp. nov., male holotype, wing and abdomen. **13.** Right wing from above. **14.** Detail of right wing, from below. Arrow points to exit of anal vein near fold in wing. **15.** Abdomen, dorsal view. **16.** Abdomen, ventrolateral view.

**Wing** (Figs. 1, 13, 14). Membrane glassy and covered with microtrichiae all over. Costa pale yellow, most other veins yellow basally, more brownish distally. Basicosta yellow, tegula yellow. Anterior edge of costa with

two regular (anterodorsal and anteroventral) rows of almost erect strong setulae longer than costal diameter. These are alternating for a long distance beyond exit of vein  $R_1$  with 2–3 thin and much less erect setulae. The remainder of the anterior edge of costa only with thin setulae of the latter type. Costal spine prominent, 2x length of erect setulae. Upper and lower side of costa with small setulae for a long distance beyond exit of vein  $R_1$ . Stem-vein bare on both surfaces of wing. Node at base of humeral crossvein bare.

Subcostal sclerite yellow, bare, no setulae or setae, only pale microtomentum present. Subcosta slightly sinuous with an inconspicuous forward bend at middle. Vein  $R_1$  brownish with a pale spot at middle. Vein  $R_{4+5}$  with thin rather long setulae on both surfaces of wing all the way to costa. Bend of vein M a gentle curve. Distal section of vein M (posterior crossvein) slightly sinuous distally so that the section closest to costa is running almost parallel to vein  $R_{4+5}$ . Cell  $r_{4+5}$  opens close to wing tip, opening as wide as length of  $r-m$  crossvein.  $dm-cu$  crossvein slightly sinuous, a little closer to bend of vein M than to  $r-m$  crossvein. Anal vein reaching margin (Fig. 14, arrow). Upper calypter small, brownish yellow. Lower calypter brownish yellow, much larger and longer than upper calypter, about as broad as long, inner edge converging with longitudinal axis of body; bare on both surfaces [many mites covering much of the upper surface making much of it invisible]. Halter with pale yellow stem and knob.

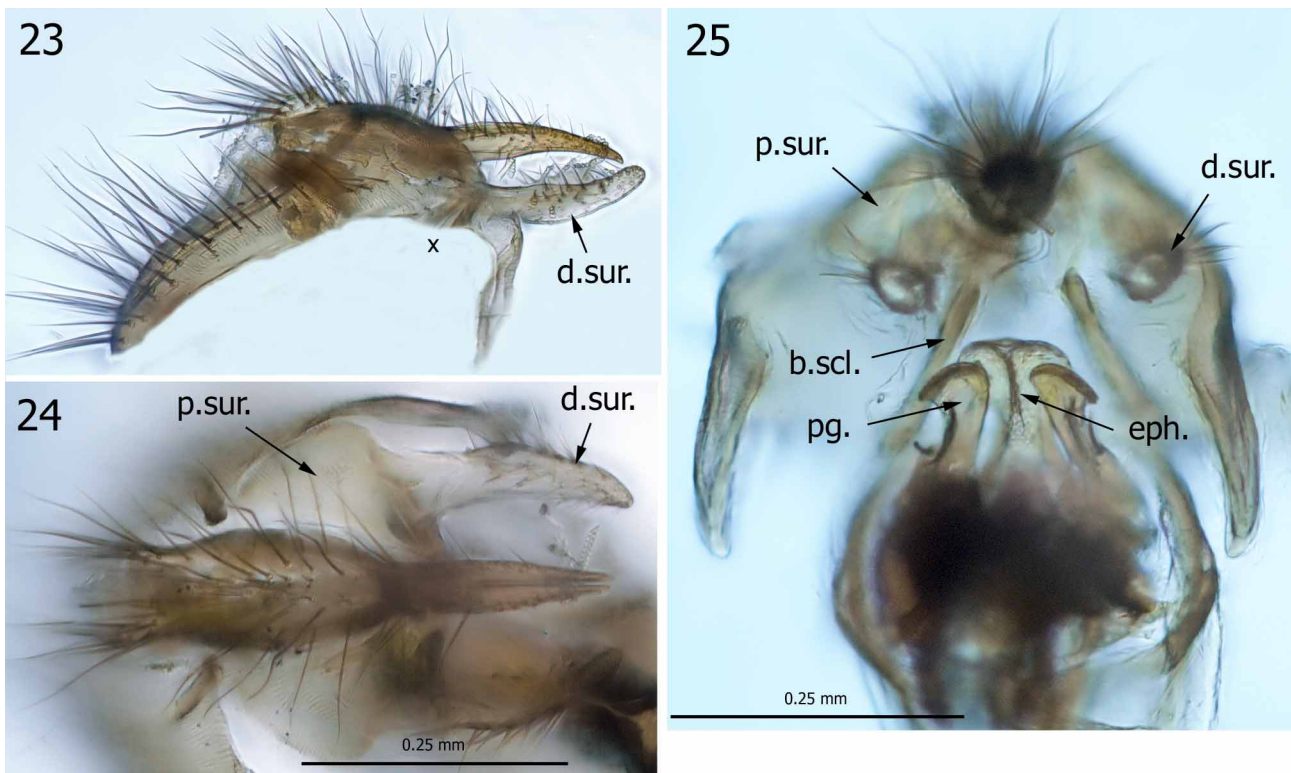
**Legs** (Figs. 17–22). All yellow, with black setae. Hind coxa bare on posterior surface. All femora thickened. No  $pv$  ctenidium on mid femur, setae in this position long and thin and widely spaced. Tibial setae moderately long. Tarsi much longer than tibiae. Claws and pulvilli on each tarsus about half as long as the distal tarsomere. Fore femur with complete row of  $pv$  setae; double row of  $ad$  setae in distal half. Fore tibia with 2 small  $ad$ , about as long as tibial diameter, and 1  $pv$  twice as long; preapical  $ad$ ,  $d$  (latter 1.5x length of former),  $pv$  and  $v$  setae (both about the size of the  $ad$  preapical) present. Mid femur with one  $ad$  at middle; a complete  $av$  row with distal 4–5 setae stronger than the rest; one  $a$  preapical seta; complete  $pv$  rows of setae shorter than femoral diameter; 2–3  $p$  preapicals. Mid tibia with 2  $ad$  [can also be described as 1  $a$  and 1  $ad$ ], 2  $pd$  and 1  $v$  seta, all longer than tibial diameter. Hind femur with complete rows of  $ad$  setae, partly doubled in middle; 5–6 strong  $av$  setae in distal half,  $av$  in proximal half weak; complete rows of  $pv$  setae, those in proximal two-thirds stronger than the rest; one weak  $pd$  seta in preapical position. Hind tibia with 2 strong  $ad$  setae; strong  $ad$ ,  $d$  and  $pd$  preapical setae, the  $d$  preapical remarkably long, 1.2x as long as first tarsomere (Figs. 1, 21, 22); 2 weak  $a$  preapicals and 1  $av$  preapical as strong as the  $ad$  preapical. A thin and short  $p$  preapical close to and just below the  $pd$  preapical, and also a short and weak  $pv$  preapical.



**FIGURES 17–22.** *Mafikengia ciliata* sp. nov., male holotype, legs. **17.** Left fore leg, posterior view. **18.** Right fore leg, posterior view. **19.** Right mid leg, anterior view. **20.** Right mid leg, posterodorsal view. **21.** Right hind leg, anterior view. **22.** Right hind leg, dorsal view.

**Abdomen** (Figs. 15, 16). Excavation at base of T1+2 very shallow, hardly present at all. Ground setulae quite long and more or less erect. Complete marginal rows of setae on all tergites, weak on T1+2, becoming stronger posteriorly, strongest on T5. Irregular transverse rows of weaker discal setae on T3–T5. T6 a small bare sclerite in front of TST7+8, the latter setose. ST1–3 cannot be described since mostly hidden by phoretic mites, but visible posterior half of ST3 with black short setae. ST4 lost. ST5 of usual shape with lateral lobes, without alpha-setae near anterior margin.

**Genitalia** (Figs. 23–37). Cerci and surstyli. Cerci fused into a single structure (Fig. 24). Proximal half narrowly oval with long upright setae. Distal half very narrow in dorsal view, also with long setae, at least basally. Distal half split for distal two-thirds into two very narrow pointed parts which do not diverge from each other. In lateral view distal half of cerci slightly curved downwards (Fig. 23). Each surstylus composed of two, broadly connected parts. A narrow distal part, situated on a level lower than the proximal part, is curved upwards towards the cerci in lateral view (Fig. 23), and curved slightly inwards in dorsal (posterior) view (Fig. 24). It has moderately long setae on distal two-thirds. The proximal part of the surstylus (*p.sur.*) is a broad microtrichiose convex plate without setae, situated between the basal parts of the cerci and the epandrium (Fig. 24). It is separated from both sclerites by unsclerotised membrane. There is a downward slope **laterodistally** that connects it with the distal part, thus placing the distal half at a lower level than the cerci. There is a similar, but narrower, downward slope **mediodistally**, i.e., close to the cerci, that connects it with the upper end of the bacilliform sclerite. The bacilliform sclerites proceed downwards, as two simple separate rods, towards the posterior end of the hypandrial arms (Figs. 23, *x*; 25, *b.scl.*). The connection between the upper end of each bacilliform sclerite is thus on the medial side of the surstylus.



**FIGURES 23–25.** *Mafikengia ciliata* sp. nov., male holotype, cerci, surstyli, epandrium and bacilliform sclerites. **23.** Cerci, surstylus, epandrium, left lateral view. The letter ‘x’ marks the position of the remainder of the bacilliform sclerite, most of it removed from figure. **24.** Cerci and surstylus, dorsal (posterior) view. **25.** Genital capsule, internal view.

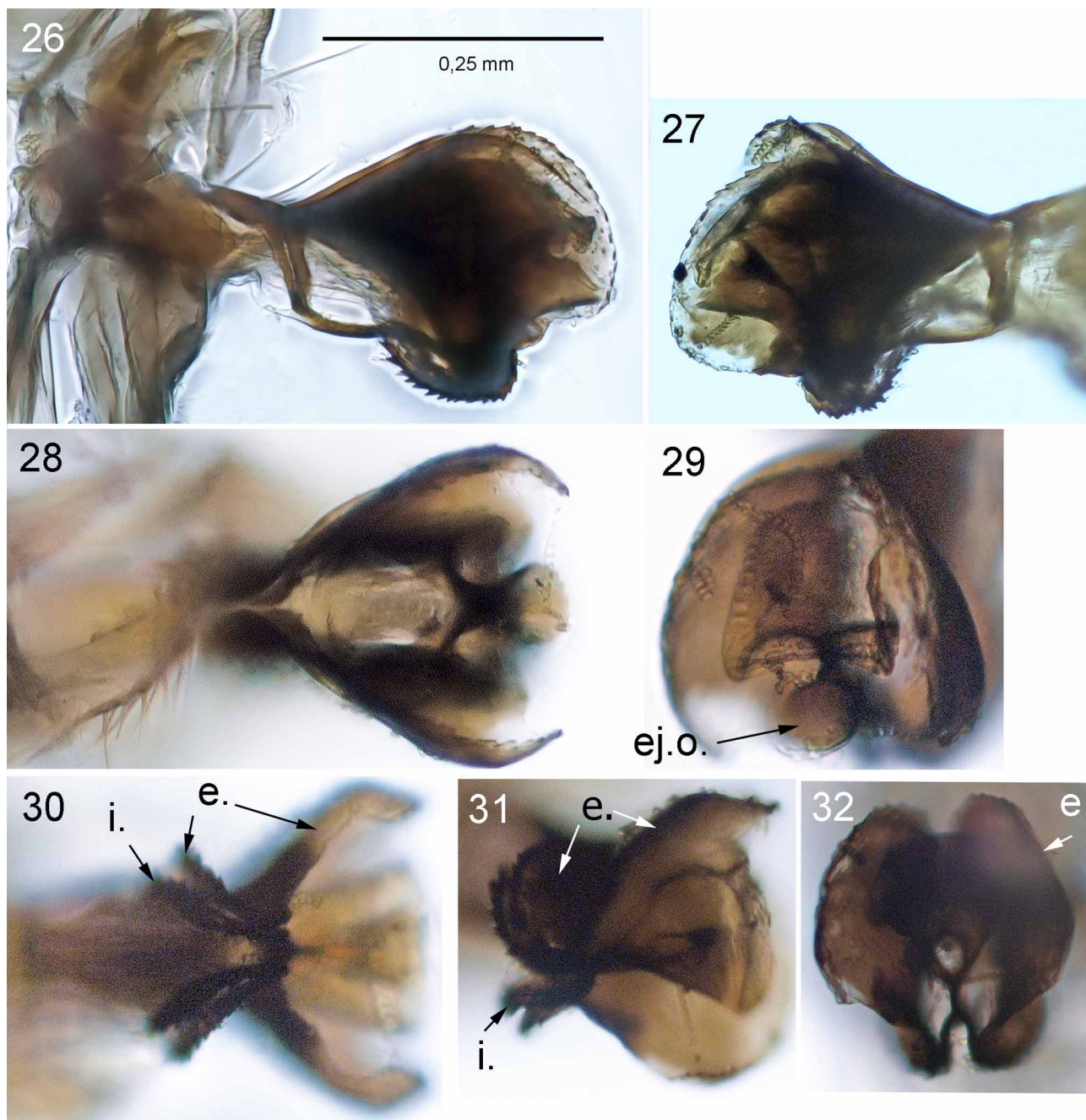
**Aedeagus.** (Figs. 25–33). Basiphallus difficult to describe since partly hidden. Epiphallus (Fig. 25) elongate and curved, with a keel on anterior side. Distiphallus globose. Ventral plate narrow, ring-like. Mesohypophallic sclerotisation (Figs. 26, 27, 33) rather broad, proceeding distally from the ventralmost point of the ventral plate, narrowing to a ridge below the ejaculatory opening and for much of its course situated in a deep groove in the ventral surface of the distiphallus (Fig. 32). Lateral wall of distiphallus (“paraphallus”) strongly sclerotised (except along its margins) and, in lateral view, an almost circular structure with a weakly serrated margin distally and a strongly dentate margin ventrally, the latter termed an external hypophallic lobe (Figs. 30–32, *e.*). In ventral view a conspicuous inward bulge present in the ventral part (Figs. 30, 31). Each “paraphallus” diverging strongly from its counterpart on the opposite side in dorsal view (Figs. 28, 29). Middorsally between the anterodorsal edges of the lateral sclerotised wall of the distiphallus, and at a slightly lower level, a broad, curved (in lateral view) shield-like hood (Figs. 28, 29, 31), probably representing much of the dorsal sclerotised wall of the distiphallus. Below it the large opening of the ejaculatory duct (Fig. 29, *ej.o.*). Between the latter and the underside of the hood a strongly sclerotised median bridge connecting the two structures (Figs. 28, 29). Between the external hypophallic lobes a

short, strongly serrated internal hypophallic lobe on each side (Figs. 30, 31, *i.*). The external and internal hypophallic lobes forming two dentate ridges ventrally on each side, at least the inner lobes converging towards midline in ventral view.

Pre- and postgonites. Postgonite a thickened elongate sclerite, curved at tip and with an apodeme at the proximal end articulating with the basiphallus. Postgonite lying alongside the epiphallus of the basiphallus (Fig. 25) in its natural position, with a long seta at middle and a field of sensillae above the seta, near the bend (Fig. 36). Pre-gonite (Figs. 33–35) a complex structure carrying a row of 5–6 setae along its dorsal ridge. This ridge strengthened and carrying a flange laterally, which is also strengthened along the middle, this strengthening forming an angle with the first strengthening. Pregonite distally with a long pointed process beyond the distalmost seta. This process lies alongside the distiphallus (Fig. 35). [It is lost on the left side.]

Ejaculatory sclerite narrow, weakly sclerotised distally (Fig. 37).

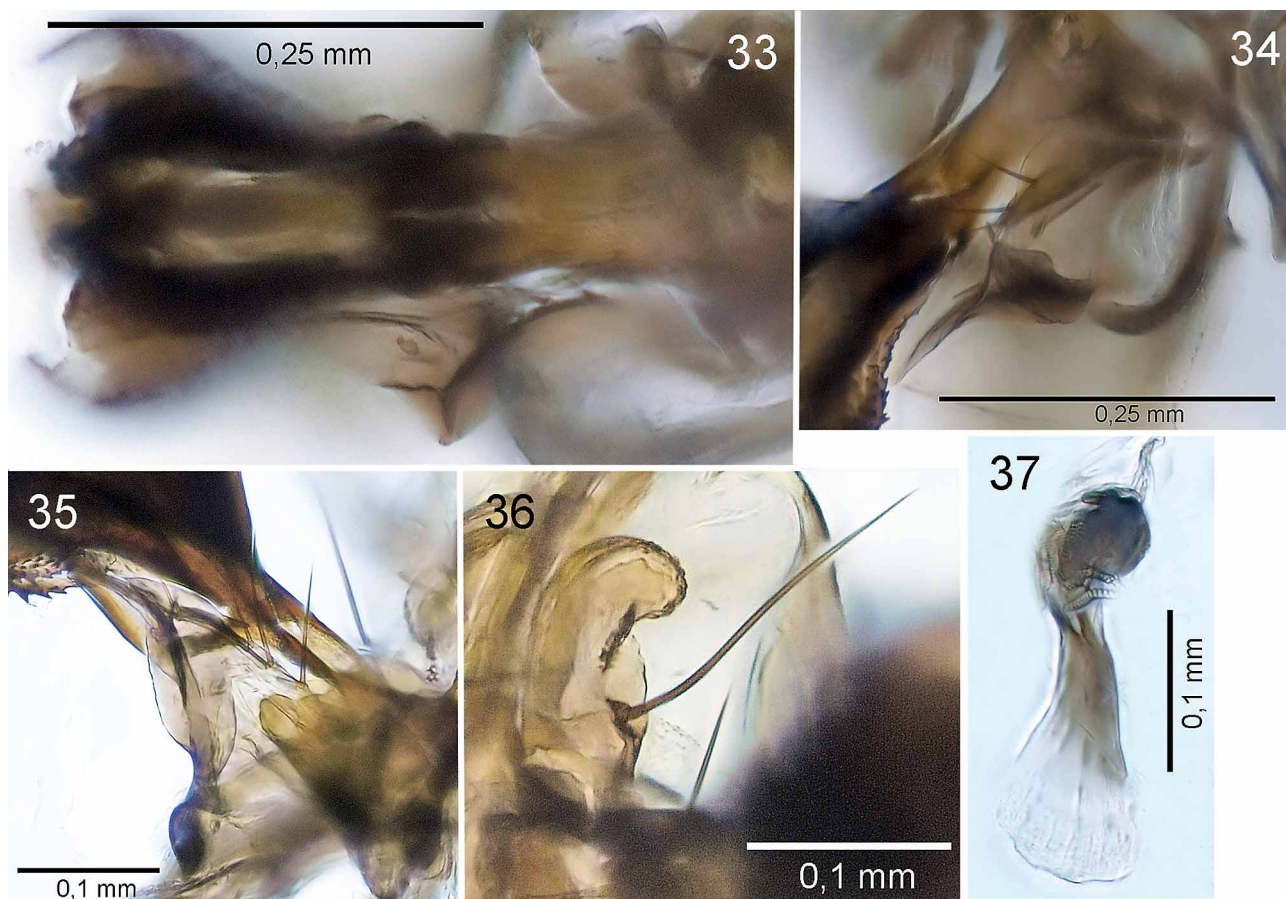
*Female.* Unknown.



**FIGURES 26–32.** *Mafikengia ciliata* sp. nov., male holotype, aedeagus. 26. Aedeagus, left lateral view. 27. Distiphallus, right lateral view. 28. Distiphallus, dorsal view. 29. Distiphallus, slightly oblique anterodorsal view. 30. Distiphallus, ventral view. 31. Distiphallus, oblique anteroventral view. 32. Anterior view.

**Biology.** The capture of the specimen on the “chimney” of a termite nest (*Odontotermes* sp.) suggests that it is biologically associated with termites. Nothing else is known. The identity of the mites found on its body might shed some light on whether they have been received from mites usually living in the termite’s nest (cf. Haq *et al.* 1990).

**Type material. Holotype:** adult ♂, labelled: (1) “SOUTH AFRICA: NORTH WEST PROVINCE // Mafikeng [as “Mafeking” on some maps] 24.ii.2007 // 25° 49' 10.10"S / 25° 37' 55.33"E, ca 1280m. // S. Dupont & J. Pedersen leg.” [printed] (Fig. 1, inset); (2) “*Neocordylobia* sp.” [printed]; (3) My red holotype label. The specimen was brought to ZMUC in 96% ethanol, and pinned and dried after dissection. The KOH macerated genitalia are now in glycerol in a glass vial on the pin. The left mid and hind legs were removed for molecular studies by ZMUC and have not been studied by me. All material is in ZMUC.



**FIGURES 33–37.** *Mafikengia ciliata* sp. nov., male holotype, right pre- and postgonites, ejaculatory sclerite. **33.** Right pregonite alongside distiphallus, dorsal view. **34.** Same, oblique anterodorsal view. **35.** Same, oblique dorsolateral view. **36.** Right postgonite. **37.** Ejaculatory sclerite.

### Monophyly and diagnosis of the Bengaliinae

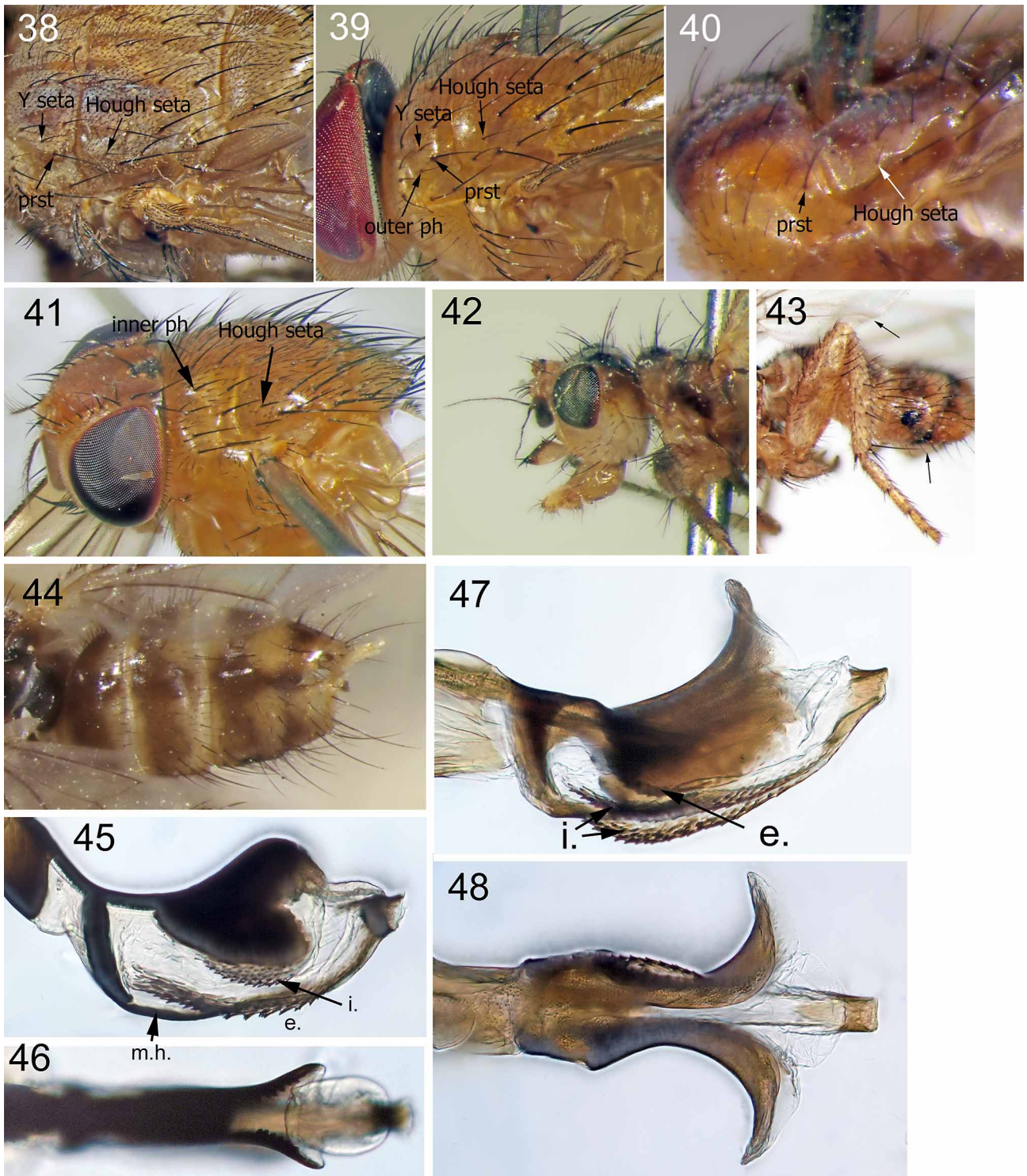
Rognes (1991, 1997, 1998, 2006), Pape (1992) and Pape and Arnaud (2001) have discussed the composition and monophyly of the Bengaliinae. Rognes (1998) ended up treating Bengaliini and Auchmeromyiini (equivalent to “Bengaliinae” and “Auchmeromyiinae”, respectively, in Rognes 1997) as separate monophyletic tribes within the subfamily Bengaliinae (s.lat.) of the Calliphoridae, whereas Pape (1992) did not attempt any such subdivision. Rognes (1997) established that among the Calliphoridae the composite group “Bengaliinae” + “Auchmeromyiinae”, the equivalent of the subfamily Bengaliinae (s.lat.) of the present paper, was a very well supported group, the best supported one according to one criterion (Farris’ Parsimony Jackknifer). The monophyly was established by Rognes (1997: 37, fig. 2, node 26) on the basis of the following synapomorphies: (1) ground colour yellow; (2) coxopleural streak absent; (3) anal vein reaching wing margin.



Other character states that often occur among the Bengaliinae and can be used to diagnose the subfamily are listed below (those with numbers in boldface are examined in detail later). Several of them, indicated by an asterisk, may be synapomorphic for the genera making up the subfamily:

- (4) \* frons in male as broad as in females, sometimes even with a proclinate orbital seta (Fig. 41);
- (5) \* a distinct but weakly developed convex subscutellum (not present in *Mafikengia*, but this apparent absence may be due to shrinkage subsequent to alcohol preservation);
- (6) a small seta (Hough's "postsutural seta", here named the "Hough seta", Figs. 38–41) situated between and on the inside of the prealar and the first supra-alar and which does not form part of the intra-alar row (more on this below);
- (7) a small seta present a little to the inside and a little in front of the presutural seta ("Y seta") (Figs. 38, 39) (more on this below);
- (8) lateral scutellar marginal setae tending to be numerous and conspicuous and to follow the lower margin of scutellum very closely and strikingly far forward toward its anterior end (except in *Bengalia* and *Cogano-myia* that have only a single seta in lateral position, although in *Bengalia* additional small erect setae may occasionally be present; and in *Tricycleala* where no row of small setulae could be found, sometimes only a single small setula is present alongside the lateral seta);
- (9) wing cell  $r_{4+5}$  opens at the wing tip, not well in front of it (in several genera, especially those with small-sized species);
- (10) \* wing vein M gently curved, not angulated;
- (11) costa setulose on underside all the way to vein  $R_1$ ;
- (12) abdominal segments usually with narrow dark posterior margins; exceptions are found e.g. in *Termitoloemus* (where the male has three broad spots along fore margins of abdominal tergites, proceeding backwards, but not reaching posterior margins which are all pale; in the female there are dark bands along fore margins, cf. Fig. 44); and e.g. in *Auchmeromyia* and *Cordylobia* (which have a more complex dark pattern, even almost totally black);
- (13) male cerci sometimes fused into a single undivided structure (*Auchmeromyia*, *Pachychoeromyia*, *Cogano-myia*, *Mafikengia*) (Figs. 24, 49, 50, 53);
- (14) surstylus differentiated in all the genera into a posterior (proximal) part, often of considerable size and bare, i.e. microtrichiose but not setose, and a distal part situated at slightly different level, usually setose; in at least one genus (*Bengalia*) these parts are completely separate sclerites (Figs. 51, 52);
- (15) \* bacilliform sclerite joined at its upper end to the **medial** side of the surstylus at the transition zone between proximal and distal part of latter, a unique feature never described by earlier authors (discussed in greater detail below) and which appears to be of great significance;
- (16) \* distiphallus with two ventral dentate bands, ridges or lobes: an internal hypophallic lobe and an external hypophallic lobe, latter not always joined to, thus independent of, the outer strongly sclerotised lateral wall of the distiphallus (Figs. 30, 31, 45, 47, 68, 82, 84, 85) (cf. also Patton [1935, 1936, for various genera]; Grunin [1949, for *Booponus inexpectatus*]; Rohdendorf [1959, for *Booponus borealis*]; Kurahashi *et al.* [1997, for *Verticia*]; Rognes [2009b, for *Bengalia*]);
- (17) \* lateral wall of distiphallus strongly sclerotised (Figs. 26–32, 45, 47, 66, 68, 82, 84, 85) a feature which mimics and has been termed a paraphallus in some genera, a term I now find misleading since the structure is just a sclerotisation originating in the dorsal wall of the distiphallus, also often strongly sclerotised for some distance, and it is never shaped as a narrow pointed process or hook free from remainder of aedeagal wall (Rognes 2010). In retrospect, the coding of char. 30 as "1" for Auchmeromyiinae by Rognes (1997) is therefore suspect;
- (18) dorsal and also distal edge of the "paraphallus" distally dentate (e.g., *Mafikengia ciliata* [Figs. 26, 27], *Hemigymnochaeta gogoiana* Lehrer [Lehrer 2009: 29, fig. 2], *Booponus borealis* [Rohdendorf 1959: fig. 2], *Booponus inexpectatus* [Grunin 1949: fig. 1 ♂]);
- (19) \* ventral plate of the distiphallus, a ring-like structure, narrow [= short in anteroposterior direction] in profile view (Figs. 26, 45, 47, 66, 68, 82, 85) and forming roughly almost a right angle with the mesohypophallic rod as seen in profile;
- (20) mesohypophallic rod continuous with and proceeding at least some distance distad from ventral end of ventral plate (Figs. 26, 45, 47, 66, 68, 82, 85);

(21) lateral wall of the distiphallus flaring out laterally as seen in dorsal view (Figs. 28, 47, 48, 83, 84; cf. also conditions in e.g. *Booponus inexpectatus* [Grunin 1949: fig. 1♂], *Cordylobia rodhaini* [Fain 1953a], *C. roubaudi* [Patton 1935] and *C. ruandae* [Fain 1953b]).



**FIGURES 38–48.** Bengaliinae, various species. **38–41.** Thorax (in part also head), lateral to dorsolateral view, showing various setae. **38.** *Cordylobia anthropophaga* (Blanchard), male (MZLU). **39.** *Hemigymnochaeta* sp. (BMSA). **40.** *Termitoloemus marshalli* Baranov, female paratype (BMNH). **41.** *Verticia* sp., male (Sarawak specimen, BMNH). **42–44.** *Termitoloemus marshalli* Baranov, holotype (BMNH). **42.** Left lateral view of head and fore part of thorax. **43.** Left lateral view of hind leg, including parts of wing and abdomen. Arrows point to exit of anal vein (upper), and tip of dorsal preapical seta on hind tibia. **44.** Dorsal view of abdomen. **45–46.** *Hemigymnochaeta gogoiana* Lehrer, male (specimen no. 15210, BMSA). **45.** Distiphallus, left lateral view. **46.** Distiphallus, dorsal view. **47–48.** *Cordylobia anthropophaga* (Blanchard), male (MZLU). **47.** Distiphallus, left lateral view. **48.** Distiphallus, dorsal view.

## Hough's postsutural seta and the Y seta

Hough (1898: 170, fig. 9a, marked "x."; 180) was the first to describe a particular seta which is widespread within the Bengaliinae. He named it the *postsutural seta* and discovered its presence in his new nominal species *Parochromyia varia* Hough, 1898 belonging in his new nominal genus *Parochromyia* Hough, 1898. The latter is now a synonym of *Hemigymnochaeta* Corti, 1895 (cf. Pont 1980). He wrote about the seta: "... I venture to apply this name [postsutural seta] to a bristle present in all the specimens of this species [*Parochromyia varia*], which I have not been able to find in any other Muscids that I have seen. It is situated caudad the transverse suture of the thorax, a little mesad and caudad the anterior supra-alar, and laterad the intra-alar No. 3 (I number the intra-alars, ..., from the caudal end of the thorax cephalad, thus the intra-alar nearest the scutellum is No. 1)." In his figure 9a he marked the seta with an "x." and drew a line between the *prst* seta and the marked seta, indicating that he considered them to belong to the same series of thoracic setae. Villeneuve (1937: 1) used Hough's term in his description of his new nominal genus *Tricycleala* which he considered "... *proche de Tricyclea* Wulp (... *présence de la soie postsuturale de HOUGH, ..., etc.*)" [... close to *Tricyclea* Wulp (... presence of Hough's postsutural seta, ..., etc.)]. Rognes (1997: 52, fig. 11) described a seta in exactly the same position but did not name it. He found it to be present in *Auchmeromyia senegalensis*, *Cordylobia anthropophaga*, *Hemigymnochaeta unicolor*, *Hemigymnochaeta* sp., *Pachychoeromyia praegrandis* and *Tricyclea* sp. and used its presence to define the subfamily Auchmeromyiinae. Finally, Sze *et al.* (2008: 29) established the presence of the same seta in *Verticia*. The "Hough seta" is present in all the genera of Bengaliinae except *Bengalia*, *Coganomyia* and *Mafikengia* (Figs. 38–41).

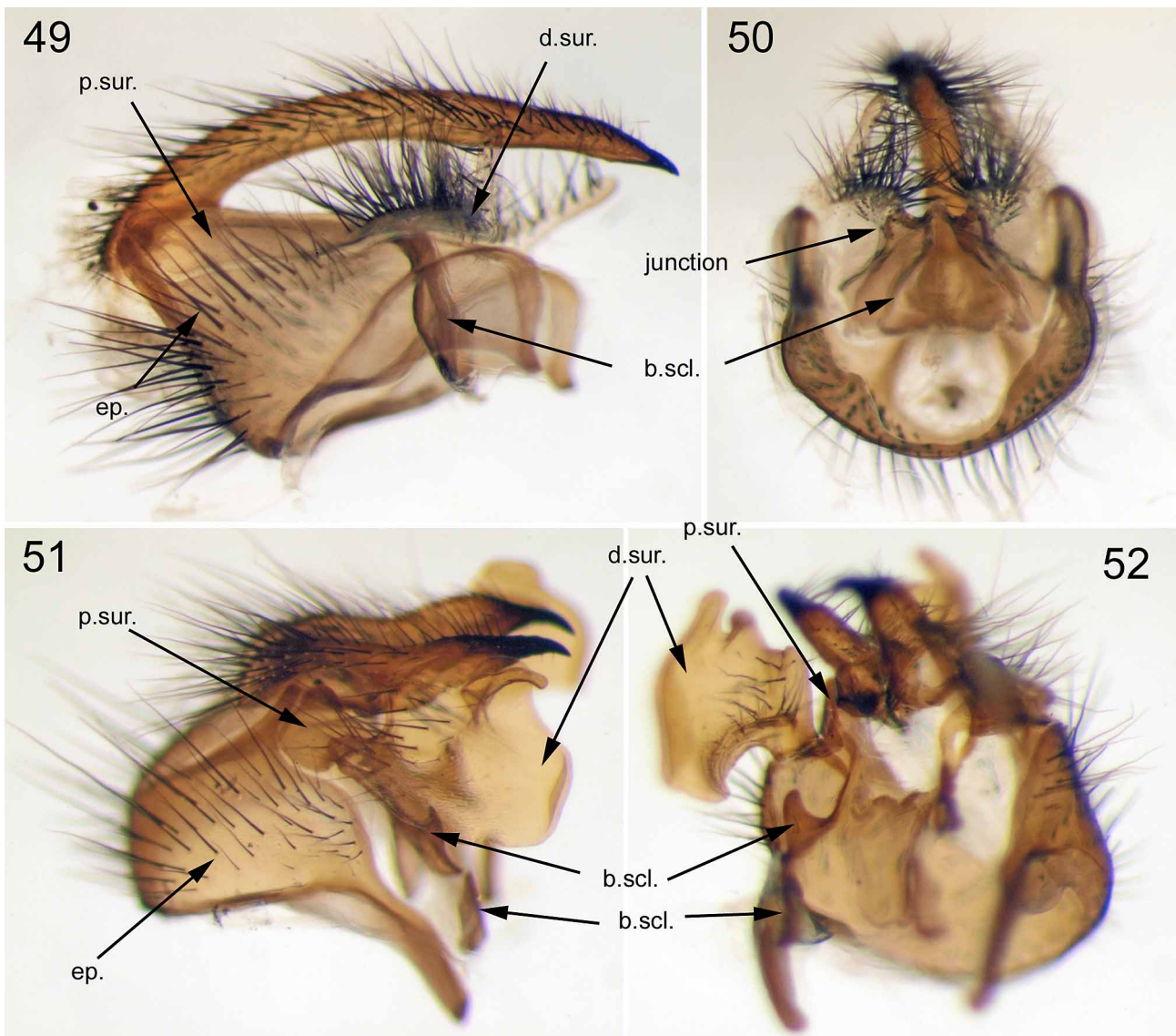
There is another seta found among the genera of Bengaliinae, but not elsewhere to my knowledge. I have called it the "Y seta" and it is shown for *Cordylobia anthropophaga* and *Hemigymnochaeta* sp. in Figs. 38, 39. It is situated somewhat in front of the *prst* seta and medially to it. It is often reckoned to be included among the post-humeral setae, but I do not think this is justified. The posthumeral setae are much closer to the humeral callus (post-pronotal lobe) than is this seta. I have noted its presence in all material I have seen of *Cordylobia*, *Booponus*, *Hemigymnochaeta* and *Pachychoeromyia*, in many species of *Tricyclea*, but only in two species of *Auchmeromyia* (*A. boueti*; and in females, but not males, of *A. choerophaga*; it is absent in *A. senegalensis* and *A. bequaerti*).

## Cerci, surstyli and bacilliform sclerites complex

*Mafikengia ciliata* was found to show two features that were quite surprising: (1) the surstylus has an extensive proximal part, and (2) the proximal part of the surstylus continues **mediodistally** directly into the upper end of the bacilliform sclerite. The connection point is where the proximal part of the surstylus dips down between the distal part of the surstylus and the lateral edge of the cercus. These two features have never before been described explicitly in any calliphorid taxon and this arrangement of the cerci, surstyli and bacilliform sclerites complex seems to be of fundamental importance. In what follows I will describe this complex of the genitalia (a) in all the bengaliine genera, and (b) in the remaining calliphorid and other groups. For some bengaliine species other genital parts are illustrated, sometimes for the first time.

### (a) – among genera of the Bengaliinae

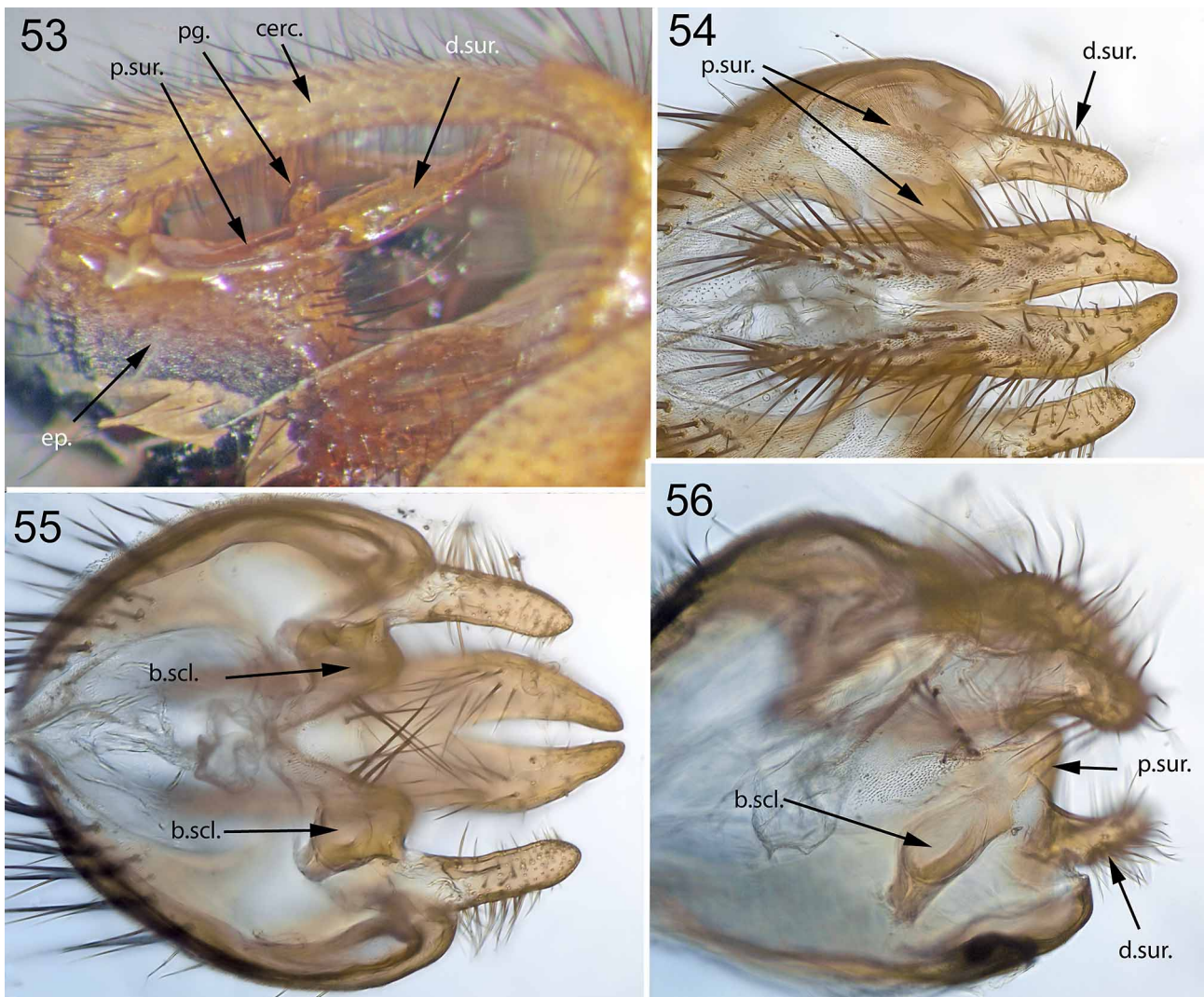
*Auchmeromyia* (Figs. 49, 50). The cerci, surstyli and bacilliform sclerites were described and illustrated by Patton (1935) for *A. senegalensis* (as *A. luteola*, preocc.), *A. bequaerti*, *A. choerophaga* and *A. boueti*. The structure of these sclerites, including the fused, strongly sclerotised and curved cerci, is essentially similar in all species, except for variation in length, shape and vestiture. The proximal part of the surstylus is more or less fused at its posterior-most narrow end with the epandrium in *A. bequaerti*, but not in *A. senegalensis* (my dissections). The essential features are shown in Figs. 49, 50. The proximal segment of surstylus (*p.sur.*) is bare and very strongly prolonged, the distal segment (*d.sur.*) is slender and more or less upturned in its distal half. The bacilliform sclerites (*b.scl.*) are fused in the midline, forming a single plate. Each upper lateral corner of this plate articulates with the medial side of the surstylus (*junction*). The upper posterior end of the epandrium terminates in a strong process which forms a conspicuous articulation with the base of the fused cerci.



**FIGURES 49–52.** 49–50. *Auchmeromyia senegalensis* (Macquart), male (ZMUN). 51–52. *Bengalia seniorwhitei* (Lehrer) (ZMUN). 49. Epandrium, cerci, surstyli and bacilliform sclerites, left lateral view. 50. Epandrium, cerci, surstyli and bacilliform sclerites, inside (anteroventral) view. 51. Epandrium, cerci, the two parts of the surstylus and bacilliform sclerites, left dorsolateral view. 52. Epandrium, cerci, left surstylus and bacilliform sclerites. Note the two sclerotisations from upper end of bacilliform sclerite, connecting to the medial side of the proximal and distal parts of surstylus, respectively.

*Bengalia* (Figs. 51, 52). In all *Bengalia* species each surstylus consists of two separate sclerites, corresponding to the proximal and distal parts of other genera, and each part is connected to the upper end of the bacilliform sclerite. The latter is also two-segmented, but only the upper piece is connected to the surstylus. From the medial side of anterior end of the proximal surstylus there is a thin sclerotised connecting lamella or string passing downwards to join the upper end of the uppermost bacilliform sclerite. Similarly, there is a thin string of sclerotised lamella passing down from the medial side of posterior end of the distal surstylus.

*Booponus*. Patton (1936: 60) figured the genitalia of *Booponus indicus* [as *Cordylobia (Elephantoloemus) indica*]. He did not illustrate or mention any “posterior prolongation” of his “ninth coxite” (proximal part of surstylus), but this part may have been overlooked, as was done in *Cordylobia anthropophaga* and *C. roubaudi* (see below). He described the bacilliform sclerite (as “the proximal segment” of his “ninth coxite”) as a stout rod. Grunin (1947, 1949) figured the genitalia of *B. inexpectatus* (originally placed by him in *Pavlovskiomyia*, subsequently in *Cordylobia*) and Rohdendorf (1959) figured the genitalia of *B. borealis*, but the figures do not give much detail about the articulation of the bacilliform sclerites with the surstyli. I did not have material of *Booponus* available for dissection to study this articulation.



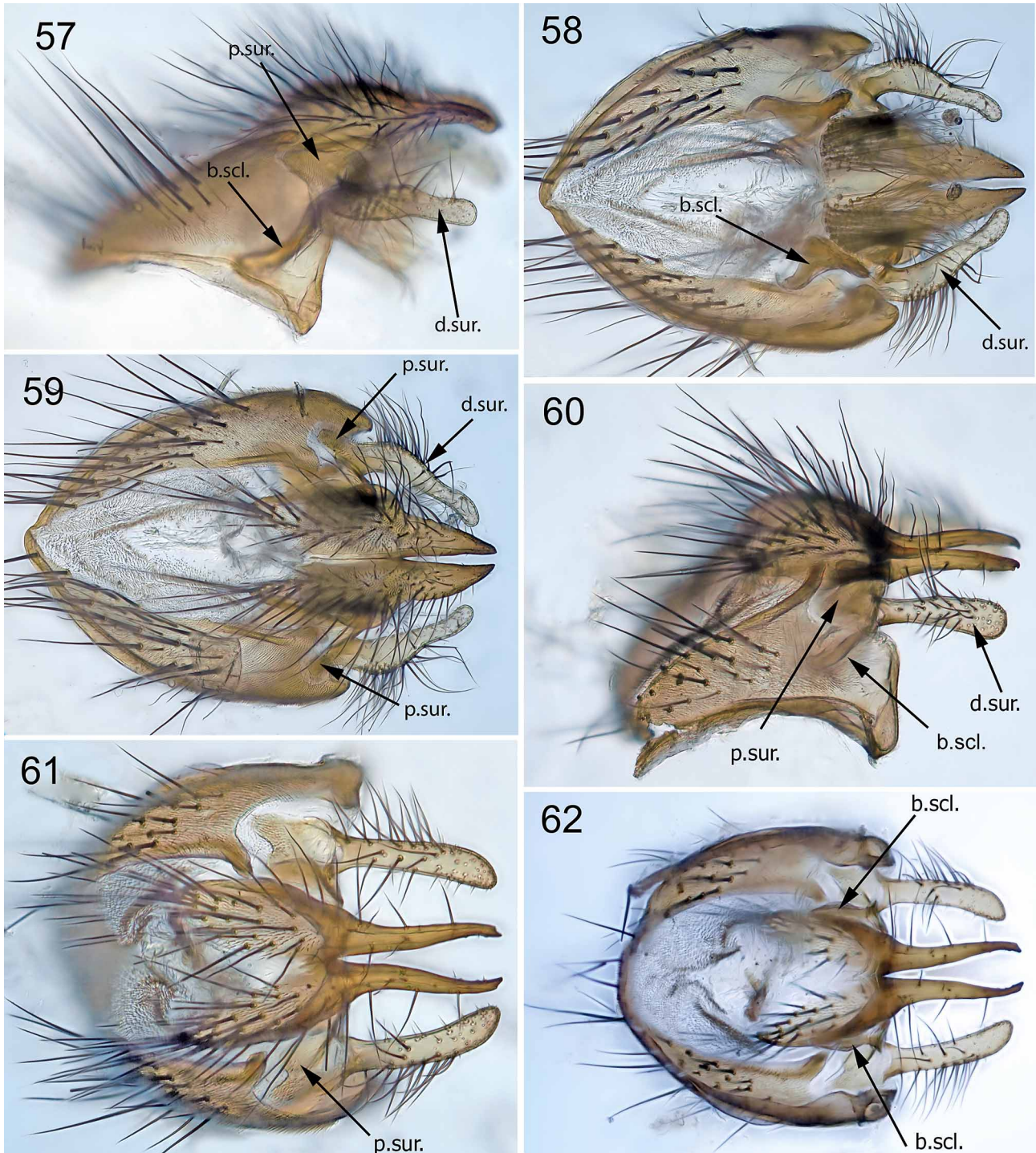
**FIGURES 53–56.** 53. *Coganomyia ornata* Dear, male holotype (BMNH). Cerci, epandrium and surstylus, oblique view. 54–56. *Cordylobia anthropophaga* (Blanchard), male (MZLU). 54. Cerci and surstyli, dorsal (posterior) view. 55. Genital capsule with bacilliform sclerites, cerci and surstyli, internal view. 56. Genital capsule with bacilliform sclerites, cerci and surstyli, oblique internal view.

*Coganomyia* (Fig. 53). Dear (1977) described the fused elongate cerci with bifid tip in his new genus, and the glossy, bare and elongate surstylus curving towards the cercal plate. The proximal part of surstylus, not mentioned by Dear, is a very elongate sclerite following and being separate from the neighbouring edge of the epandrium by weakly sclerotised membrane. The distal part of the surstylus is also elongate and, exceptionally, quite bare. I did not want to dissect the only available male (the holotype in BMNH) so I could not determine whether the bacilliform sclerites are fused in the midline, or whether they attach to the medial side of surstylus. Judging from the similarity of the surstylus and cerci with those of *Auchmeromyia* it is most likely that the upper end of the bacilliform sclerite joins the medial side of the junction of the proximal and distal parts of the surstylus.

Peris & González-Mora (2004) created a separate subfamily for this genus, Coganomyiinae, excluding the genus from both their Auchmeromyiinae (which included several genera) and their Bengaliinae (encompassing *Bengalia* only). The anal vein reaching the wing margin, the absence of a coxopleural streak, a yellow ground colour and a small subscutellum all speak in favour of placing the genus in Bengaliinae (s. lat.). I find that to keep a separate subfamily for this genus with the same rank as Auchmeromyiinae, Bengaliinae, and the other subfamilies of the Calliphoridae is quite unnecessary and therefore sink Coganomyiinae as a junior synonym of Bengaliinae **syn. nov.**

*Cordylobia* (Figs. 54–59). Patton (1936) described the genitalia of both *C. anthropophaga* Blanchard and *C. roubaudi* Villeneuve. Villeneuve (1929) described *C. roubaudi* in a new subgenus, *Neocordylobia* (under *Cordylobia*), but Zumpt (1956) later raised this taxon to a full genus. Patton overlooked the presence of the proximal part of

the surstylus (Figs. 54, 56, 57, 59) in both species (Patton 1936: 58, fig. 1f; 62, fig. 5b). In *C. anthropophaga* the proximal part of the surstylus is broad and dips down medial to the base of the distal part to form a junction with the bacilliform sclerite on each side (Figs. 54–56). The latter are separate simple sclerites. In *C. roubaudi* (Figs. 57–59) the proximal part of the surstylus is small when seen in dorsal view. It dips down medial to the distal part of the surstylus and joins the bacilliform sclerite. Between the bacilliform sclerites there are two large sclerotisations in the ventral epandrial membrane each carrying a dense brush of long, fine, pale setae (Fig. 58); a very good distinguishing character, previously unknown or at least not mentioned by Patton or other workers, for *C. roubaudi*.



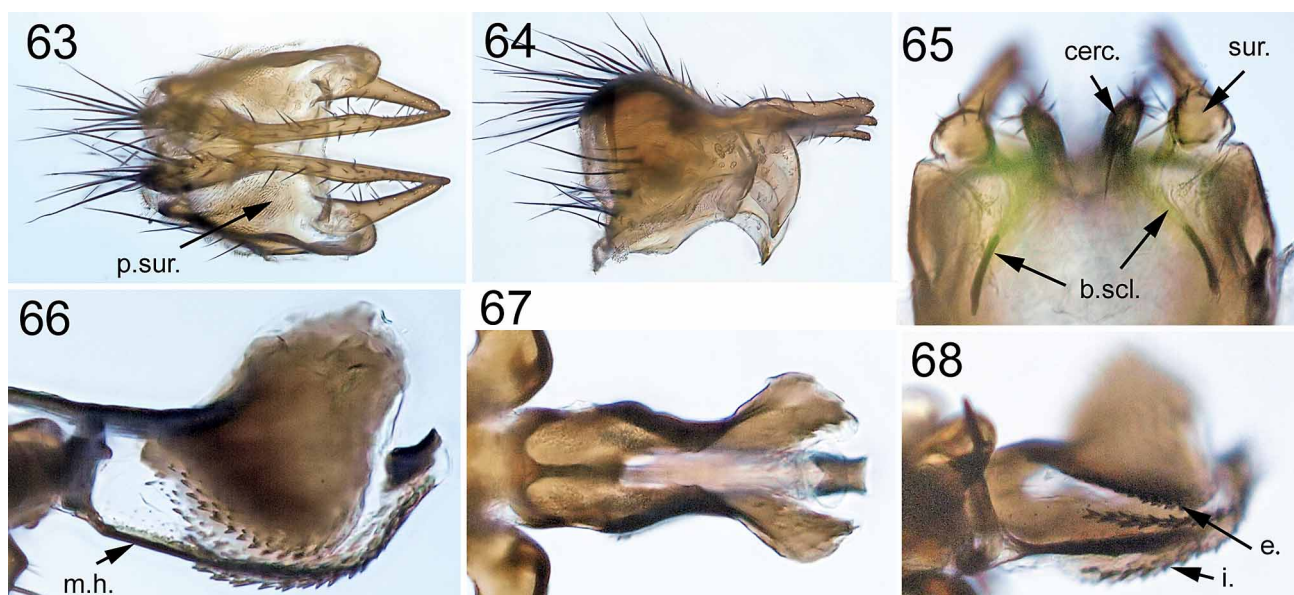
**FIGURES 57–62.** 57–59. *Cordylobia roubaudi* (Villeneuve), male (specimen no. 00719, BMSA). 57. Epandrium, surstylus, cerci and bacilliform sclerite, left lateral view. 58. Epandrium, surstyli, cerci and bacilliform sclerites, ventral (internal) view. 59. Epandrium, surstylus, cerci and bacilliform sclerite, dorsal (posterior) view. 60–62. *Hemigymnochaeta gogoiana* Lehrer, male (specimen no. 15210, BMSA). 60. Epandrium, surstylus, cerci and bacilliform sclerite, left lateral view. 61. Epandrium, surstyli and cerci, dorsal (posterior) view. 62. Epandrium, surstyli and cerci, ventral (internal) view.

*Hemigymnochaeta* (Figs. 60–62). Again, the proximal and the distal parts of the surstylus are easily identifiable and the medial edge of the former dips down on the inside to join the bacilliform sclerite. The junction is thus on the medial side of the surstylus.

*Pachychoeromyia*. The male and female genitalia of *Pachychoeromyia praegrandsis* were described and figured by Patton (1935, as *Auchmeromyia praegrandsis*). He found the male genitalia to be very similar to those of the other species of *Auchmeromyia* in all essential features regarding the cerci, surstyli and bacilliform sclerites, and argued against keeping *Pachychoeromyia* as a genus distinct from *Auchmeromyia*. I dissected a male from South Africa, and can confirm Patton's descriptions. The long bare proximal part of the surstylus continues directly into the very densely long setose distal part, with almost no angle between them, as seen in profile. Seen from above, the distalmost section of the proximal part of the surstylus divides into two short separate longitudinal bands, with a weakly sclerotised zone between them. The medial band bends down and continues directly into the upper lateral corner of the fused bacilliform sclerites. The lateral band continues into the distal part of the surstylus. A part of the upper lateral corner of the fused bacilliform sclerites seems to form a loose articulation with the inside of the basal part of the distal surstylus. Again, the bacilliform sclerite joins the surstylus on the medial side of the latter.

The *Pachychoeromyia praegrandsis* aedeagus is very high (dorsoventrally) as seen in profile, the ventral plates are also very high (dorsoventrally) and narrow (anteroposteriorly) and the opening of the ejaculatory duct is carried on a long narrow apical projection. It has no trace of sclerotised hypophallic lobes and dentate bands on the ventral side of the distiphallus alongside the well developed mesohypophallic sclerotisation. The only denticles present are situated on the distalmost parts of the paraphallus; the paraphallus has two lappets on each side high up on the sides of the distiphallus and about halfway to the tip.

*Termitocalliphora* (Figs. 63–68). The cerci and surstylus of *T. nana* in posterior (dorsal) view and the aedeagus in lateral view were illustrated by Bauristhene (1964). No clues about the connection between the posterior part of the surstylus and the upper end of the bacilliform sclerite are given in her figures. I examined the genitalia of a male specimen from Nigeria, and they are shown in Figs. 63–68. A long slender bacilliform sclerite joins the proximal part of the surstylus on its medial side, as usual.



**FIGURES 63–68.** *Termitocalliphora nana* (Zumpt), male (CNC). **63.** Epandrium, cerci and surstyli, dorsal (posterior) view. **64.** Epandrium, cerci, surstyli and bacilliform sclerites, left lateral view. **65.** Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view. **66.** Distiphallus, left lateral view. **67.** Distiphallus, dorsal view. **68.** Distiphallus, oblique ventral view.

*Termitoemus marshalli* (Figs. 69–72). Only a single male is known of this species, given a very detailed description in German by Baranov (1936). The genitalia of the male holotype is mounted with some lateral compression on a slide with the left side up. Baranov figured the genitalia in lateral view (this figure is easily compared with the slide), and in posterior (dorsal view) (Fig. 72), but gave no interpretation of the structures he illustrated. He diagnosed the genitalia as follows: “*Hypopygium des ♂ mit sehr kompliziert gebautem Phallus (kein Calliphora-*

*Typus!*) und sehr grossem *Spinus ditillatorius*” [Hypopygium of the ♂ with an aedeagus of very complex build (no *Calliphora*-type!) and very large epiphallus]. Baranov assigned his new genus to the “*Townsend'sche Tribe Bengaliini*” although he thought it “*viel besser für diese Art eine besondere Tribe zu schaffen*” [much better to create a separate tribe for this species].

Senior-White *et al.* (1940) gave a comprehensive English description. Sabrosky and Crosskey (1970), examining Baranov's types, saw “no relationship to the Bengaliini” and for reasons of “general facies and chaetotaxy, the open metathoracic spiracle with reduced lappets, and the small rounded calypteres” suggested it be referred to the Rhinophoridae. Crosskey (1977a) keyed the species in a brief review of the Oriental Rhinophoridae, and was the first to refer to features of the slide-mounted genitalia of the holotype in BMNH. According to him, “the slide shows that the cerci are extremely reduced, the surstyli long and very narrow (but both broken and with missing apices), and the ejaculatory sclerite of an extraordinary umbrella-like or mushroom-like shape (different from that of other rhinophorids)”. Crosskey (1977b) catalogued it in the Rhinophoridae in accordance with his earlier view (Sabrosky & Crosskey 1970). Pape (1986) re-examined both the adult and the genital slide, noted peculiarities of the lower calypter, claimed that “its ventral plates are not fused” in the aedeagus, and transferred it back to the Calliphoridae. Finally, Pape (1992) listed *Termitoloemus* Baranov, 1936 among several genera he assigned to the calliphorid subfamily Bengaliinae, together with “... *Auchmeromyia, Bengalia, Cordylobia, ..., Tricyclea...*” all found by Pape to have an elongate anal vein reaching the wing margin.

I have examined the male holotype, the two female paratypes and the slide of the male genitalia of *Termitoloemus marshalli* in BMNH. Although I am reluctant to accept that it is possible to claim from an examination of Baranov's slide-mount that the ventral plates are not fused, I agree with Pape that *Termitoloemus* belongs in the Bengaliinae (*s.lat.* of Pape 1992 and Rognes 1998).

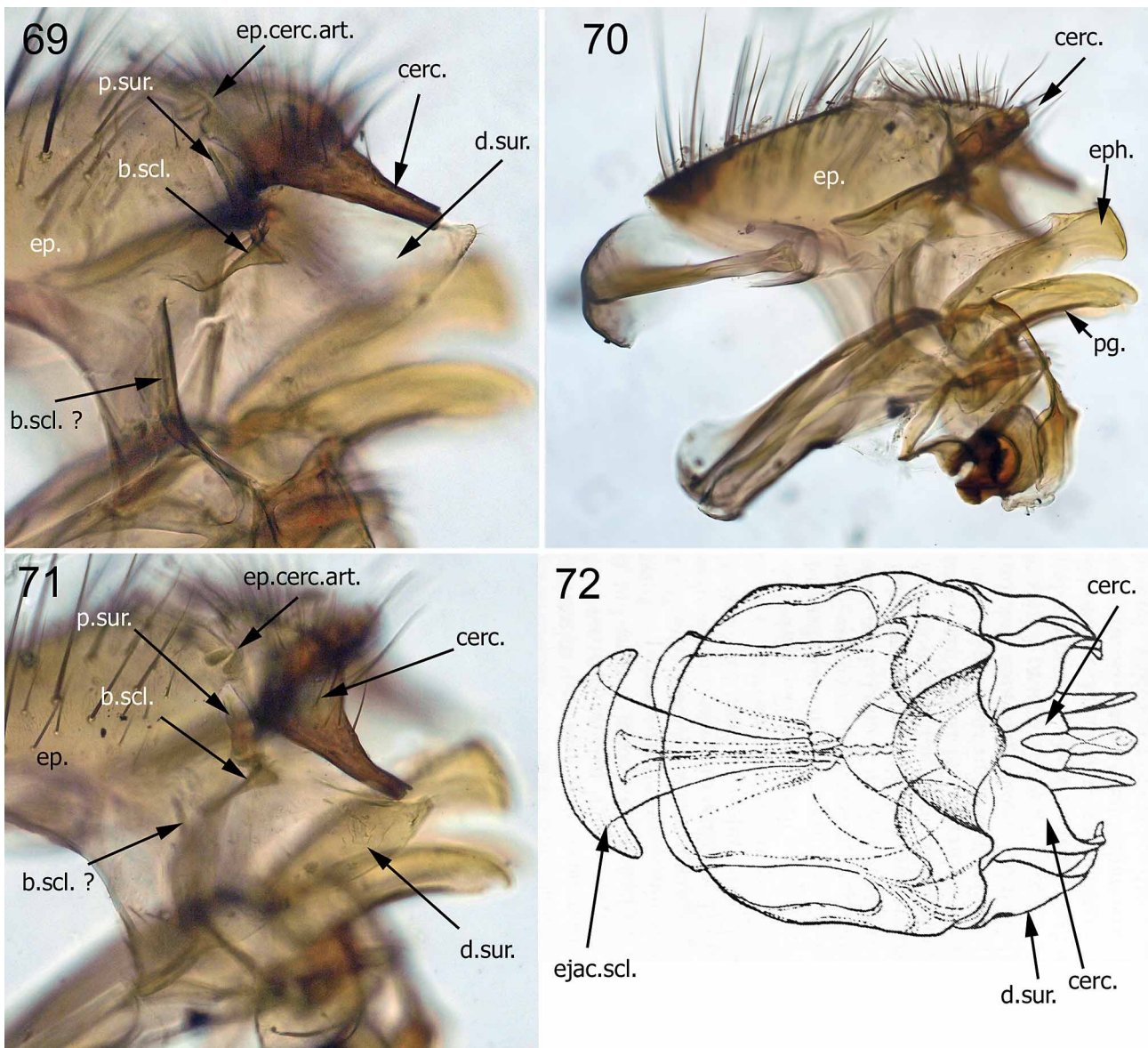
It is also evident to me, both from a close study of one of Baranov's figures (Baranov 1936: 649, fig. 2, reproduced here as Fig. 72) and from a re-examination of the genital slide, that Crosskey (1977a) both misinterpreted the complex cerci of *Termitoloemus*, and was unable to offer an interpretation of the structure (Figs. 69, 71, 72, labelled “*d.sur.*”) situated outside of the strongly sclerotised sclerite he interpreted as the “surstyli” in Baranov's fig. 2 (those with “broken and with missing apices”). He simply did not mention it at all. It is very weakly sclerotised and it is possible that it was simply overlooked. I would like to offer an alternative interpretation of the various structures of the genital slide.

In both the left (Fig. 69) and right (Fig. 71) part of the capsule there is present a large almost triangular very weakly sclerotised structure with a curved lower edge and an almost straight upper edge. It is furnished with a number of very small pale setulae at the tip. This bilateral structure is the one overlooked by Crosskey (1977a). It was drawn by Baranov not only in his fig. 1, although with a not quite correct outline as I see it, but also in his fig. 2 (Fig. 72, *d.sur.*). I interpret it as the distal part of the surstylus. The structure that Crosskey (1977a) took to be the surstyli (described as very narrow, broken and with missing apices) I interpret as a lateral component of the complex paired cerci (*cerc.*). Another component of the cerci are the two small paired median struts directed obliquely upwards in Fig. 70. Furthermore, the structure to the right in the exact middle of Baranov's figure (Fig. 72) is the epiphallus (cf. Fig. 70, *eph.*) [his “*Spinus ditillatorius*”], flanked by a postgonite on either side. Having thus established some fixed points, I think it is possible to identify the bacilliform sclerites (*b.scl.*, *b.scl.* ?), possibly double on each side (as in *Bengalia*) and not fused with its fellow in the midline. These are present both in the left and the right part of the genital capsule. The upper part even has a tooth-like projection on both sides, similar in form to the one in many *Bengalia* species. It is also possible to recognise the articulation of the posterior part of the cerci with the upper part of the epandrium (*ep.cerc.art.*), also present symmetrically on both sides. Finally one can distinguish the proximal part of each surstylus (*p.sur.*) as a sclerotised thin strut wedged in between the anterior edge of the epandrium and the lateral part of the cercus (exactly where it belongs) and surrounded by paler membrane. It is impossible to determine whether the proximal and distal parts of the surstylus are separate sclerites (as in *Bengalia*) or fused.

The structures I interpret as bacilliform sclerites are situated medial to the corresponding distal part of surstylus on both sides, therefore I think it is justified to assume that there is, in this genus too, a junction between the upper part of the bacilliform sclerite and the *medial* side of the zone of transition between the proximal and distal parts of the surstylus.

The peculiar cerci in *Termitoloemus*, consisting of paired long narrow main structures with paired short struts in between them, are similar to the ones found in some species of *Tricyclea*, discussed in the next entry.

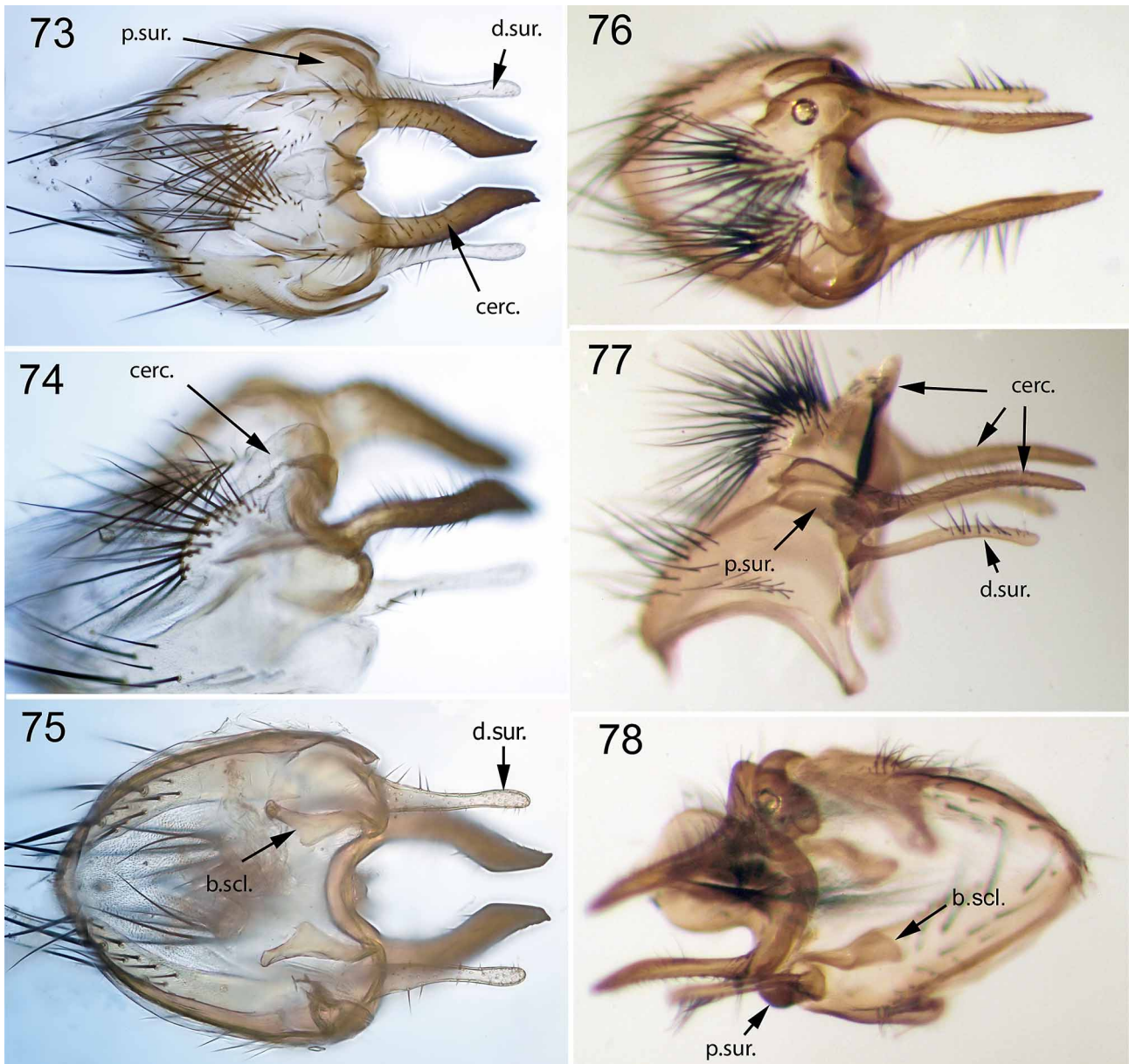




**FIGURES 69–72.** *Termitoemus marshalli* Baranov, male holotype. **69–71.** Genital capsule, left side view, at various depth of focus (from genital slide in BMNH). For a detailed explanation, see Material and methods, section Photography, above. **69.** Genital capsule, left part (exposure #9492, i.e., no. 10 from top). **70.** Genital capsule, middle part (“focus-fused from exposures #9506–#9511, i.e., nos. 24–29 from top). **71.** Genital capsule, right part (exposure #9523, i.e. no. 8 from deepest level). **72.** Genital capsule, dorsal (posterior) view, reproduced from Baranov (1936: 649, fig. 2) with permission from Taylor & Francis. The labelling is added by KR.

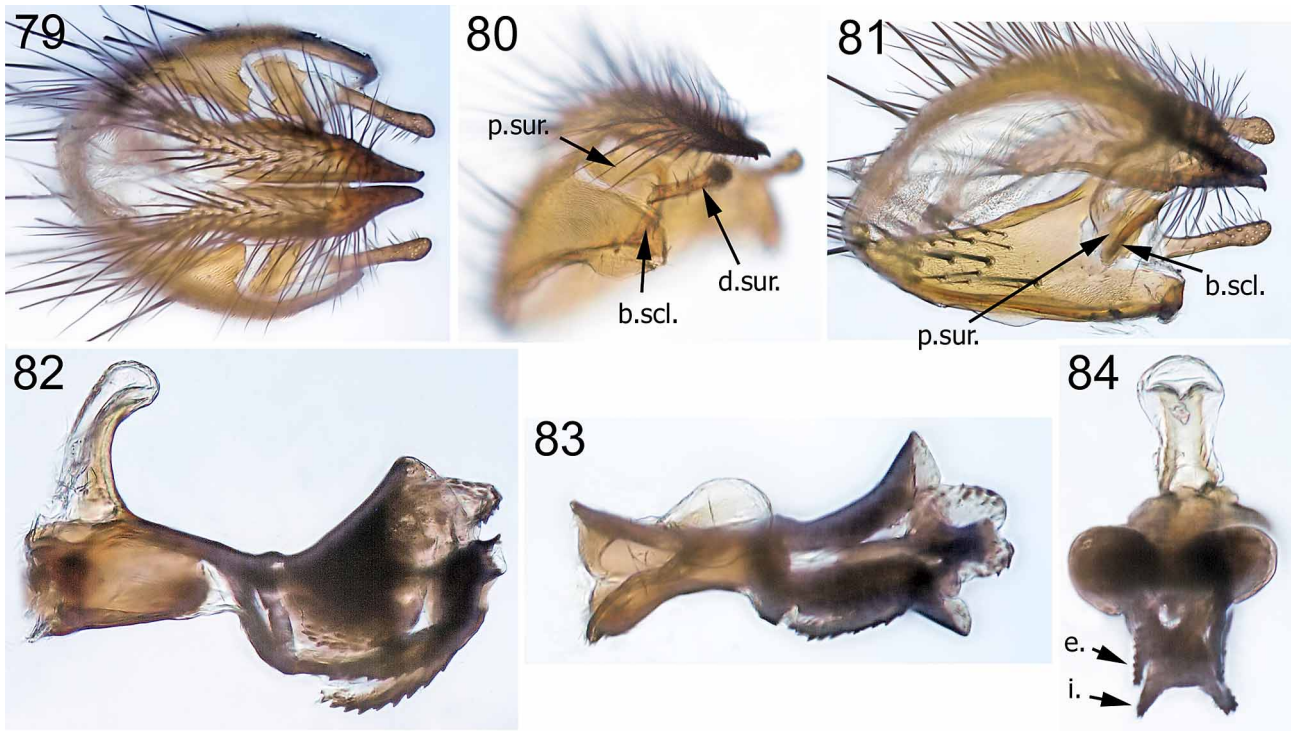
I have not been able to recognise any presence of dentate bands on the ventral part of the distiphallus of *Termitoemus marshalli* (cf. Fig. 70).

*Tricyclea* (Figs. 73–84). The cerci, surstyli and bacilliform sclerites of *T. fasciata ferruginea* are shown in Figs. 73–75, and those of *T. tauffliebi* in Figs. 76–78. In both species the proximal part of the surstylus curves down medially between the cerci and distal part of the surstylus so as to articulate with the upper end of the bacilliform sclerite, which is of the simple type. In both species the cerci are complex, consisting of two long narrow lateral prongs united by a transverse gently curved sclerotised bridge from which arises an upward-pointing structure. This consists of two small, flat and sagittal lamellae in *T. fasciata*, but a single transverse and much more conspicuously projecting process in *T. tauffliebi*. Similarly projecting medial cercal structures are also present in *T. perpendicularis* and *T. kivuensis* (Zumpt 1956). The genitalia of *T. semicinerea* are illustrated in Figs. 79–84 from a specimen from South Africa (KwaZulu-Natal). The cerci are much simpler, but the bacilliform sclerite joins the medial part of the proximal part of the surstylus, as usual (Figs. 79–81).



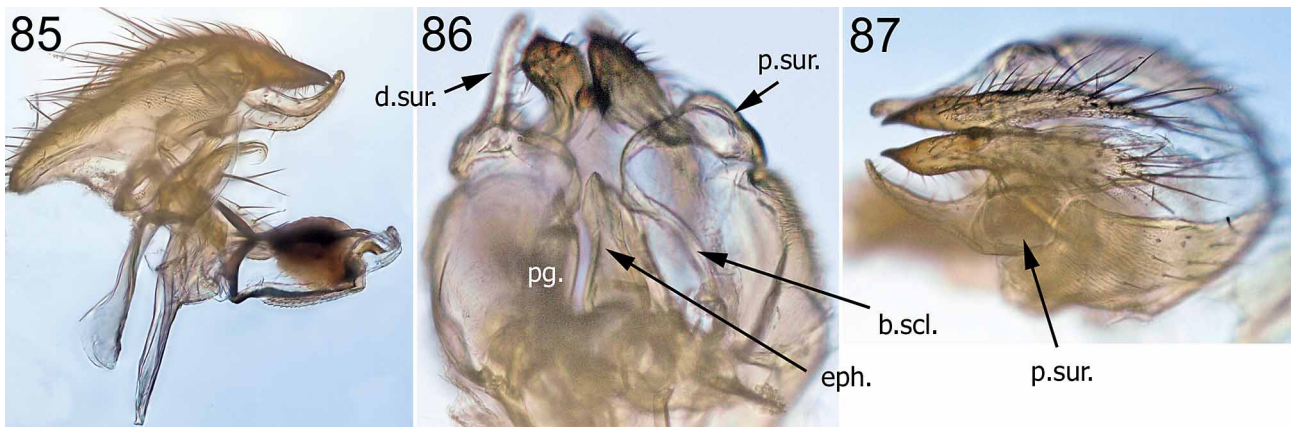
**FIGURES 73–78.** 73–75. *Tricyclea fasciata* (Macquart), subsp. *ferruginea* Wulp, male (specimen no 15029 in BMSA). 76–78. *Tricyclea tauffliebi* (Zumpt), **comb. nov.**, male (BMNH). 73. Epandrium, cerci and surstyli, dorsal (posterior) view. 74. Epandrium, cerci and surstyli, oblique dorsolateral view. 75. Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view. 76. Epandrium, cerci and surstyli, dorsal (posterior) view. 77. Epandrium, cerci and surstyli, oblique lateral view. 78. Epandrium, cerci, surstyli and bacilliform sclerites, slightly oblique ventral (internal) view.

Note that I have transferred the nominal species *Neocordylobia tauffliebi* Zumpt, 1958 to the genus *Tricyclea*, **comb. nov.**, because of the projecting medial cercal structure similar to the one in the *Tricyclea* species mentioned above.



**FIGURES 79–84.** *Tricyclea semicinerea* Bezzi, male (specimen no. 13747, BMSA). **79.** Epandrium, cerci and surstyli, dorsal (posterior) view. **80.** Epandrium, cerci, surstyli and bacilliform sclerites, oblique left antero-lateral view. **81.** Epandrium, cerci, surstyli and bacilliform sclerites, oblique ventral (internal) view. **82.** Aedeagus, left lateral view. **83.** Aedeagus, oblique dorsal view. **84.** Aedeagus, apical view.

*Tricycleala* (Figs. 85–87). I dissected a male from Nigeria of the only species of this genus, *T. maculipennis*. The male genitalia are illustrated here for the first time. There is a slight projection on the upper half of the bacilliform sclerite, though weaker than in *Termitoloemus marshalli* and very much weaker than in most *Bengalia* species. Fig. 86 shows that the bacilliform sclerites join the medial side of the proximal part of the surstylus.



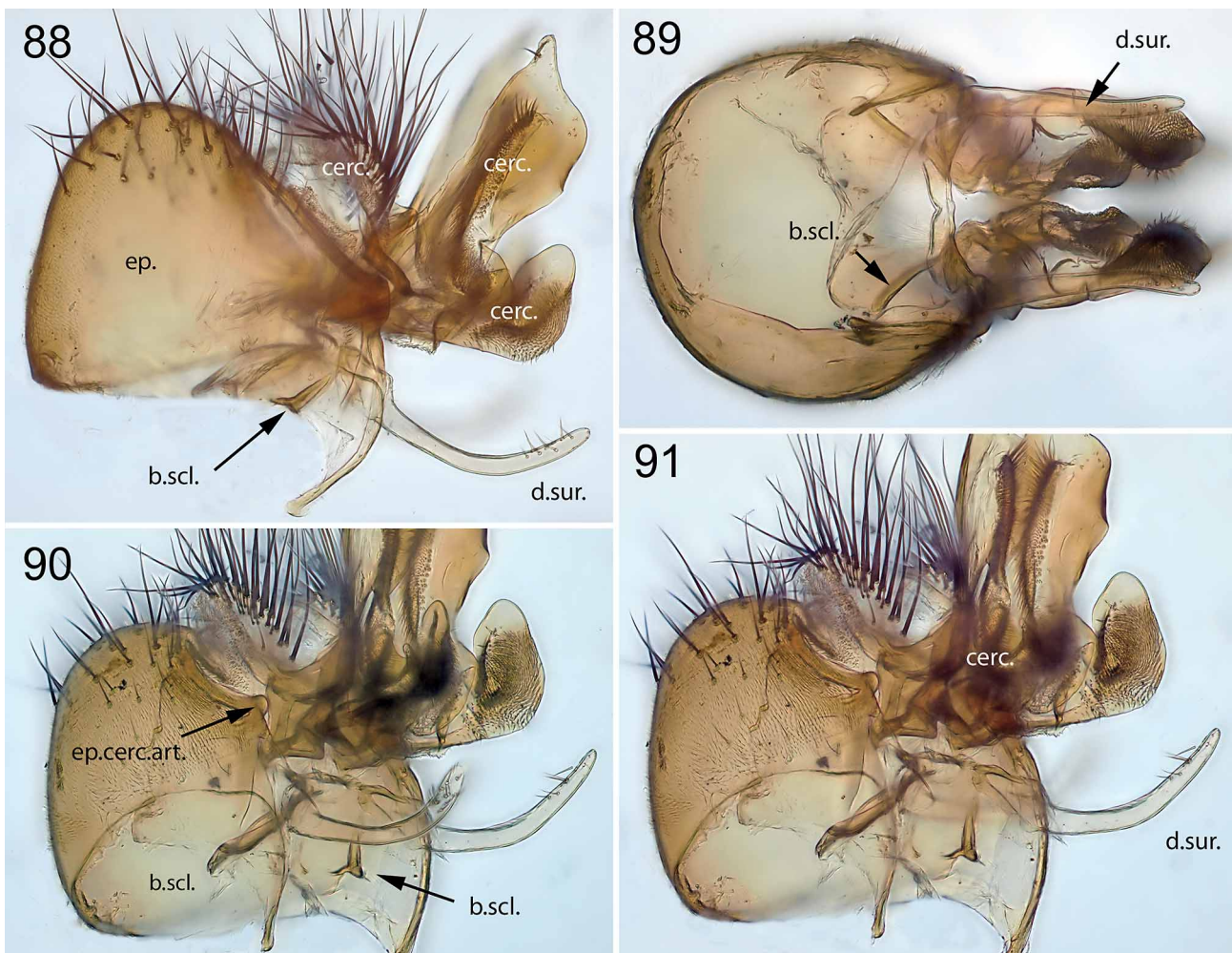
**FIGURES 85–87.** *Tricycleala maculipennis* Villeneuve, male (CNC). **85.** Epandrial complex, left lateral view. **86.** Epandrial complex, slightly oblique internal view. **87.** Epandrium, cerci and surstyli, oblique right dorsolateral view.

*Verticia* (Figs. 88–91). I examined a male specimen of an undescribed species from Sarawak (in BMNH, misidentified by myself as “*Verticia orientalis*”), which I had dissected many years ago. It is very small. The cerci are extremely complicated and consist of a pair of large three-lobed structures, of which the posterior lobe is strongly setose with long ordinary setae, and the two anterior lobes have complex patterns of densely-set short setae or setulae on their inner sides. The cerci are closely appressed along the midline but not connected through sclerotised tissue. Externally each cercus articulates with the epandrium by means of a distinct joint (*ep.cerc.art.*). The surstylus,

very weakly sclerotised and thus easily overlooked, is long, narrow and slightly curved, carrying a group of about 7 small setae near the tip and a few even smaller ones near the base. I have not been able to identify any proximal part of the surstylus, which was expected to be found between the cerci and the epandrium distal to the cercus-epandrium joint. At the base of the surstylus there is a sizable medial projection, which articulates with the simple rod-like bacilliform sclerite. The medial projection of each surstylus joins their fellow on the opposite side through a sclerotised bridge. The two bacilliform sclerites diverge downward toward their junction with the distal ends of the hypandrial arms, and the ventral epandrial membrane between them appears somewhat sclerotised.

The surstylus occupies a position similar to the long slender epandrial projection figured by Kurahashi *et al.* (1997: 47, fig. 5a) for *Verticia chani*. However, the surstylus in the Sarawak specimen I dissected is clearly separate from and has no connection whatsoever with the epandrium. So what I interpret as the surstylus is clearly not an epandrial projection.

Kurahashi & Chowanadisai (2001: 208, fig. 2c) may have misinterpreted parts of the cerci as “paralobes” (= surstyli) in *Verticia quatei*. The structure labelled “pa” seems to me to be the middle part of a tripartite cercus. The posterior part is labelled “ce”; the fore part, which is very small, is not labelled; cf. also their fig. 2d (“ce” and “pa”).



**FIGURES 88–91.** *Verticia* sp., male (dissected and misidentified by me as “*Verticia orientalis* Malloch”, BMNH). **88.** Epandrium, left cercus, left surstylus and bacilliform sclerite, left lateral view. **89.** Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view. **90.** Epandrium, cerci, surstyli and bacilliform sclerites, oblique anterolateral view. **91.** Epandrium, cerci, surstyli and bacilliform sclerites, oblique anterolateral view; slightly different focus than Fig. 90.

**(b) – among calliphorid and other groups outside the Bengaliinae**

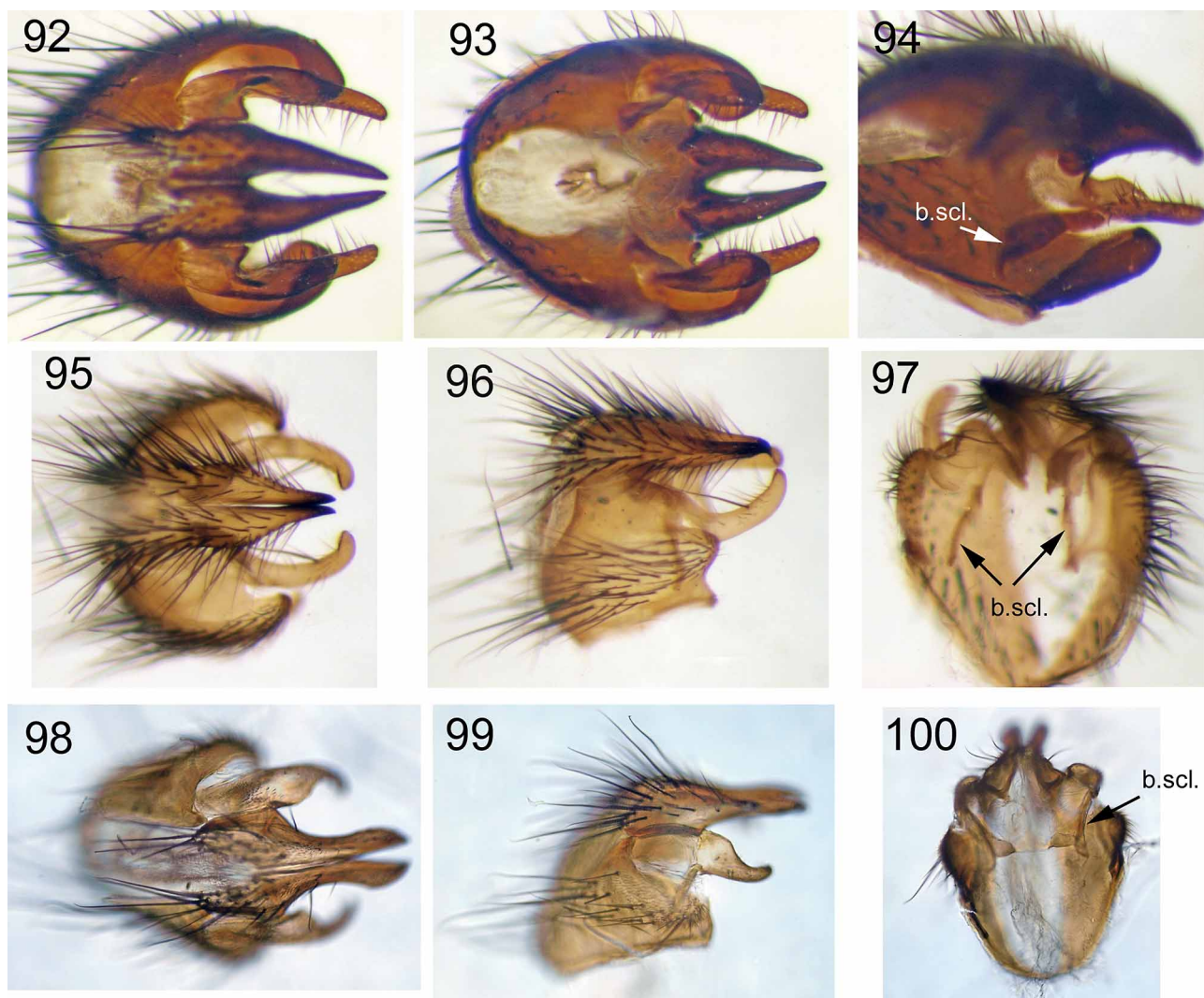
Hennig (1976) discussed this part of the genitalia (sclerotisations of the ventral epandrial membrane) in connection with his treatment of the Anthomyiidae.

Tschorsnig (1985a) described the bacilliform sclerite (as “processus longus”) in Rhinophoridae, but did not describe the position of the attachment point of the upper end of the bacilliform sclerite; i.e., as to whether is situated laterally or medially on the surstylus. In *Alvamaja* Rognes the attachment point of the upper end of the bacilliform sclerite is ventrolaterally on the posterior end of the distal portion of the surstylus (Rognes 2010: 9, figs. 9–10).

Tschorsnig (1985b: 32, figs. 50–60) illustrated the connection between the bacilliform sclerite and the surstylus for several genera of the Tachinidae and described it for numerous subgroups. He did not state explicitly whether the upper end of the bacilliform sclerite articulates with the lateral or medial side of the surstylus, but from the figures he presented it seems that the most common arrangement is the lateral attachment.

It would be an interesting task to follow up in detail the relative position of the cerci, surstyli and the bacilliform sclerite in other calyptrate groups but this is beyond the scope of this work.

In the following I report upon the feature in all calliphorid subgroups. It will be evident that in none of them a medial position of the junction of the bacilliform sclerite with the surstylus is found.



**FIGURES 92–100.** 92–94. *Silbomyia fuscipennis* (Fabricius), male (BMNH). 95–97. *Mesembrinella bicolor* (Fabricius), male (KR). 98–100. *Phumosia lutescens* (Villeneuve), male (KR). 92. Epandrium, cerci and surstyli, dorsal (posterior) view. 93. Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view. 94. Area around right surstylus and right bacilliform sclerite, oblique internal view. 95. Epandrium, cerci and surstyli, dorsal (posterior) view. 96. Epandrium, cerci, surstyli, and bacilliform sclerites, left lateral view. 97. Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view. 98. Epandrium, cerci and surstyli, dorsal (posterior) view. 99. Epandrium, cerci and left surstylus, left lateral view. 100. Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view.

Ameniinae (Figs. 92–94). I examined and dissected a male of *Silbomyia fuscipennis* (in BMNH). The proximal part of surstylus is moderate in size. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus, at the anterior end of which is a knob-like strong rounded protuberance on the surstylus which may serve as a “landmark”. The bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion, at the opposite side of the landmark.

Aphyssurinae. The junction of the bacilliform sclerite with the surstylus is shown in all the illustrations by Norris (1999: 513, fig. 1e and *passim*) to be ventrolaterally at the base of its distal portion (“outer base” in Norris’ terminology).

Calliphorinae. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all the illustrations by Rognes (1991) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion (*Bel-lardia* Robineau-Desvoidy, *Calliphora* Robineau-Desvoidy, *Cynomya* Robineau-Desvoidy, *Onesia* Robineau-Desvoidy). The same applies to *Pericallimya perlata* (Walker) of which a male specimen (BMSA # 08049) was dissected.

Chrysomyinae. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all the illustrations by Rognes (1991) and Rognes & Paterson (2005) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion (*Phormia* Robineau-Desvoidy, *Protophormia* Townsend, *Protocalliphora* Hough, *Trypocalliphora* Peus, *Chrysomya* Robineau-Desvoidy).

*Euphumosia* Malloch, 1926 (Figs. 101–103). I examined a male paratype of *E. evittata* and a male *E. papua*, both from New Guinea, in BPBM. The proximal part of the surstylus has a superficial microtrichiose part wedged between the cercus and the epandrium, and another more deeply situated part which forms a long strongly sclerotised median shelf articulating with a groove on the lateral side of the cercus. The upper end of the bacilliform sclerite joins a ventral point on the proximal part of the surstylus well laterad of the median shelf and well behind the distal end of the ridge. Thus the type of articulation does not agree with the one in Bengaliinae, and neither with the one in most calliphorids.

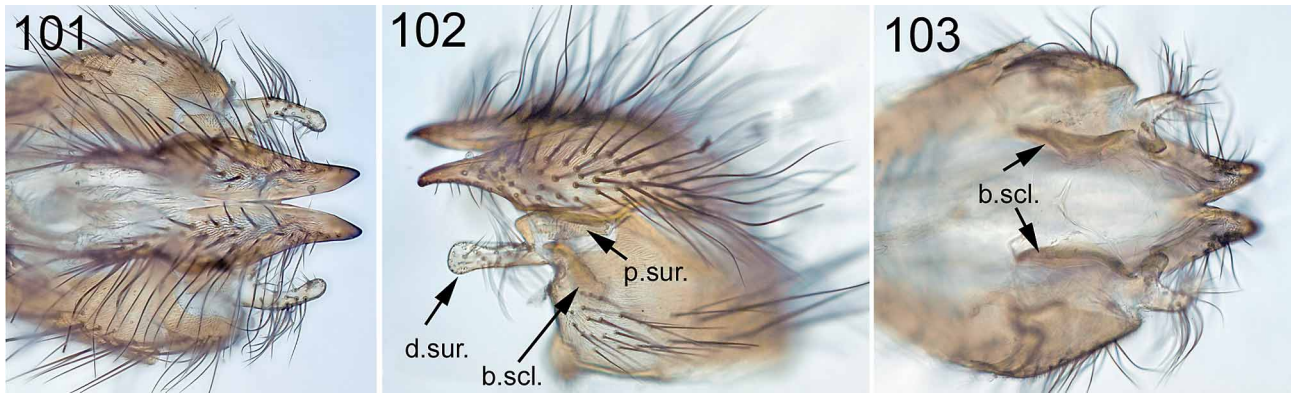
Helicoboscinae. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all the illustrations by Rognes (1991, 1993) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion (*Eurychaeta* Brauer & Bergenstamm, *Gulmargia* Rognes).

Luciliinae. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all the illustrations by Rognes (1991) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion (*Lucilia* Robineau-Desvoidy). In a male of *Hemipyrellia ligurriens* the base of the distal portion of the surstylus is very narrow and the junction with the upper end of the bacilliform sclerite occupies the whole ventral width of the surstylus. The epandrial projection which runs alongside the surstylus (cf. Aubertin 1931: 504, fig. 4) has no relation to the bacilliform sclerites or surstylus.

Melanomyinae. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all the species treated by Rognes (1991) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion (*Angioneura* Brauer & Bergenstamm, *Eggisops* Rondani, *Melanomya* Rondani, *Melinda* Robineau-Desvoidy). The same relation exists in *Adichosina eos* (Fig. 104), *A. munroi*, *Ochromelinda thoracica* (Figs. 110–112), *Onesihoplisa umbrosa* (Fig. 124) and *Zernyiella dubia* (Figs. 134–136). All these taxa are shown below to belong in the Melanomyinae.

Mesembrinellinae (Figs. 95–97). I examined and dissected a male of *Mesembrinella bicolor*. There is an articulation between a ventromedially expanded part of the proximal part of the surstylus and the cercus. The bacilliform sclerite is fused with the midventral part of this medial expanded part of surstylus. The superficial part of the proximal part of surstylus is large and fused with the epandrium. Mesembrinellinae species have a gently curved vein M and a cell  $r_{4+5}$  that opens near the wing tip (Guimarães 1977).

Phumosiinae (Figs. 98–100). I examined a male of *Phumosia lutescens* from Yemen and *P. coomani* (several specimens, including the lectotype of *Caiusa coomani*, cf. Rognes 2011a). There is a long articulation between the proximal part of the surstylus and the side of the basal part of the cercus. The upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion.



**FIGURES 101–103.** *Euphumosia papua* (Guérin-Ménéville), male (BPBM). **101.** Epandrium, cerci and surstyli, dorsal (posterior) view. **102.** Epandrium, cerci, right surstylus and bacilliform sclerite, right lateral view. **103.** Epandrium, cerci, surstyli and bacilliform sclerites, ventral (internal) view.

Polleniinae. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all the illustrations by Rognes (1991) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion (*Pollenia* Robineau-Desvoidy). In *Morinia doronici* (Scopoli) (= *melanoptera* Fallén) the bacilliform sclerite is not differentiated in the ventral epandrial membrane, but there is a suggestion of an upper part (Tschorsnig 1985a; Rognes 1991: 210, fig. 571). In this species there is also a kind of pointed process or knob medially in the proximal part of the surstylus fitting into a hollow in the cercus (Tschorsnig 1985a: 6, fig. 8; Rognes 1991: 210, fig. 572).

Rhiniinae [= Rhiniidae of Pape & Thompson (2010), Kutty *et al.* (2010)]. There is a longitudinal articulation between the medial side of the proximal part of the surstylus and the lateral part of the proximal part of the cercus. In all species examined by Rognes (1991, 2002), i.e., species of *Cosmina* Robineau-Desvoidy, *Rhinia* Robineau-Desvoidy, *Rhyncomya* Robineau-Desvoidy and *Stomorhina* Rondani, the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion.

Toxotarsinae. In all illustrations by Dear (1979) it is evident that the upper end of the bacilliform sclerite joins the surstylus ventrolaterally at the proximal end of its distal portion.

### (c) – conclusion: raise the rank of Bengaliinae to a family?

From the analysis above it is evident that in all calliphorid groups except Bengaliinae there is a more or less elongate articulation between the medial part of the surstylus and the lateral side of the proximal part of the cercus; and, more importantly for our purpose, the proximal end of the distal portion of the surstylus joins or articulates laterally and ventrally with the upper end of the bacilliform sclerite. In Bengaliinae the medial part of the proximal portion of surstylus is often freed from an articulation with the cerci, and this portion of the surstylus is in direct, more or less sclerotised, continuation distally, medially and ventrally with the upper end of the bacilliform sclerite; i.e., to the inside of all distal parts of the surstylus. Thus the construction of the genital parts in this region in Bengaliinae is fundamentally different from all other “calliphorids”, and definitely constitutes a unique autapomorphic feature corroborating the monophyly of this subfamily (an “objective synapomorphy” in Sæther’s [1983] terminology). For this and other reasons (see section “Monophyly and diagnosis of the subfamily Bengaliinae”, above) the Bengaliinae is an extraordinarily well founded group within the Oestroidea, and it should be seriously considered to raise the status of Bengaliinae to a family of its own, in view of the artificial nature of the group “Calliphoridae” (Rognes 1997, Pape & Arnaud 2001). A similar action has been widely accepted for Rhiniinae by Pape & Thompson (2010) and by Kutty *et al.* (2010). The former authors treated it as a family in *Systema Dipteroorum* and, according to their “Notes on Family Classification”, mainly on the basis of my own earlier work (Rognes 1997). This means of course that under such a concept the Bengaliidae will be a much more inclusive taxon than Lehrer’s concept of the family, which was created for *Bengalia* only (Lehrer 2005a).

## Key to world Bengaliinae

The key below is based on original observations of one or more specimens of one or more species of all the genera included in the Bengaliinae (cf. Appendix 2). I have abandoned the genus *Neocordylobia* Villeneuve, 1929 and synonymised it under *Cordylobia* Grünberg, 1903. Its type species *N. roubaudi* Villeneuve, 1929 has been transferred to *Cordylobia*, whereas *N. tauffliebi* Zumpt, 1958 has been transferred to *Tricyclea* Wulp, 1885. No further species have been catalogued under *Neocordylobia* (cf. Pont 1980).

- 1 Lateral broad continuous dark band along body from posterior part of head, across thoracic pleura to tip of abdomen, contrasting strongly with yellow body elsewhere; arista long plumose; frontal vitta bare; prosternum and proepisternal depression setose; 0 + 1 *acr*; ST5 in male with a medial triangular backward projection, no cleft or bay in posterior edge; inner edge of lower calypter diverging from long axis of body; size about 8.5–9.5 mm . . . . . *Coganomyia* (Afrotropical)
- No dark continuous band along side of body contrasting with yellow colour elsewhere . . . . . 2
- 2 Frontal vitta very broad, with setulae all over; proepisternal depression bare; 0 *prst acr*; ST5 in male with a median flap of various shapes appended to its posterior edge, no bay or cleft in posterior edge; outer posthumeral seta absent; large species, body length 8–15 mm . . . . . *Bengalia* (Afrotropical, Oriental, immigrant Australasian)
- Frontal vitta narrow or broad, bare; ST5 in male normal shaped, with a bay or cleft in posterior edge, no median flap; small to large species, body length 3–17mm . . . . . 3
- 3 Arista appearing pectinate, with long hairs above, longest hairs about as long as width of first flagellomere, a few very short hairs below (high magnification necessary); arista much longer than first flagellomere; palpus enlarged distally, narrow basally; strong erect setae along facial ridge at least halfway to lunula; both male and female with one proclinate orbital seta in addition to the exclinate orbital seta; proepisternal depression and prosternum setose; wing vein  $R_1$  with setulae all the way to wing margin on upper side of wing; vein  $R_{4+5}$  with setulae on upper side of wing at least reaching halfway to wing margin from r-m crossvein; lower calypter narrow, inner edge diverging from long axis of body; abdominal dark bands along posterior margins of tergites; male frons about as wide as an eye as seen from above; male hind tibia with dorsal preapical seta much shorter than first tarsomere; wing with a rounded dark spot at exit of vein  $R_{2+3}$ , posterior rim of spot reaching halfway to  $R_{4+5}$ ; very small species, body length 3–5 mm . . . . . *Tricycleala* (Afrotropical)
- Arista not pectinate; usually long or short plumose; if appearing pectinate then the hairs above are very short, hardly longer than width of arista at base and arista rather short and strongly thickened basally; very small to very large species, body length 4–17 mm . . . . . 4
- 4 Arista very strikingly thickened along basal 0.4 to 0.8; arista almost pectinate with very short hairs above, hairs hardly longer than width of thickened part of arista, in some species a few very inconspicuous hairs below; proepisternal depression bare; frons at least as wide as an eye seen from above; prosternum setulose; parafacial at narrowest about 0.66x–1.50x width of first flagellomere (0.66 in *indicus*, 1.5 in *intonsus*), with several rows of black setulae for its whole length; facial membrane very deeply sunk; lower part of facial ridge curving towards midline almost horizontally, distance between vibrissal corners much less than width of facial membrane at its middle; outer posthumeral seta present, but sometimes weak and easily overlooked; body length 5–6 mm . . . . . *Booponus* (Oriental and Palaearctic)
- Arista not strikingly thickened at the same time as pectinate . . . . . 5
- 5 Outer posthumeral seta absent; proepisternal depression bare; 0–3 *prst acr*; prosternum bare or setose; small to large species, body length 4–17 mm . . . . . 6
- Outer posthumeral seta present, outside or in line with the *prst* seta; if absent, then proepisternal depression setose (*Termitocaliphora*, *Tricyclea semicinerea*, *T. diffusa*, *T. bifrons*); 1–2 *prst acr*; prosternum setose . . . . . 10
- 6 Small to very small species, less than 6 mm; prosternum bare; lower calypter narrow or broad . . . . . 7
- Large species, about 14–17 mm; prosternum setose; lower calypter broad, inner edge converging with long axis of body . . . . . 9
- 7 Wing vein  $R_{4+5}$  ciliate on dorsal surface at most in proximal 0.33 of distance between r-m crossvein and wing margin; vein  $R_1$  usually bare, but sometimes with 1–2 small setae above; arista long-plumose and of normal length; palpus not projecting strongly beyond lower facial margin; male frons about as wide as an eye seen from above, with outer vertical seta and a single strong proclinate orbital seta in posterior half of fronto-orbital plate; parafacial less than 0.5x width of first flagellomere; cerci and ST5 in male prominent, peculiarly formed, and sometimes projecting well beyond tip of abdomen; male hind tibia with a short dorsal preapical seta . . . . . *Verticia* (Oriental)
- Wing vein  $R_{4+5}$  ciliate for about 0.66 of distance between r-m crossvein and wing margin; wing vein  $R_1$  either bare or with setulae for whole length on upper side of wing; arista with short or long hairs above and below; arista very long, about twice as long as first flagellomere; palpus strongly projecting beyond lower facial margin; male frons extremely broad, almost 1.5–2.0x width of an eye in dorsal view; male hind tibia with dorsal preapical seta 1.2–1.5x longer than first tarsomere; genitalia not projecting beyond tip of abdomen . . . . . 8



- 8 Wing vein R, ciliate above for whole length; parafacial very narrow, hardly twice as wide as base of arista; arista hairs hardly longer than width of arista stalk at base; a single laterocline orbital seta of normal size in middle of frons, a single small proclinate seta in front of it; mentum very large, *Bengalia*-like; no setae along facial ridge above vibrissa; palpus darkened at tip; occiput very strongly expanded; lower calypter narrow (though with a peculiar base, figured by Pape 1986: 22, fig. 6); abdominal dark bands along anterior margin of tergites . . . . . *Termitoloemus* (Oriental)
- Wing vein R, bare above; parafacial very broad, broader than width of first flagellomere; arista hairs about as long as width of first flagellomere; two strong laterocline orbital setae; mentum broad, boat-shaped; several long setulae along facial ridge above vibrissa; palpus yellow throughout; occiput slightly expanded; lower calypter broad; abdominal dark bands along posterior margin of tergites . . . . . *Mafikengia* **gen. nov.** (Afrotropical)
- 9 Lower calypter setose above; T6 (not to be confused with TST7+8) present in male, but not projecting beyond posterior edge of T5; Y seta present . . . . . *Pachychoeromyia* (Afrotropical)
- Lower calypter bare above; T6 (not to be confused with TST7+8) absent in male; Y seta absent or present . . . . . *Auchmeromyia* (Afrotropical)
- 10 Proepisternal depression setose; frons varying from very narrow to very broad; male cerci close together or separated by an upright lobe between their bases . . . . . 11  
 Note. Also keyed out here is *Tricyclea tauffliebi*, with bare proepisternal depression; costal area of wing with two darkened elongate spots; Hough seta very strong, 0.75x length of *pra*; male frons at narrowest 2x distance between posterior ocelli inclusive; male cerci long and very narrow, widely separated from each other and with an upright lobe between their bases; also with very long and narrow surstylus
- Proepisternal depression bare; frons at most as wide as an eye seen from above, sometimes almost obliterated; cercal halves always close together, never an upright lobe between them and separating their proximal parts 12
- 11 Three *post dc*; lower calypter narrow, with inner edge diverging from longitudinal axis of body; frons varying from about as wide as the anterior ocellus (*T. nana*) to 3–4x width of anterior ocellus (*T. machadoi*); parafacial plates with numerous erect rather strong setae all over; outer posthumeral seta absent . . . . . *Termitocalliphora* (Afrotropical)
- Four *post dc*; lower calypter with inner edge converging with longitudinal axis of body, closely following scutellar margin; frons varying from very narrow to almost as wide as an eye; parafacial plates bare or with a few or numerous setae, these never very strong; outer posthumeral seta usually present (absent in a few species: *Tricyclea semicinerea*, *T. diffusa*, *T. bifrons*, and possibly others) . . . . . *Tricyclea* (Afrotropical)
- 12 Parafacial broader than third antennal segment, if narrower (*Cordylobia ruandae*), then broader than half the width of third antennal segment and parafacial with densely set black setulae for whole length; parafacial setose with not very densely set setulae which are black or yellow and usually confined to upper half; eyes in male broadly separated, except in *C. anthropophaga* where the frons is narrow, about 2x width of anterior ocellus; hind tibia without *av* setae (sometimes a very inconspicuous *av* seta in *C. anthropophaga*), but often with a conspicuous row of densely set short *ad* setae; lower calypter broadly truncate with inner edge closely following margin of scutellum . . . . . *Cordylobia* (Afrotropical)
- Parafacial narrower than third antennal segment, bare or with only scattered setulae in extreme upper part; eyes in male touching, frons narrower than anterior ocellus; hind tibia usually with a conspicuous *av* seta in distal third; lower calypter narrow with inner edge diverging from longitudinal axis of body . . . . . *Hemigymnochaeta* (Afrotropical)

## Phylogenetic relationship of the genera of Bengaliinae

The strict consensus tree output by NONA from the 11 most parsimonious trees of length 56 steps is shown in Fig. 138. There are two main monophyletic groupings within the strongly supported monophyletic subfamily Bengaliinae: (1) *Bengalia* + (*Coganomyia* + *Tricycleala*), and (2) the remaining genera as a collapsed clade with two resolved subgroups, i.e., *Auchmeromyia* + *Pachychoeromyia* and *Verticia* + (*Mafikengia* + *Termitoloemus*). This means that a division of the subfamily into two separate tribes Auchmeromyiini and Bengaliini as suggested by Rognes (1997) may be upheld. Rognes (1997) did not consider the genera *Tricycleala* and *Coganomyia* at the time. The support is very low for both groups and I am reluctant to keep these as tribes now. I see no reason for keeping the separate subfamily Coganomyiinae for *Coganomyia* only, as was proposed by Peris & González-Mora (2004).

Below are listed the monophyletic groups present in the consensus tree and the character state transformations that support their monophyly. The Bremer support values are entered in parentheses.

### Bengaliinae (>5)

ground colour (0): black → yellow

male frons (1): very narrow → broad

outer posthumeral seta (7): present → absent

subscutellum (12): absent → present

anal vein (14): ends before wing-margin → reaches margin  
bend of vein M (16): sharp → gently curved  
length of proximal part of surstylus (22): very short → moderate  
bacilliform sclerite attachment to surstylus (25): lateral → medial  
dentate bands on distiphallus (27): simple → double

*Bengalia* + (*Coganomyia* + *Tricycleala*) [= Tribe Bengaliini] (1)  
bacilliform sclerite tooth (26): absent → present

*Coganomyia* + *Tricycleala* (1)  
propleuron (9): bare → setose  
lower calypter shape (17): broad → narrow

*Termitocalliphora* + (*Verticia* + (*Mafikengia* + *Termitoloemus*)) + *Hemigymnochaeta* + *Cordylobia* + *Booponus* + *Tricyclea* + (*Auchmeromyia* + *Pachyoeromyia*) [Tribe Auchmeromyiini] (1)  
Hough seta (11): absent → present  
row of numerous setae along whole lower edge of lateral scutellar declivity (13): absent → present

*Verticia* + (*Mafikengia* + *Termitoloemus*) (1)  
prosternum (10): setose → bare

*Mafikengia* + *Termitoloemus* (4)  
male frons (1): broad → extremely broad  
aristal length (3): normal → very long  
palpus length (5): normal → very long and projecting  
vein R<sub>4+5</sub> (15): bare → setose almost all the way to wing margin  
dorsal preapical seta of hind tibia in male (19): normal → very long

*Auchmeromyia* + *Pachyoeromyia* (2)  
cerci (20): broad, separate, not fused → narrow, fused  
length of proximal part of surstylus (22): moderate → very long  
bacilliform sclerites (24): separate → fused in midline

It is interesting that the Afrotropical *Mafikengia* according to this analysis, has its closest relative in the genus *Termitoloemus* from the Oriental Region, and that the clade formed by these genera is very well supported. This fact and the fact that both genera are associated with termites might suggest that these monotypic genera should be merged. I have refrained from such an action which I consider premature, in view of the paucity of material of both species, the incomplete knowledge of the *Termitoloemus* male genitalia and the wide geographic separation of the genera. Keeping in mind the very scant knowledge of the female genitalia among all the Bengaliinae one might well expect the cladogram (Fig. 138) to be perturbed when such knowledge becomes available. Since, in addition, *M. cilata* and *T. marshalli* are dissimilar in several easily accessible external and non-genital features I keep them in monotypic genera.

The grouping of *Pachyoeromyia* with *Auchmeromyia* comes as no surprise, since e.g. Patton (1935) could see no reason to keep a separate genus (*Pachyoeromyia*) for *praegrans*.

More surprising is that *Coganomyia*, in spite of sharing the apomorphic state in characters 20 and 22 with the group (*Auchmeromyia* + *Pachyoeromyia*) and the apomorphic state in character 28 (heavily sclerotised distiphallus) with *Auchmeromyia*, did not group with these two genera, neither in the consensus, nor in any of the 11 shortest trees. It might be the case that lack of information on the *Coganomyia* genitalia (not dissected) accounted for this. To examine this problem, a test matrix was created (filename: *mafistp.ss*) where the state “?” was replaced with an hypothetical state “1” in characters 24, 25, 27 [assuming that the bacilliform sclerites are fused (24), with a medial attachment to the surstylus (25), and that there are double dentate bands on the ventral side of the distiphallus (27)], and where the state “?” was replaced with an hypothetical state “0” in character 26 [assuming the lack of

a tooth on the bacilliform sclerite]. This resulted in 191 trees of length 58 steps, the consensus of which showed the Bengaliinae to be completely unresolved except for the group *Mafikengia* + *Termitoloemus*. The group *Auchmeromyia* + *Pachychoeromyia* + *Coganomyia* was present as a monophyletic group in only 37 of the 191 trees. An almost identical test matrix (filename: *mafistpx.ss*), where the state “?” was replaced with an hypothetical state “1” in character 26 [assuming the presence of a tooth on a the bacilliform sclerite] gave the same 11 trees of 56 steps as the original matrix (filename: *mafip.ss*), showing that NONA optimised the lacking character states as in the original matrix.

A constrained tree search in NONA on the basis of the original data matrix showed that the group *Auchmeromyia* + *Pachychoeromyia* + *Coganomyia* was monophyletic in only 61 of 27765 trees of length 58 steps, thus two steps away from the optimal tree.

## Biology of the Bengaliinae

The brief summary given below is mostly based on Zumpt (1953, 1965, 1973) and Ferrar (1987a, 1987b).

*Auchmeromyia*. Larvae are temporarily blood-sucking ectoparasites of burrowing mammals such as warthogs (*Phacochoerus aethiopicus*) and antbears (*Orycteropus afer*) all having a more or less naked skin. Occasionally hairy mammals such as hyaena can act as hosts (Boreham & Geigy 1976). Larvae of *A. senegalensis* (= *luteola* Fabricius) also occupy simple human dwellings, the adults laying eggs in dry dusty soil in the dwellings, hence the name “Congo floor maggot”. *Auchmeromyia senegalensis* was thought to be unique to man, but this is an error (Boreham & Geigy 1976, Noireau 1992). The adults of *A. senegalensis* nourish themselves on excrement, fallen fruits and fermenting vegetables.

*Bengalia*. Larval biology unknown, but Altson (1932: 37) observed a female “digging her way backwards into a small heap of soil freshly excavated by a pair of the sexual form of a termite” so it may be the case that *Bengalia* larvae feed in termite nests. Adults are predaceous on the prey of ants (summarised in Rognes 2009b). There is also an observation of an adult *Bengalia* sucking the abdomen of a termite (Bezzi 1911, citing an observation by Poulton of *B. jejuna* during the night in lamp light).

*Booponus*. Larvae are obligatory skin parasites of bovids, cervids and elephants; a case of human myiasis in a child is also known (Gomoyunova *et al.* 1973). The Philippine species *B. intonsus* (“Oriental foot fly”) oviposits on the legs below the knees of bovids, subsequently the larvae find their way downwards and dig into the skin between the toes.

*Coganomyia*. Biology unknown.

*Cordylobia*. As far as is known, larvae are myiasis producers in mammals (including man) producing skin boils. The adult *C. anthropophaga* is known as the “Tumbu Fly”, its larvae as “ver de Cayor”. The eggs are laid on dry shaded ground, especially if contaminated with urine and faeces. According to Cuthbertson (1933: 93) the “young larvae wander on the ground and attach themselves to children, puppies, etc”. Ovipositing may also occur on drying laundry (Hall & Wall 1995). The “forest mouse fly” (*C. ruandae*) is only known to parasitise the forest mouse *Grammomys dolichurus surdaster*. “Lund’s fly” (*C. rodhaini*) is named after the name of the man from whose arm a larva had been extracted. The main reservoir are antelopes and the African giant rat (*Cricetomys gambianus*) (Rodhain & Bequaert 1916), but it also attacks a number of other mammals including monkeys. The biology of *C. roubaudi* (formerly in *Neocordylobia*) is unknown, but adults are found in the entrances of warthog burrows (Zumpt 1965: 69).

*Hemigymnochaeta*. Associated with termites (fungus gardens), also reared from wild fungus and mushrooms. “The Namibian species appear to be primarily associated with the fungus gardens of termites and the fruiting bodies of associated fungi” (Kurahashi & Kirk-Spriggs 2006: 67).

*Mafikengia*. Biology unknown. The capture of the holotype on the “chimney” of a termite nest (*Odontotermes* sp.) suggests some kind of biological association with termites. The phoretic mites on its body may possibly have been received from mites living inside the termite nest (cf. Haq *et al.* 1990), and the identity of the mites might give some clues as to whether the nest is the source of the mites.

*Pachychoeromyia*. Larvae are blood-sucking ectoparasites living in the burrows of warthogs (*Phacochoerus aethiopicus*) (Zumpt 1965: 65).

*Termitocalliphora*. A number of larvae, pupae and adult flies of *T. machadoi*, a termitophilous fly from Angola, were found living in the sawdust store of the nests of *Bellicositermes natalensis* (Haviland) (Isoptera) (Bauristhene 1964).

*Termitoloemus*. Unknown biology, though Baranov (1936) cited the text of a letter by G.A.K. Marshall, who sent him the three flies to become syntypes of *T. marshalli*, to the effect that they were predaceous on termites in India.

*Tricyclea*. Associated with ants and/or termites. *Tricyclea deemingi* Zumpt has been reared from larvae found in the “humus layer” of mounds of *Macrotermes*. Other species were attracted to damaged mounds of *Macrotermes bellicosus* (Smeathman) (Deeming in Zumpt 1973). Ferrar (1987a: 87) reported to have seen larvae collected from food stores of this termite species. He also cited a report of *Tricyclea fasciata* larvae in Nigeria being found in the heaps of rubbish piled up by ants of the genus *Paltothyreus* outside their nests. In some *Tricyclea* species females have been observed ovipositing in the nest openings of “driver ants” (*Dorylus*) in Nigeria (Engel & Cuthbertson 1937).

*Tricycleala*. Biology unknown.

*Verticia*. Sze *et al.* (2008) reported on a larva of *V. fasciventris* developing as an internal parasitoid in the head capsule of a termite soldier of *Macrotermes barneyi* (Isoptera), finally filling the head capsule entirely. The larva found its way out of the head through the neck foramen and traversed the whole body to emerge between the cerci of the host. The host lived for 2–3 days after the larva had departed. Nothing is known about how the first instar of the fly entered the termite head.

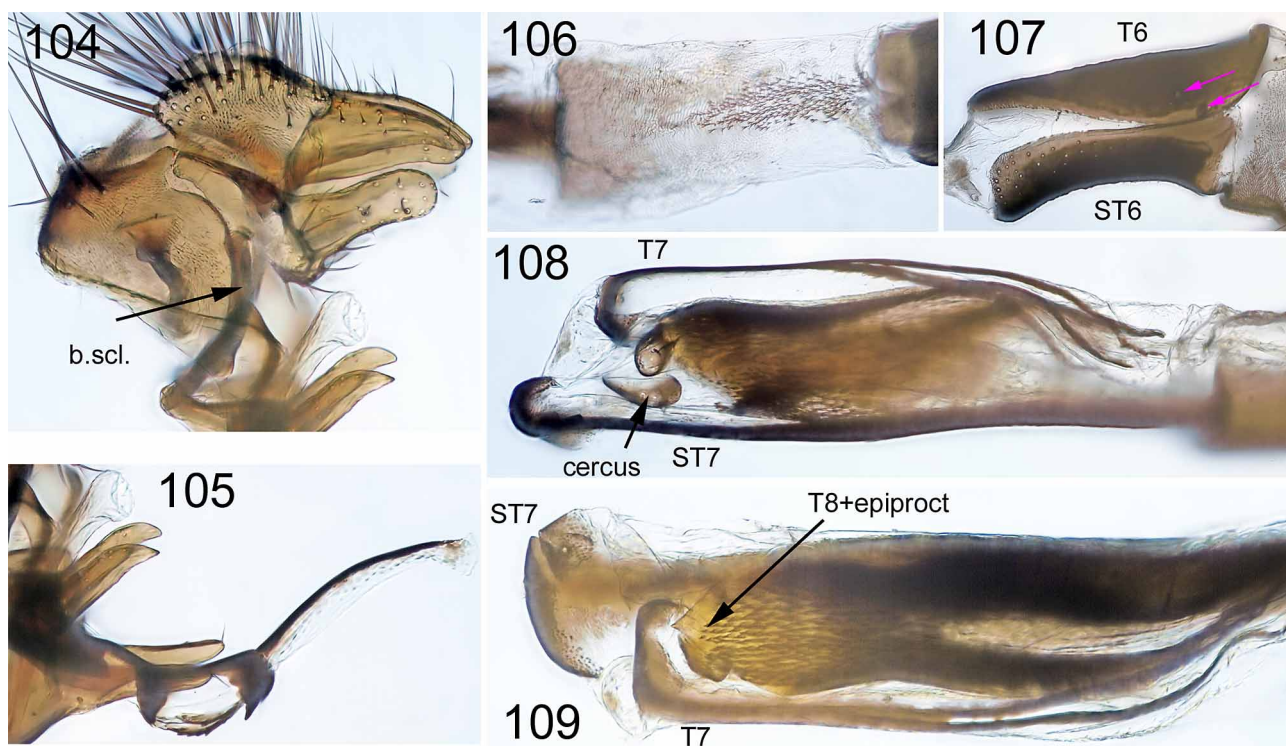
Given the low resolution of the basal branches of the consensus cladogram, it is not easy to deduce what is the ground plan substrate for larval development among the Bengaliinae. Widely dissimilar animals as man and termite are used for their growth, with a varied source of larval nourishment, from human blood to the contents of a termite head. Perhaps an important common denominator is the oviposition habit, in combination with larvae being very resistant to desiccation and able to stay alive for a long time without nourishment (Roubaud 1913). In almost all cases where the egg-laying habit is known the eggs are deposited on the ground or in loose sand, either close to the host in their burrows or dwellings (*Auchmeromyia*, *Pachychoeromyia*) or in a place where the host will turn up (*Cordylobia*, *Tricyclea*). A derived feature seems to be the one displayed by *Booponus*: ovipositing directly on the host skin.

### **Systematic position of the Afrotropical genera *Adichosina* Villeneuve, *Ochromelinda* Villeneuve, *Onesihoplisa* Villeneuve and *Zernyiella* Zumpt in the subfamily Melanomyiinae**

Recently, Peris & González-Mora (2004) included the four Afrotropical genera *Adichosina* Villeneuve, *Ochromelinda* Villeneuve, *Onesihoplisa* Villeneuve and *Zernyiella* Zumpt in the subfamily Auchmeromyiinae, as they conceived this taxon, alongside *Auchmeromyia*, *Booponus*, *Cordylobia*, *Hemigymnochaeta*, *Neocordylobia*, *Pachychoeromyia*, *Tricyclea* and *Verticia*. They maintained this subfamily as a taxon coordinate with their taxon Bengaliinae (for *Bengalia* only). The structure of the distiphallus, ovipositor and first instar larva (as far as it is known) in these genera speaks strongly against such an assignment and provides incontrovertible evidence for an assignment with Melanomyiinae. Here follows a description of the genitalia of representatives of these genera.

*Adichosina* Villeneuve. *Male*. The genitalia of *A. eos* are shown in Figs. 104, 105. Noteworthy are the narrow pre- and postgonites, the strong hook-shaped paraphallic tip, the very elongate acrophallus, the dentate edge of the hypophallic lobes, and the almost unsclerotised acrophallic membrane. *Female*. The female ovipositor of *Adichosina munroi* is shown in Figs. 106–109. In females of *Adichosina* the ovipositor is often protruding from the posterior end of the abdomen and the protruding tip forms a flat almost circular shining spatula-like structure separated from the more basal parts by a constriction. The projecting part consists of the tips of T7 and ST7, and especially the latter is distally rounded (Fig. 109). I never succeeded in drawing the T8 and ST8 out from their telescoped position within the seventh segment, but close examination of the eighth segment and the cerci was nevertheless possible through the integument of the seventh segment and the intersegmental membrane 7–8. T6 and ST6 are without setae; many sensillae are present on ST6, especially on posterior third, also along margin (Fig. 107). Spiracles 6 and 7 are within the confines of T6 (Fig. 107, pink arrows). Pleural membrane 6 is without microtrichiae. Intersegmental membrane 6–7 with anteriorly directed dentate sclerotisations middorsally in anterior half (Fig. 106). T7 and ST7 very elongate and slender, T7 cleft proximally and widening out like a “T” distally; ST7 widen-

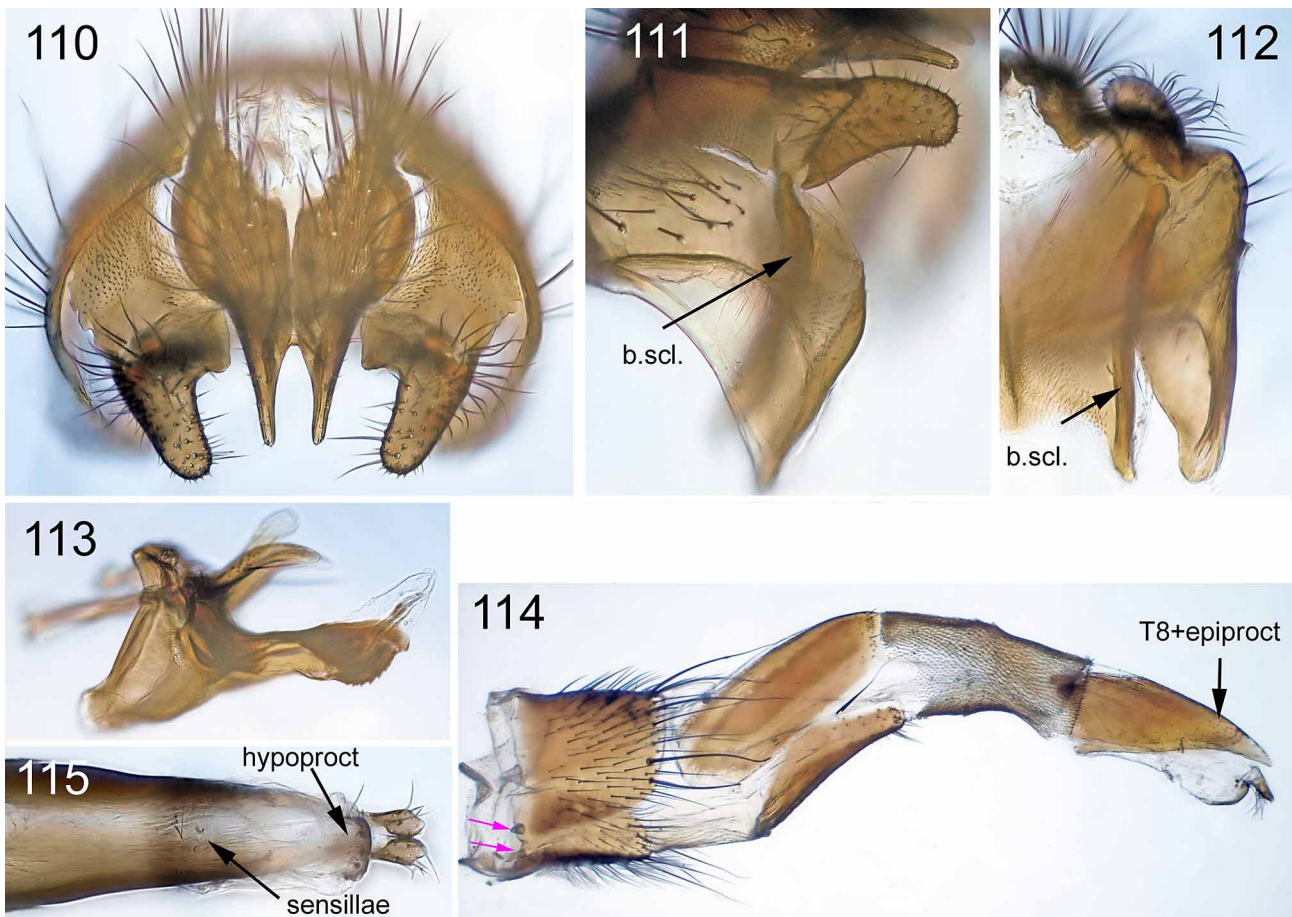
ing out into an almost flat circular sclerotisation distally. Intersegmental membrane 7–8 with dentate sclerotisations directed proximad (visible in Fig. 109 as a layer covering the T8 + epiproct). T8 + epiproct fused and pointed distally. Cerci small and wart-like. It was not possible to determine if a hypoproct is present, since the eighth segment remained unexposed.



**FIGURES 104–109.** **104–105.** *Adichosina eos* Zumpt (CNC). Male genitalia. **104.** Epandrium, cerci, surstyli and bacilliform sclerites, left lateral view. **105.** Aedeagus, pre- and postgonites, left lateral view. **106–109.** *Adichosina munroi* (Curran) (MZLU). Female ovipositor. **106.** Dorsal intersegmental membrane 6–7 (behind T6). **107.** Segment 6, right lateral view. Pink arrows point to spiracles 6 and 7. **108.** Segment 7, with segment 8 and cerci telescoped within it, right lateral view. **109.** Dorsal view of T8+epiproct telescoped within segment 7. Note tooth-like microtrichiae on intersegmental membrane 7–8 superimposed on the compound T8+epiproct sclerite; these are pointing towards hind end of T7. They seem to be pointing backwards, but if segment 8 had been drawn out from segment 7, they would have been pointing forwards.

Note. Some unidentified specimens possibly related to *A. eos* (cf. Zumpt 1972) in CNC have an anal vein reaching the wing margin, whereas in other *Adichosina* species the anal vein terminates well before the wing margin. This means that an anal vein reaching the wing margin is a feature that must have emerged independently from the Bengaliinae.

*Ochromelinda* Villeneuve. *Male.* The genitalia of *O. thoracica* are shown in Figs. 110–113. The bacilliform sclerite joins the ventrolateral part of the distal part of the surstylus. The distal part of the paraphallus is a strongly sclerotised plate, dentate along margin. The membrane of the aedeagus is elsewhere without denticles. Pre- and postgonites are narrow. *Female.* The ovipositor of *O. thoracica* is shown in Figs. 114, 115. T6 and ST6 are setose and rather short. The spiracles 6 and 7 are situated at the anterior edge of T6 (Fig. 114, pink arrows). Pleural membrane 6 without microtrichiae. The intersegmental membrane 6–7 is without dentate sclerotisations. T7 consists of two elongate sclerotisations that are close together distally but separate proximally. ST7 is a single piece. T7 and ST7 both with some short inconspicuous setae along the posterior margin. Pleural membrane 7 without microtrichiae. Intersegmental membrane 7–8 all covered with densely set dentate sclerotisations pointing towards base of ovipositor. T8 fused with epiproct, combined sclerite pointed distally, sensillae present middorsally slightly behind tip and along lateral margin in distal third. Cerci small and wart-like. Hypoproct present. On the ventral side, midway along the eighth segment there is a transverse row of a few small sensillae (Figs. 114, 115). They are probably marking the posterior end of the unsclerotised ST8 and forming the ventral border of the opening of the uterus or “birth” canal.

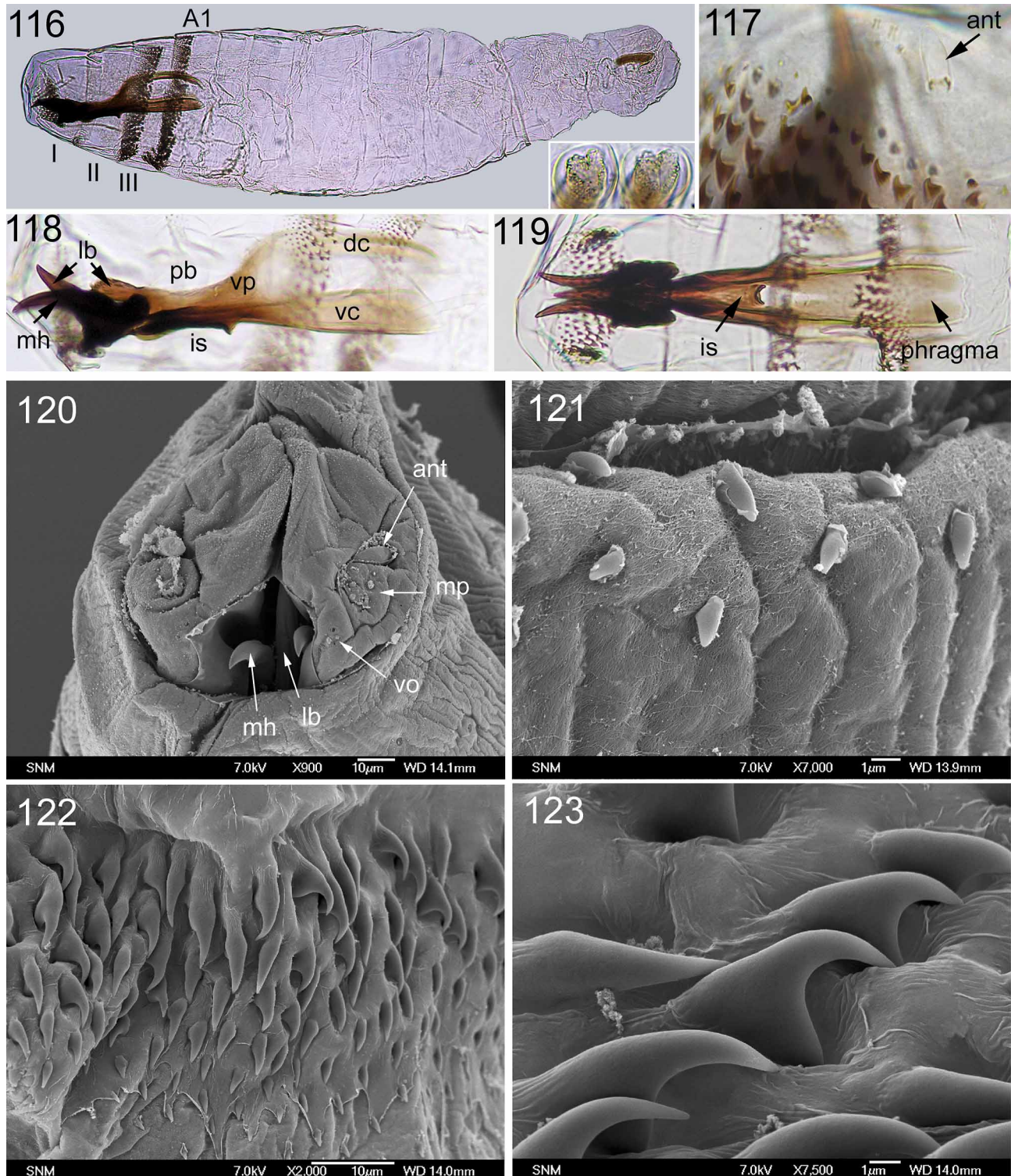


**FIGURES 110–115.** *Ochromelinda thoracica* Villeneuve (CNC). **110–113.** Male genitalia. **114–115.** Female ovipositor. **110.** Epandrium, cerci and surstyli, posterior (dorsal) view. **111.** Epandrium, surstylus and bacilliform sclerite of left side, left lateral view. **112.** Parts of right side of epandrium, right cercus, surstylus and bacilliform sclerite, anterior (inside) view. **113.** Hypandrium with aedeagus and gonites, left lateral view. **114.** Fully extended ovipositor, left lateral view. Pink arrows point to spiracles 6 and 7. **115.** Ovipositor, terminal segment, ventral view.

*First instar larvae* (Figs. 116–123). In the dissected uterus I found about 10 first instars about to free themselves from their egg membranes. They were subsequently mounted and are described in Appendix 4 by Krzysztof Szpila. The labrum (*lb.*) is dorsally concave (upturned) and firmly fused with the tentoropharyngeal sclerite (= parastomal bar, *pb.*) (Fig. 118). The larva resembles the first instar of the European melanomyine fly *Eggisops pecchiolii*. Like in this species, *Ochromelinda* first instars have a small projection dorsally on the labrum, and reduced spinulation on abdominal segments and anal division.

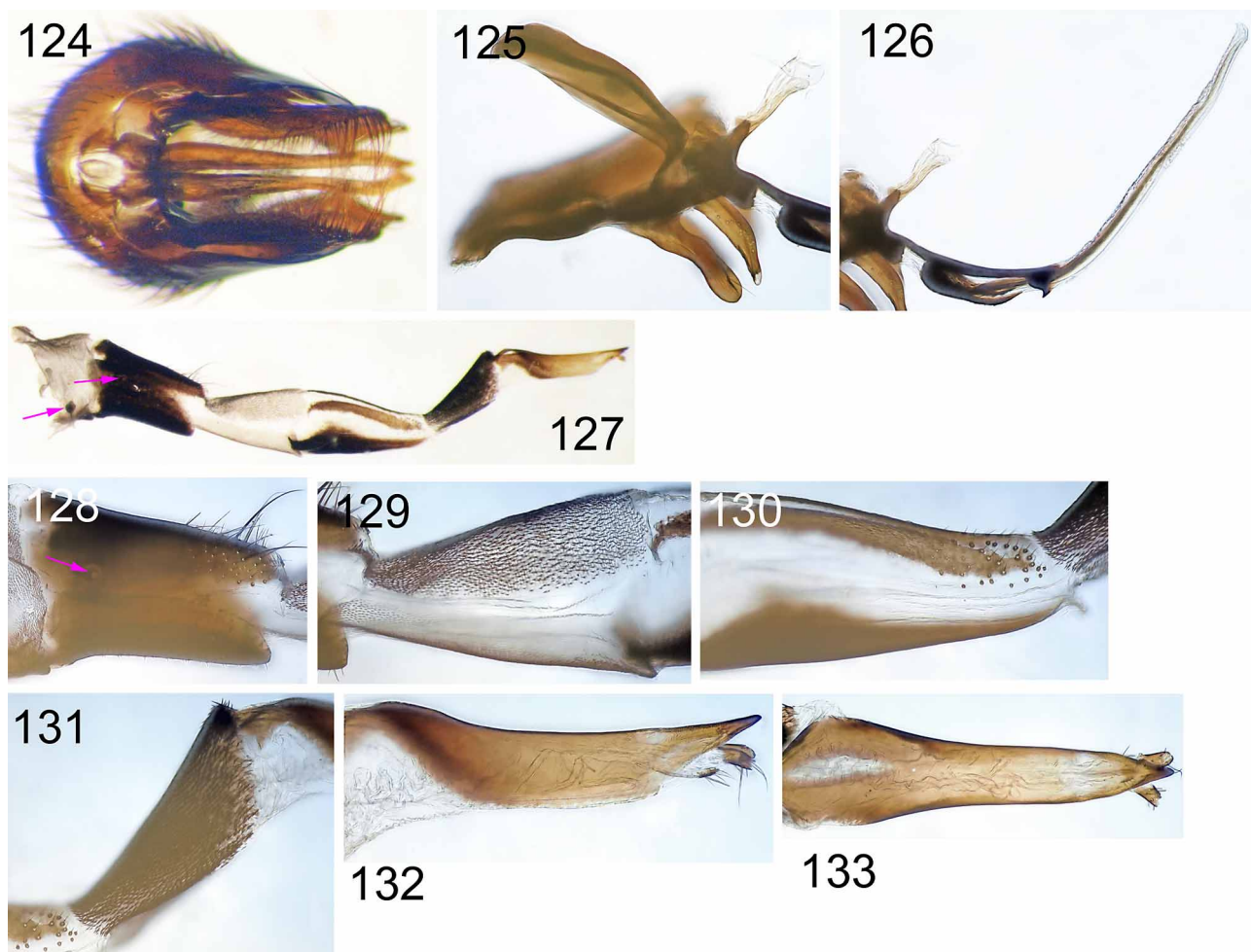
*Onesihoplisa* Villeneuve. *Male.* The male genitalia of *Onesihoplisa umbrosa* are shown in Figs. 124–126. The pre- and postgonites are very narrow. The paraphallic tip is a small strong hook with a single point, and the acrophallus is extremely long. The latter has two thin sclerotisations for its whole length, and is very narrow and without denticles. The hypophallic lobe is a long dentate ridge. *Female.* The ovipositor is shown in Figs. 127–133. T6 is a little more than twice as long as broad, and a little narrower posteriorly than anteriorly. Proximal edge of T6 slightly concave. In the posterior half it has a pair of long setae and numerous short ones. Pleural membrane 6 is without microtrichiae. ST6 is much broader than T6 and covered with small sensillae all over. Abdominal spiracle 6 is situated laterally and rather far forward in the intersegmental membrane 5–6, slightly on the ventral side of the ovipositor tube, whereas spiracle 7 is within the confines of the anterolateral corner of T6 (Figs. 127, 128, pink arrows). The intersegmental membrane 6–7 carries dorsally a broad band of densely set small denticles directed proximad (Fig. 129). Laterally it is without denticles. Ventrally it has a broad band of denticles similar to the one dorsally, but the denticles are finer and paler. T7 consists of two long and slender sclerotisations, which are slightly curved, and which are closest together at a point a third of their length from the posterior end. In the distal third they are provided with a number of sensillae (Fig. 130). Pleural membrane 7 is without microtrichiae. ST7 is also a long single sclerite, broadest at about the proximal third and narrowing to a point at its distal end (Fig. 130). The

intersegmental membrane 7–8 is covered with very dark and densely set denticles both dorsally, laterally and almost on the whole ventral side giving it the appearance of being totally sclerotised (Figs. 127, 131). There is a narrow bare gap in the posterior part of the midventral part of the membrane. T8 is fused with the epiproct into a single sclerotised piece, partly cleft proximally and pointed distally (Fig. 133). ST8 is absent. The cerci are small,



**FIGURES 116–123.** *Ochromelinda thoracica* Villeneuve (CNC). First instar uterine larva. **116–119.** Photomicrographs. **120–123.** Scanning electron micrographs (SEM). **116.** Whole mount in Hoyer's medium, left lateral view. Inset: posterior spiracles. **117.** Pseudocephalon and first thoracic segment, lateral view. **118.** Cephalopharyngeal skeleton, left lateral view. **119.** Cephalopharyngeal skeleton, ventral view. **120.** Pseudocephalon, ventral view (SEM). **121.** Spines from anterior spinose band on second thoracic segment. **122.** Spines from anterior spinose band on third thoracic segment. **123.** Spines from anterior spinose band on third thoracic segment, enlarged. [All photographs by Krzysztof Szpila]. Abbreviations, see Material and methods chapter.

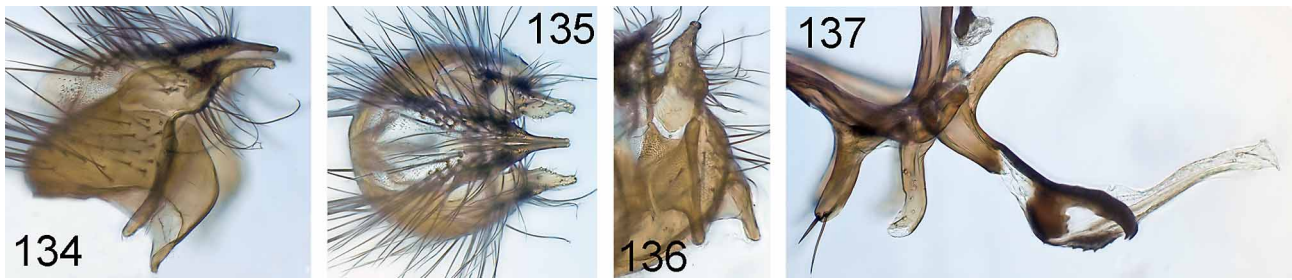
oval wart-like sclerotisations carrying a few setae. The hypoproct is sclerotised distally where it carries a few setae (Figs. 132, 133). Proximally it proceeds proximad and forms the roof of the genital orifice (Fig. 132).



**FIGURES 124–133.** *Onesihoplisa umbrosa* Villeneuve (CNC). **124–126.** Male genitalia. **127–133.** Female ovipositor. **124.** Epanandrium, cerci and surstyli, posterior (dorsal) view. **125.** Hypandrium, phallapodeme and gonites, left lateral view. **126.** Aedeagus, left lateral view. **127.** Fully extended ovipositor, left lateral view. Pink arrows point to spiracles 6 and 7. **128.** Segment 6, left lateral view. Pink arrow points to spiracle 7. **129.** Intersegmental membrane 6–7, left lateral view. **130.** Segment 7, left lateral view. **131.** Intersegmental membrane 7–8, left lateral view. **132.** T8+epiproct, cerci and hypoproct, left lateral view. **133.** T8+epiproct and cerci, dorsal view.

*Zernyiella* Zumpt. *Male.* The male genitalia of the lectotype of *Zernyiella dubia* Zumpt are shown in Figs. 134–137 (for lectotype designation, see Appendix 3). Epanandrium, surstylus and cerci with long, thin slightly wavy setae. The cerci are pointed apically and close together all the way to the tip. The tips of the cerci are shown to diverge in Zumpt's (1956: 98, fig. 54, left side) figure but this is an artifact resulting from his habit of squashing these organs flat. Postgonite narrow without basal seta, numerous small sensillae present along stalk. Pregonite narrow with two short setae at tip. Epiphallus large, widened distally. Hypophallic lobes sclerotised along ridge edge, latter with 3–4 teeth on each side. Distiphallus elsewhere quite bare. Ventral plates strong, not joined midventrally, open. Paraphallic processes separate at level of ventral plates in dorsal view. Paraphallic tip hook-shaped with a pointed apex. Acrophallus long, slender. Bacilliform sclerite joining the ventrolateral corner of the middle part of surstylus. Articulation between medial part of proximal surstylus and lateral part of basal part of cercus with strong sclerotisations on each articulating part. Each bacilliform sclerite with a broad, medially directed almost rectangular sclerotisation in the ventral epanandrial membrane, almost touching its counterpart on the other side. *Female.* Unknown.

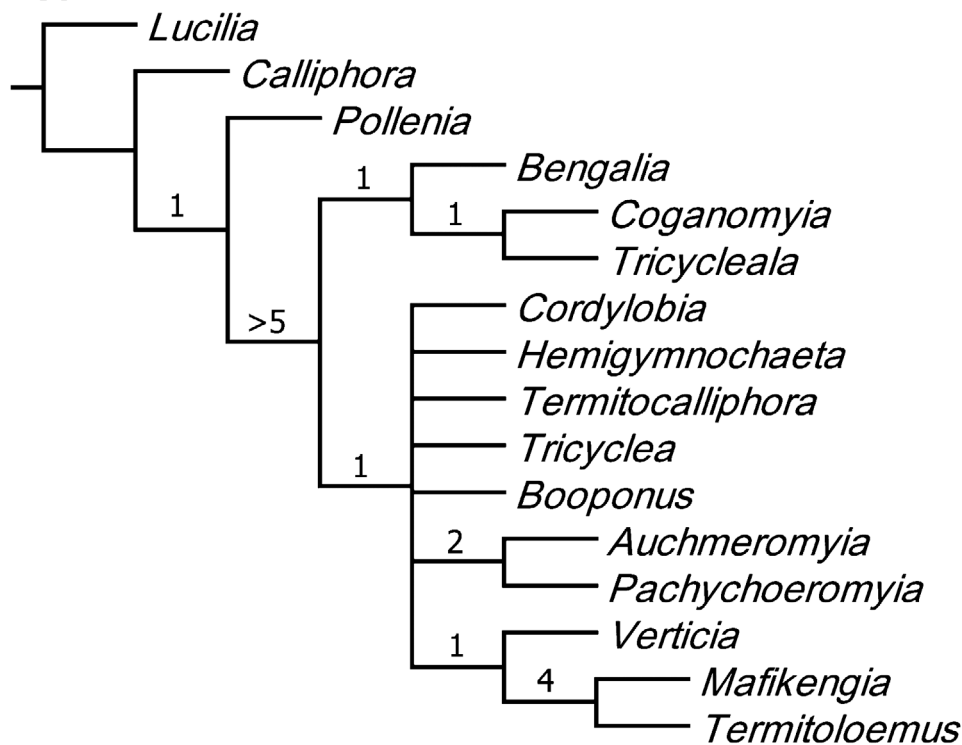




**FIGURES 134–137.** *Zernyiella dubia* Zumpt, male lectotype (NMSA). **134.** Epandrium, cerci and surstyli, left lateral view. **135.** Epandrium, cerci and surstyli, posterior (dorsal) view. **136.** Part of epandrium with right surstylus and right bacilliform sclerite, internal view. **137.** Pre- and postgonites, aedeagus, left lateral view.

Conclusion. Rognes (1991: 184) gave a list of ten autapomorphies defining the subfamily Melanomyiinae:

- (1) Epiproct in ovipositor fused with T8, the combined T8+epiproct often appearing shovel-shaped posteriorly.
- (2) Cerci in ovipositor short and broad, wart-like, with hairs.
- (3) Ovipositor sclerites (except hypoproct) without microtrichiae, thus shining black without dust (except posterior edge of T6 in *Melinda gentilis*, and T6 of *Opsodexia*).
- (4) ST8 in ovipositor completely absent or very strongly reduced.
- (5) Sclerites of segment 7 and 8 in ovipositor strongly elongated.
- (6) Sclerites of at least segments 7 and 8 in ovipositor devoid of setae or setulae, these replaced by numerous small sensillae.
- (7) Intersegmental membranes in ovipositor without microtrichiae of usual form; these entirely absent or replaced with armature of a peculiar form.
- (8) Pleural membranes of ovipositor entirely without microtrichiae.
- (9) Acrophallus and other parts of aedeagal walls bare, without denticles.
- (10) First instar larva with labrum dorsally concave (i.e. upturned) and firmly fused with tentoropharyngeal sclerites.



**FIGURE 138.** Strict consensus of the 11 most parsimonious trees of 56 steps found by NONA. Numbers above branches indicate Bremer support values.

The genitalia found in the genera *Adichosina*, *Ochromelinda* and *Onesihoplisa* satisfy all the synapomorphies nos. 1–9. The first instar larvae extracted from the abdomen of *Ochromelinda thoracica* also satisfy the synapomorphy no. 10. No females are known in the genus *Zernyiella*, but the male genitalia satisfy the only synapomorphy listed for males; i.e., the acrophallus and other parts of the aedeagal wall being bare, without denticles (no. 9). All these Afrotropical genera also share very narrow pre- and postgonites, a feature which is widespread also in Palaearctic genera: *Angioneura* Brauer & Bergenstamm, *Eggisops* Rondani, *Melinda* Robineau-Desvoidy (cf. Rognes 1991) and also in several Oriental ones: *Gymnadichosia* Villeneuve (cf. Fan 1997), *Paradichosia* Senior-White (cf. Fan 1997), *Tricycleopsis* Villeneuve (cf. Kurahashi 1998). On the basis of present knowledge of the male and female genitalia and the morphology of the first instar larva the inescapable conclusion is that all these Afrotropical genera belong to Melanomyiinae. The subfamily is thus demonstrated to occur in the Afrotropical Region. It is already known to occur in the Palaearctic, Nearctic, Neotropical and Oriental Regions (Rognes 1991; Whitworth 2010).

## Acknowledgements

I would like to thank Nigel Wyatt (BMNH), Ashley Kirk-Spriggs (BMSA), Neal Evenhuis (BPBM), Jim O'Hara (CNC), Christophe Daugeron (MNHN), Eliane De Coninck (MRAC), Fabrizio Rigato (MSNM), Roy Danielsson (MZLU), Burgert Muller (NMSA), Peter Sehnal (NMW), Amnon Freidberg (TAU), Thomas Pape (ZMUC) and Vladimir Gusarov (ZMUN) for loan of material. Thanks also to Hans-Peter Tschorsnig, Stuttgart, Germany, for help in locating the source for the term “soie postsuturale de Hough” used by Villeneuve; to Michelle Whittaker, Taylor & Francis Group (<http://www.informaworld.com>), UK, for permission to use Baranov's figure of the genitalia of *Termitoloemus marshalli* Baranov, reproduced here as Fig. 72; and to Krzysztof Szpila, Toruń, Poland, for his generosity in examining the uterine first instar larvae of *Ochromelinda thoracica* with light and scanning electron microscopy, for providing a description and a discussion of important larval features, and for providing images for use in this paper, and to Hiromu Kurahashi, Tokyo, Japan, for providing important reprints. A special thank to the reviewers Thomas Pape and Hans-Peter Tschorsnig and to the *Zootaxa* editor Jim O'Hara for their conscientious work and invaluable comments and suggestions.

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- Note. I follow Sabrosky (1999: 97) in regarding the author of the name *anthropophaga* to be Blanchard who also assigned it to the genus *Ochromyia* Macquart. Pont (1980: 792) seems to have been in error when assigning the authorship of the name *anthropophaga* to both Bérenger-Féraud and Blanchard, but the former provided only the description of the larva, not the name (cf. ICZN 1999, Code Article 50.1.1).
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## Appendix 1. Characters and states used for data matrix and the phylogenetic analysis

Character 0—ground colour

0: black

1: yellow

Character 1—width of male frons

0: very narrow, usually narrower than, at most as broad as, the ocellar triangle

1: broad, at most as broad as an eye seen from above, always broader than the ocellar triangle

2: extremely broad, about 2x width of an eye or more as seen from above

*Cordylobia*, *Termitocalliphora* and *Tricyclea* are scored as polymorphic, since both states 0 and 1 occur among their species.

Character 2—aristal stalk thickness

0: normal

1: thickened

Character 3—aristal length

0: normal, about 1.5x length of first flagellomere

1: unusually short, about as long as first flagellomere

2: very long, about 2x length of the first flagellomere

*Booponus* is scored for state 1, *Mafikengia* and *Termitoloemus* for state 2.

Character 4—aristal hair length

0: normal

1: very short

*Booponus* and *Termitoloemus* are both scored for very short aristal hairs.

Character 5—palpus length

0: normal, not projecting beyond mouth-edge

1: very long, projecting far beyond mouth-edge

Only *Mafikengia* and *Termitoloemus* are scored for state 1, cf. Figs. 4, 42.

Character 6—number of humeral (postpronotal) setae

0: 3 or 4

1: 2

2: 1

*Bengalia* and *Mafikengia* are scored for state 1. Only *Coganomyia* has a single humeral seta.



Character 7—outer posthumeral seta

0: absent

1: present

An outer posthumeral seta is present in *Cordylobia*, *Hemigymnochaeta* (and *Lucilia* and *Calliphora*). It is variably present or absent in *Booponus* and *Tricyclea* (thus scored as polymorphic).

Character 8—Y seta

0: absent

1: present

The Y seta is present in *Cordylobia*, *Hemigymnochaeta*, *Booponus* and *Pachychoeromyia*, but variably present or absent in *Auchmeromyia* and *Tricyclea*.

Character 9—proepisternal depression (propleuron)

0: bare

1: setose

*Termitocalliphora* is coded with both states, following Bauristhene (1964: 15). I have done the same for *Tricyclea* to accommodate *T. tauffliebi* that has a bare proepisternal depression, contrary to other *Tricyclea* species.

Character 10—prosternum

0: bare

1: setose

Character 11—Hough seta

0: absent

1: present

Character 12—subscutellum

0: absent

1: present

Character 13—lower edge of lateral scutellar declivity, row of numerous setae

0: absent

1: present

Character 14—anal vein

0: not reaching wing margin

1: reaching wing margin

Character 15—vein  $R_{4+5}$ , setosity

0: setose on at most proximal third of distance between *r-m* and wing margin

1: setose on more than proximal half of distance between *r-m* and wing margin

*Termitocalliphora* is coded with both states, as the setosity varies according to Bauristhene (1964: 18).

Character 16—bend of vein M

0: sharp

1: gently curved

Character 17—lower calypter, shape

0: narrow

1: broad

Character 18—lower calypter, vestiture

0: bare

1: hairy

*Pachychoeromyia* has the lower calypter covered with pale hairs except on the posterolateral corner, contrary to the condition in *Auchmeromyia* which has a bare lower calypter.

Character 19—dorsal preapical seta of hind tibia in male, length

0: short, much shorter than first tarsomere

1: strikingly long, 1.2–1.5 times length of first tarsomere (Figs. 21, 22, 43)

Character 20—male cerci

0: broad, separate, not fused in midline

1: narrow, fused in midline (Figs. 24, 49, 50, 53)

Character 21—surstylus

0: a single undivided sclerite

1: divided into two separate sclerites (Figs. 51, 52)

I have coded *Termitoemus* as “?”. It is impossible to decide from the genital slide of the holotype whether the proximal and distal parts of the surstylus (Figs. 69, 71, *p.sur.* and *d.sur.*) are separate or fused.

Character 22—length of proximal part of surstylus

0: very short

1: moderately long

2: very long

3: absent

Character 23—bacilliform sclerite, simple or double

0: simple

1: divided into two separate sclerites

I have coded *Termitoemus* as “?”. To judge from Fig. 69 it may well be the case that the bacilliform sclerite is double, but a definite answer must await examination of further males.

Character 24—bacilliform sclerites, separation

0: separate from one another

1: fused in midline (Fig. 50)

Character 25—bacilliform sclerite, attachment to surstylus

0: proximally on lateral or ventrolateral side of distal part of surstylus

1: distally on medial side of proximal part of surstylus

*Termitoloemus* is coded as having a medial connection between the upper end of the bacilliform sclerite and the surstylus (cf. discussion of the *Termitoloemus* genital slide, above).

Character 26—bacilliform sclerite, projection or tooth

0: absent

1: present

A prominent projection, of varying shape, is present in all species of *Bengalia* (Figs. 51, 52). In *Termitoloemus marshalli* the projection is much smaller (Figs. 69, 71). A very slight projection is visible on the upper part of the bacilliform sclerite in *Tricycleala maculipennis* (Fig. 86).

Character 27—dentate bands on ventral side of distiphallus

0: simple, one on each side

1: double, two on each side

2: absent

I have not been able to recognise the presence of dentate bands on the ventral part of the distiphallus of *Termitoloemus marshalli* (cf. Fig. 70), neither are dentate hypophallic lobes present in *Pachychoeromyia praegrans* (own dissection; cf. also Patton 1935: 219, fig. 18a).

Character 28—degree of sclerotisation of distiphallus

0: normal, not strong

1: very strongly sclerotised

In the holotype male of *Coganomyia ornata* a small part of the tip of the distiphallus can be observed. It is very heavily sclerotised, black and shining. *Pachychoeromyia praegrans* has a much less strongly sclerotised aedeagus than the species of *Auchmeromyia* (own dissections; Patton 1935).

## Data matrix

					111111	1111	22222	2222
	01	234567	8	9	012345	6789	01234	5678
<i>Lucilia</i>	00	000001	0	1	100000	0100	00000	0000
<i>Calliphora</i>	00	000001	0	1	100000	0110	00000	0000
<i>Pollenia</i>	00	000001	0	0	000000	0100	00000	0000
<i>Bengalia</i>	11	000010	0	0	101010	1100	01110	1110
<i>Cordylobia</i>	1[01]	000001	1	0	111110	1100	00100	1010
<i>Hemigymnochaeta</i>	10	000001	1	0	111110	1000	00100	1010
<i>Termitocalliphora</i>	1[01]	000000	0	[01]	111111[01]	1000	00100	1010
<i>Tricyclea</i>	1[01]	00000[01]	[01]	[01]	111110	1100	00100	1010
<i>Verticia</i>	11	000000	0	0	011110	1100	00300	1010
<i>Booponus</i>	11	11100[01]	1	0	111110	1100	00100	?010
<i>Auchmeromyia</i>	11	000000	[01]	0	111110	1100	10201	1011
<i>Pachychoeromyia</i>	11	000000	1	0	111110	1110	10201	1020
<i>Coganomyia</i>	11	000020	0	1	101010	1000	1020?	???1
<i>Mafikengia</i>	12	020110	0	0	000111	1101	10100	1010
<i>Termitoloemus</i>	12	021100	0	0	011111	1001	0?0?0	1120
<i>Tricycleala</i>	11	000000	0	1	111011	1000	00100	1110

## Appendix 2. Check-list of genus-group and species-group names included in Bengaliinae

Synonyms are mainly based on James (1977), Pont (1980) and Rognes (2006, 2009a, 2011b).

*Auchmeromyia* Brauer & Bergenstamm, 1891

*Choeromyia* Roubaud, 1911

*bequaerti* Roubaud, 1913 (= *pattoniella* Lehrer, 2005b, **unavailable** [no type designation], not validated in Lehrer, 2006b)

*boueti* Roubaud, 1911

*choerophaga* Roubaud, 1911

*reidi* Zumpt, 1959

*senegalensis* Macquart, 1851 (= *luteola* Fabricius, 1805, preocc.; = *kurahashi* Lehrer, 2005b, **syn. nov.** [cf. Appendix 3])

*Bengalia* Robineau-Desvoidy, 1830

*Ochromyia* Macquart, 1835

*Anisomyia* Walker, 1859

*Homodexia* Bigot, 1885

*Parabengalia* Roubaud, 1913

*Pollenoides* Matsumura, 1916

*Eubengalia* Townsend, 1926

*Afridigalia* Lehrer, 2005a

*Ashokiana* Lehrer, 2005a

*Bezzigalia* Lehrer, 2005a

*Gangelomyia* Lehrer, 2005a

*Kenypyga* Lehrer, 2005a

*Laoziana* Lehrer, 2005a

*Maraviola* Lehrer, 2005a

*Ochromyia* Lehrer, 2005a. Permanently invalid. Junior homonym of *Ochromyia* Macquart, 1835

*Shakaniella* Lehrer, 2005a

*Temaseka* Lehrer, 2005a

*Tsunamia* Lehrer, 2005a

*Sindhigalia* Lehrer, 2006a

*Anshuniana* Lehrer, 2010. *Nomen nudum*.

*Anshuniana* Lehrer & Wei, 2010

—about 60 species, cf. Lehrer 2005a; Rognes 2006, 2009b, 2011b

*Booponus* Aldrich, 1923

*Elephantoloemus* Austen, 1930 [as *Elephantolæmus*]

*Pavlovskiomyia* Grunin, 1947

*aldrichi* Senior-White, Aubertin & Smart, 1940

*borealis* Rohdendorf, 1959

*indicus* Austen, 1930

*inexpectatus* Grunin, 1947

*intonsus* Aldrich, 1923

*malayana* Kurahashi, Benjaphong & Omar, 1997

*Coganomyia* Dear, 1977

*ornata* Dear, 1977

*Cordylobia* Grünberg, 1903

*Stasisia* Surcouf, 1914

*Neocordylobia* Villeneuve, 1929 (as subgenus of *Cordylobia*), **syn. nov.**

*anthropophaga* Blanchard in Larrey, 1872

*rodhaini* Geddoelst, 1910 (= *ebadiana* Lehrer & Goergen, 2006, **syn. nov.** [cf. Appendix 3])

*roubaudi* Villeneuve, 1929

*ruandae* Fain, 1953b

*Hemigymnochaeta* Corti, 1895

*Parochromyia* Hough, 1898

*Auchmeromyiella* Townsend, 1918

- Tricyclodes* Curran, 1927  
—numerous species, in need of revision
- Mafikengia* **gen. nov.**  
*ciliata* **sp. nov.**
- Pachychoeromyia* Villeneuve, 1920  
*praegrandis* Austen, 1910 (= *kanemia* Lehrer, 2011, **syn. nov.** [cf. Appendix 3].
- Termitocalliphora* Bauristhene *in* Pont, 1980  
*machadoi* Bauristhene, 1964  
*nana* Zumpt, 1953
- Termitoemus* Baranov, 1936  
*marshalli* Baranov, 1936
- Tricyclea* Wulp, 1885  
*Zonochroa* Brauer & Bergenstamm, 1891  
*Kenia* Malloch, 1927  
*Keniella* Malloch, 1929  
—numerous species, cf. Pont 1980; in need of revision; also *tauffliebi* Zumpt, 1958, **comb. nov.**
- Tricycleala* Villeneuve, 1937  
*maculipennis* Villeneuve, 1937
- Verticia* Malloch, 1927  
*chani* Kurahashi, Benjaphong & Omar, 1997  
*fasciventris* Malloch, 1927  
*indochinica* Kurahashi & Chowanadisai, 2001  
*nigra* Malloch, 1927  
*orientalis* Malloch, 1927  
*quatei* Kurahashi & Chowanadisai, 2001  
—plus several undescribed species

Note. It has been suggested that *Wilhelmina* Villeneuve *in* Schmitz & Villeneuve, 1932 “may be closely related to the genus *Bengalia*” because of the shape and coloration of the abdomen (Kurahashi & Omar 2007). I do not accept this point of view, briefly discussed here.

*Wilhelmina* was created for a single species *W. nepenthicola* Villeneuve *in* Schmitz & Villeneuve, 1932. Of its two syntypes, both females, one was bred from a larva found in the pitchers of a *Nepenthes rafflesiana* in Mandor, district of Pontianak, Borneo (Indonesia, Kalimantan Barat), the second from a puparium found floating in the liquid in the pitcher of *Nepenthes ampullaria* (Schmitz & Villeneuve 1932). Apart from Villeneuve’s detailed original description of the adult, third instar larva and puparium, a species description is also found in Senior-White *et al.* (1940: 133–134) who reproduced Schmitz & Villeneuve’s figures of the third instar larva and the puparium. Kurahashi & Omar (2007) re-described *Wilhelmina nepenthicola* Villeneuve on the basis of a female specimen reared from a larva found in the pitcher of *Nepenthes rafflesiana* in Sarawak (Malaysia), the third adult specimen known. Sidhu & Singh (2005) described a second species, *Wilhelmina indica*, from India (Uttarakhand [formerly Uttarachal], Almora).

The wing of *Wilhelmina* shows an almost right-angled bend to the vein M carrying a small appendix (Kurahashi & Omar 2007: 326, fig. 1). Villeneuve (in Schmitz & Villeneuve 1932) also described the occasional presence of “*un court prolongement réel*” [a short prolongation] at the angle of vein M, both of which are very different from *Bengalia* and any other Bengaliinae. Further, Villeneuve (in Schmitz & Villeneuve 1932), Senior-White *et al.* (1940), Sidhu & Singh (2005) and Kurahashi & Omar (2007) did not describe the presence of a Hough seta. Interestingly, Sidhu & Singh (2005: 257) described the supraspiracular convexity (katatergite) as “hairy”, and Kurahashi & Omar (2007: 326) as “pubescent, clothed with yellowish white upstanding hairs”. This is not a feature known among Bengaliinae, but is reminiscent of *Phumosia* Robineau-Desvoidy, which is characterised by long upstanding setulae on the katatergite. Kurahashi & Omar also described the facial plate (“*mediana*”) “with a few black setulae”, another *Phumosia* feature. However, Villeneuve (in Schmitz & Villeneuve 1932: 117), in a quite detailed description, did not mention any particular setosity on the katatergite, but recorded the presence of “*une plage de cils noirs sur l’expansion latérale du mésophragme, au-dessous du cuielleron thoracique*” [an area with black hairs on the lateral expansion of the mesophragma, under the lower calypter]. He is clearly referring to the group of small hairs on the anatergite, a different sclerite than the supraspiracular convexity (katatergite).

Villeneuve (in Schmitz & Villeneuve 1932) assigned *Wilhelmina* to the Polleniinae, because of “*prosternum et propleures glabres, soies sternopleurales 1+1, etc.*” [prosternum and propleuron bare, sternopleural setae 1+1, etc.], in addition to describing the pleura as having “*longue pilosité blanchâtre*” [with long pale hairs], as is the case in *Pollenia*. Fan (1965) also classified *Wilhelmina* in the subfamily Polleniinae, together with *Pollenia* Robin-eau-Desvoidy, 1830, *Xanthotryxus* Aldrich, 1930 and *Dexopollenia* Townsend, 1917. Rognes (1991: 206) also treated it as a member of the Polleniinae, because of the bare prosternum and proepisternal depression and setose postalar wall. Fan (1992, 1997) did the same (although lowered the rank of the subfamily to the tribe Polleniini). In addition, it is apparent from the figure of the posterior spiracles of the third instar larva published by Schmitz & Villeneuve (1932: 116, fig. 3) that the three spiracular slits are separated from each other by a right angle. This is reminiscent of the position of the spiracular slits in several species of the *Pollenia rudis* species-group published by Rognes (1987), although the upper slit in *W. nepenthicola* is leaning towards the midline, whereas in *Pollenia* it is leaning outwards.

Recently, Kurahashi & Tan (2010) described the male of *W. nepenthicola* for the first time. The illustrated genitalia and ST5 bear no resemblance to the corresponding structures in *Bengalia*, so an inclusion in Bengaliinae can safely be ruled out. The supraspiracular convexity in the male is also described as being “clothed with yellowish white upstanding hairs”. Kurahashi & Tan considered *Wilhelmina* “a member of Calliphoridae”, but found that “the [t]axonomical position and relationship remain problematic”. I suggest that the genus be transferred to the Phumosiinae, in view of the “upstanding hairs” on the katatergite and the presence of small setulae on the facial plate.

### Appendix 3. List of material examined

*Adichosina eos* Zumpt – CNC

*Adichosina munroi* (Curran) – BMSA, MZLU

*Adichosina thoracica* (Villeneuve) – CNC

*Adichosina* sp. (in *eos*-group) – CNC

*Adichosina* sp. – CNC

*Auchmeromyia senegalensis* (Macquart) – BMSA, KR, ZMUN (as *luteola* F.)

*Auchmeromyia bequaerti* (Roubaud) – BMNH, BMSA

*Auchmeromyia boueti* (Roubaud) – BMNH

*Auchmeromyia choerophaga* (Roubaud) – BMNH

*Auchmeromyia kurahashi* Lehrer – TAU (holotype)

Note. The holotype of *Auchmeromyia kurahashi* Lehrer, 2005b: 46 from Kenya, Nairobi (in TAU), carried a big plastic vial attached to the pin. In it were three genital pieces in glycerol: (1) An unattached syncercus; (2) epandrium + bacilliform sclerites + surstyli all in one piece; (3) the aedeagus. Lehrer's figure of the latter is not quite correct when it comes to the ventral distal lobes. They are sclerotised centrally as in Patton's figure in lateral view (Patton 1935: 204, fig. 3a). In ventral view, the distal lobe is heart-shaped with a central sclerotisation in each half with a clear V-shaped area in the middle, also fitting well with Patton's figure (1935: 204, fig. 3d). The distiphallus of the holotype is somewhat compressed dorsoventrally compared to Patton's drawing. The holotype belongs in my opinion to *Auchmeromyia senegalensis* (Macquart), **syn. nov.**

*Bengalia akamanga* (Lehrer) – MSNM

*Bengalia floccosa* (Wulp) – BMSA, KR, MNHN (as *mercenaria* Séguy)

*Bengalia gaillardi* Surcouf & Guyon – ZMUN (as *spurca* B.B.)

*Bengalia minor* Malloch – MNHN (as *lepineyi* Séguy)

*Bengalia peuhi* Villeneuve – BMSA, MNHN (as *bekilyana* Séguy), ZMUN

*Bengalia racovitzai* (Lehrer) – MRAC

*Bengalia seniorwhitei* (Lehrer) – MRAC, ZMUC, ZMUN

*Bengalia smarti* (Lehrer) – BMSA, MRAC

*Bengalia spinifemorata* Villeneuve – MRAC

*Bengalia wangariae* (Lehrer) – MRAC

+ numerous other species (cf. Rognes 2009a, 2009b, 2011b)

*Booponus indicus* (Austen) – BMNH

*Booponus intonsus* Aldrich – BPBM

*Coganomyia ornata* Dear – BMNH (holotype and two paratypes)

*Cordylobia anthropophaga* Blanchard – BMSA, KR, MZLU

*Cordylobia ebadiana* Lehrer & Goergen – TAU (holotype)

Note. The holotype of *Cordylobia ebadiana* Lehrer & Goergen, 2006: 17 from Togo, Kloto (in TAU) carried a big plastic tube on the pin with the right hind leg + genitalia, the latter were completely dried out. Contents were removed from vial, and the leg transferred to a fresh big plastic vial. Genitalia consisted of (1) a poorly dissected, flattened and folded cerci + surstyli + epandrium part, and (2) a hypandrium + aedeagus + gonites + phallapodeme + ejaculatory sclerite part, all dry and distiphallus surrounded by a layer of greyish substance typical of genitalia prepared by Lehrer, probably consisting of a kind of glycerol jelly. Dried genitalia were moistened with KOH and subsequently transferred via water and alcohol to glycerol in a glass microvial.

Frons is stated by Lehrer & Goergen (2006: 17) to measure 1/3 of the width of an eye (“[l]e front, vue du dessus et au lieu le plus étroit, mesure 1/3 de la largeur d’un œil.”) (the same information is repeated in key on p. 18), but that is an error. I have measured the frons of the holotype of *C. ebadiana* to be 0.74x width of an eye (0.27x head width), and of a *C. rodhaini* male in BMNH to be 0.60x width of an eye (0.23x head width). The



holotype is somewhat teneral, as evidenced by the incompletely everted face, and crimped lateral parts of thorax and base of wings. The hind tibia is somewhat curved, as described by Zumpt (1956) for *C. rodhaini*. In view of the poorly dissected and flattened nature of the piece consisting of the epandrium, cerci and surstyli I would not trust the drawings of these parts (Lehrer & Goergen 2006: 17, figs. 5A, B) to be representative of the parts in natural position. The holotype was collected in Togo, at Kloto, on 11.VIII.2003 (by G. Goergen). At exactly the same time and place Goergen collected a male specimen which was identified by Lehrer & Goergen as *C. rodhaini* Gedoelst. Rather than assuming that the material consisted of two species, I think it reflects individual differences. Note also that Lehrer & Goergen did not study any type material of *Cordylobia rodhaini* so they could not be sure what name to apply to what species, should two species actually be involved here. The holotype of *Cordylobia ebadiana* belongs in my opinion to *Cordylobia rodhaini* Gedoelst, **syn. nov.**

*Cordylobia rodhaini* Gedoelst – BMNH

*Cordylobia roubaudi* Villeneuve – BMNH (formerly in *Neocordylobia*), BMSA

*Cordylobia ruandae* Fain – BMNH

*Eggisops pecchioli* Rondani – KR

*Euphumosia evittata* Torgerson & James – BPBM

*Euphumosia papua* (Guérin-Méneville) – BPBM

*Hemigymnochaeta apicifera* Curran – BMNH

*Hemigymnochaeta gogoiana* Lehrer – BMSA

*Hemigymnochaeta laticeps* Zumpt – BMNH

*Hemigymnochaeta unicolor* (Bigot) (as *lutea* Corti) – ZMUN

*Hemigymnochaeta unicolor* Bigot – BMNH

*Hemigymnochaeta varia* (Hough) – BMNH, ZMUN

*Hemigymnochaeta* sp. – BMNH, BMSA

*Hemipyrellia ligurriens* (Wiedemann) – KR

*Mafikengia ciliata* **sp. nov.** – ZMUC

*Mesembrinella bicolor* (Fabricius) – KR

*Ochromelinda thoracica* Villeneuve – CNC

*Onesihoplisa umbrosa* Villeneuve – CNC, NMW

*Pachychoeromyia praegrans* (Austen) – BMSA

Note. Lehrer (2011: 22) described a new species *Pachychoeromyia kanemia* on the basis of a male from Nigeria which he designated as holotype on p. 21. I do not accept this nominal species as separate from *P. praegrans* on the basis of Lehrer's descriptions. Since Lehrer did not study any type material of *P. praegrans* he could not be sure what name to apply to what species, should two species actually be involved here. Thus I treat *P. kanemia* Lehrer as a synonym of *P. praegrans*, **syn. nov.**

*Pericallimya majuscula* Villeneuve – CNC

*Pericallimya perlata* (Walker) – BMSA

*Pericallimya spinigera* Villeneuve – CNC

*Pericallimya* sp. – BMSA

*Phumosia coomani* (Séguy) – KR

*Phumosia indica* (Surcouf) – CNC

*Phumosia lutescens* (Villeneuve) – KR, ZMUC

*Phumosia testacea* (Senior-White) – CNC

*Silbomyia fuscipennis* (Fabricius) – BMNH

*Stilbomyella nitens* Malloch – BMNH

*Termitoemus marshalli* Baranov – BMNH (holotype and two paratypes)

*Termitocalliphora nana* Zumpt – CNC

*Tricyclea bifrons* Malloch – BMNH

*Tricyclea fasciata fasciata* (Macquart) – BMNH

*Tricyclea fasciata ferruginea* (Wulp) – BMNH, BMSA

*Tricyclea perpendicularis* Villeneuve – BMNH

*Tricyclea semicinerea* Bezzi – BMSA

*Tricyclea tauffliebi* (Zumpt) **comb. nov.** – BMNH (as *Neoordylobia tauffliebi*)

*Tricyclea* sp. – BMNH, BMSA, CNC

*Tricycleala maculipennis* Villeneuve – CNC

*Verticia fasciventris* Malloch – ZMUC

*Verticia orientalis* Malloch – ZMUC

*Verticia* spp. – BMNH (one male from Sarawak dissected by myself in 1985 and misidentified by me as “*Verticia orientalis* Malloch”; two other undissected specimens)

*Zernyiella dubia* Zumpt – NMSA

Note. *Zernyiella dubia* was described by Zumpt (1956: 93) from three males borrowed from NMW. The locality data given by Zumpt were “[Ugano, Matengo Hochl. wsw. Songea, Tanganyika Terr., 15–1.700 m, 11–20.III.1936 (3 ♂♂ leg. ZERNY)]”. No holotype or paratypes were designated in the original publication, but in the descriptive text (p. 94) it is stated that the T4 was furnished “in one paratype with 2 pairs of median discals” suggesting he had labelled the specimens with holo- and paratype labels. No syntypes are now present in NMW (Peter Sehnal, correspondence January 2011). One syntype has been recovered in NMSA. It is labelled: (1) Ugano / 15–1700m [print on white label]; (2) Tanganyika-Terr., / Matengo-Hochland / wsw. v. Songea, / 11.–20.III.’36.Zerny [print on white label]; (3) PARATYPE [black print on yellowish label]; *Zernyiella* ♂ / *dubia* n. sp. / det. Zumpt 54 [in Zumpt’s handwriting, label with a blue stripe a little above middle]; (4) NMSA-DIP / 56535 [black print on white label]. The specimen has only a single pair of median discal setae on T4 so it cannot have been the specimen mentioned by Zumpt (1956: 94), but it fits the original description. It was not dissected by Zumpt, so it cannot have been the basis for Zumpt’s fig. 54. The specimen is obviously one of the original syntypes. In order to fix the interpretation of the name I have labelled it and here designate it as lectotype of *Zernyiella dubia* Zumpt, 1956. It has been dissected by me. The genital parts and ST1–5 are kept in glycerol in a glass microvial. The T1–5 are glued to a piece of card on the pin above the labels.

#### Appendix 4. Description of uterine larvae of *Ochromelinda thoracica* Villeneuve by Krzysztof Szpila.

Material examined. 6 larvae, obtained from a dissection by Knut Rognes of a dry pinned female specimen labelled "Ruenzori Mts / 2450m UGANDA / Dec. 23, 1972 / H. Falke in CNC.

First instar of *Ochromelinda* (Figs. 116–123) is typical for the Calyptratae in having a distinct pseudocephalon, three thoracic segments, seven abdominal segments and terminal anal division. Pseudocephalic lobes have an antennal complex situated typically on anterodorsal surfaces. Antennal dome is elongated, with rounded tip, antennal basal ring is low or absent. Maxillary palpus is shaped as a flat disc clearly distinguished from surrounding surface of pseudocephalon. Number, distribution and size of sensillae resemble pattern observed in necrophagous Calliphoridae. Sensillae of ventral organ are situated level with integument. Oral ridges are absent. Surface of pseudocephalon is smooth without ridges or warts. SEM pictures revealed existence of dense cuticular ridges on whole surface of thoracic and abdominal segments. However, it is difficult to decide whether this character is an artifact caused by the previous treatment of dissected female abdomen with strong KOH or not.

Cephaloskeleton is clearly visible through cuticle. It is composed of mouthhooks, labrum, intermediate sclerite and basal sclerite consisting of parastomal bars, vertical plate and ventral and dorsal cornua. Labrum is strong, gradually tapered to a sharp tip and curved upward. The basal part of labrum has a strong process with tip equipped with numerous small spines. Mouthhooks are strong with broad basal parts and sharp, tapered anterior parts curving downward. Intermediate sclerite is massive, strongly sclerotised and partly hidden behind parastomal bars in lateral view. In ventral view intermediate sclerite has a rectangular shape. Parastomal bars are long and massive, well sclerotised. Vertical plate is broad, about twice as wide as dorsal cornua and about as wide as posterior part of ventral cornua. Dorsal bridge is absent. Phragma between ventral cornua is slightly sclerotised.

All thoracic segments have anterior spinose bands. Band on the first thoracic segment is incomplete, 6–7 rows of spines are present on ventral surface, the width of band gradually decreases upwards on lateral surfaces with dorsal surface without spines. Spines are strongly sclerotised and hook-shaped with single tips directed toward posterior end of the body (retracted edges of segments of larvae may create impression of anterior direction of spines). Size of spines is variable, the biggest spines are located on the ventral surface, most anteriorly. Anterior spinose band on the second thoracic segment is complete but narrow (4–5 rows of spines) and spines are very small and with conical shape. Third thoracic segment is also with complete anterior spinose band, which is very broad (9–11 rows of spines) with shape and arrangement of spines resembling spinulation on the first thoracic segment (the biggest spines are situated the most anteriorly on ventral surface).

Abdominal segments except the first one are without spinose bands. Spinulation on the first abdominal segment is identical with the one observed on the third thoracic segment (only anterior spinose band is developed). Anal division is also without anterior spinose band. Anal tuft consists of several small spines. Several other small conical spines are also located on posterior surface of the anal division below posterior spiracles. Hair-like spines around spiracular field are absent. Posterior spiracles are with typical V-shaped slits.

#### Comparative analysis.

According to morphological details the highest level of similarity to the larva of *Ochromelinda* is observed in the first instar of *Eggisops pecchiolii* Rondani (comparison with description given by Thompson 1921 and original material). Larvae of both species share the following characters:

- 1) antennal complex with elongated antennal dome and low/absent basal ring;
- 2) strong labrum curving upward;
- 3) labrum of *Ochromelinda* firmly fused with the basal (= tentoropharyngeal) sclerite like in *Eggisops* and *Melinda*;
- 4) presence of a dorsal process on the basal part of labrum;
- 5) strong mouthhooks with a broad basal part and a narrow anterior part curving downward and gradually tapering to sharp tip;
- 6) massive parastomal bars and intermediate sclerite; and
- 7) reduced spinulation on abdominal segments and anal division.

## About the author

Knut Rognes was born in 1943 in Oslo, Norway. He studied botany and chemistry at the University in Oslo and zoology at the University in Bergen, where he was employed for nine years teaching comparative vertebrate anatomy. He got his Master's degree in 1970 on the morphology of the head skeleton in wrasses (Teleostei). Rognes was employed at the University in Stavanger in 1976 and has worked as a science teacher mainly for students in early childhood education since then. His interest in entomology was awakened when studying flies captured in his garden. He got his Doctor's degree in 1988 on a revision of North European blowflies with contributions to the phylogeny of the genus *Pollenia* Robineau-Desvoidy (Diptera: Calliphoridae). Rognes is now partly retired. He has been working on calypterate Diptera for more than 30 years, in later years mostly on Calliphoridae.