First-instar larva of *Palaestra rufipennis* (Westwood, 1841) and other Australian blister beetles (Coleoptera, Meloidae, Nemognathinae)

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Abstract  
This is the first study of Australian blister beetle larvae. The first-instar larva of one species of the endemic genus *Palaestra* Laporte de Castelnau, 1840, is described as well as those of other phoretic species without adult association and consequently unplaced to genus. Two main larval types (Groups 1 and 2) are recognised, as are distinct morphotypes within each group. Although both groups are assign able to the Nemognathinae, they are characterised by traits not paralleled by subfamily representatives from other regions of the world. Group 1, which includes *Palaestra*, is the more distinctive, whereas Group 2 shares most characteristics with members of the cosmopolitan tribe Nemognathini. A tabular comparison of larval groups and morphotypes is included.

Key words  
larval morphology, phoresy, systematics, triungulin.

INTRODUCTION

The Meloidae is a widespread family of Tenebrionoidea found throughout the World except New Zealand, Antarctica and most Polynesian islands. It includes more than 120 genera and ca 3000 species (Bologna and Pinto 2001). This family is well known for its production of cantharidin, a chemical defensive substance and hypermetabolic larval development, common to all taxa except possibly the basal subfamily Eleticinae (Bologna 1991; Pinto et al. 1996; Bologna et al. 2001). Phylogenetic studies using morphological and bionomic characters (Bologna & Pinto 2001) recognised four subfamilies, Eleticinae, Nemognathinae, Tetraonycinae and Meloinae, whereas analyses based on molecular and combined characters (Bologna et al. 2008) recognised only three, the tetraonycin e being referred as a tribe in the Meloinae.

Meloidae are most diverse in tropical and subtropical zones, particularly in arid and semiarid environments. The most widespread subfamily, Nemognathinae, is the only meloid group in Australia, where it is represented by two of the three tribes recognised by Bologna and Pinto (2001), the Horiini and Nemognathini.

The approximately 65 described species of Australian Meloidea are virtually unknown. Only 25 taxonomic papers have been published on this fauna, the latest almost one century ago (Lea 1914, 1917; Blair 1920). Thus far the only genera recorded from Australia are *Horia* Fabricius, 1787 in the tribe Horini, and *Palaestra* Laporte de Castelnau, 1840, *Palestrida* Hope, 1842 and *Zonitis* Fabricius, 1775 in the Nemognathini. Studies showing the presence of additional horiine and nemognathine genera common to other Gondwanian areas, as well as a complex of possibly new genera close to *Palaestra* will be the focus of a separate contribution (MA Bologna et al. unpublished 2007–2010). Preliminary work also suggests that there remains a considerable number of undescribed species on the continent.

The morphology of meloid first-instar larvae (also called triungulins) has been useful for phylogenetic studies (e.g. Cros 1940; MacSwain 1956; Bologna & Pinto 2001). All Nemognathinae triungulins are phoretic with the possible exception of the relatively plesiomorphic genus *Stenodera* Eschscholtz, 1818 (Bologna et al. 2002), and consequently their morphology is less heterogeneous than in the nominate subfamily (e.g. Bologna & Pinto 2001; Di Giulio & Bologna 2007). Triungulins of Australian blister beetles have never been described specifically. Silvestri (1920) cited, and superficially figured and described a phoretic triungulin collected near Adelaide on a Zygentoma of the family Nicoletiidae (*Subbrinimura excelsa* (Silvestri 1920)). A biological association of blister beetles with silverfishes is unknown and this record could have been accidental. We failed to locate this triungulin in the Silvestri collection at the Portici University (Napoli). More recently Houston (1984, 1987) reported triungulins phoretic on Australian Stenotritidae bees. These larvae, incorporated by Bologna and Pinto (2001) in their phylogenetic study of Meloidae (as sp. I), are described here together with other larvae of Nemognathini collected in the field, and of *Palaestra rufipennis* (Westwood, 1841) obtained recently from eggs. Larvae from one of these field collections also were incorporated in the 2001 phylogenetic study (as sp. K).

The main purposes of this study are to describe and illustrate the morphology of all available first-instar larvae of Australian Meloidae and to compare them with nemognathine
Materials and Methods

Descriptions of first-instar larvae are based on the following material deposited in the M.A. Bologna collection (CMB) (Roma, Italy), and the collection of the University of California (UCR) (Riverside, CA, USA).

Palaestra rufipennis (Westwood, 1841): AUSTRALIA: Queensland, Main Range Nat’l Park, Cunningham’s Gap Area, Mt. Cordeaux; XII-8-2002, 28°03′S, 152°24′E, J. George, A. Owen & J. Munro, colls. Site #45; larvae hatched from egg mass in the lab. CMB: vial 474 (ca 20 larvae); stub 147 (8 larvae); slides 374, 375, 376 (2 larvae each). UCR: 2 slides (2 larvae each). The identification of this species is based on Fairmaire (1880) and Blair (1920). Adults were collected feeding on Pimelea (Thymelaeaceae). A1: AUSTRALIA: Western Australia, Kununurra, 10 km NE, Mulligans Lagoon Rd., III-23-1991, s.s. (= screen sweeping), J.D. Pinto. CMB: slide M180. Referred to as ‘species K’ in Bologna and Pinto (2001). - AUSTRALIA: Western Australia, Kununurra, 10 km NE, Mulligans Lagoon Road., III-23-1991, s.s., J.D. Pinto. UCR: one slide (JP Coll. A). B1: AUSTRALIA: Western Australia, Hyden, 75 km E, X-24/27-1985, T.F. Houston, coll.; one larva attached to hair of bee Ctenocolletes smaragdinus (Smith) female. CMB: slide M323. Referred to as ‘species H’ in Bologna and Pinto (2001). - AUSTRALIA: Western Australia, Wannoo, 13 km S, VIII-24/28-1984, T.F. Houston, coll.; two larvae attached to hair of adult bee Ctenocolletes nicholsoni (Cockerell) female. CMB: slides M274, M324. - AUSTRALIA: Western Australia, Wannoo, 13 km S, 26°49′S, 114°37′E, VIII-24/28-1984, T.F. Houston & B. Hanich, colls. – specimen attached to hair of bee: Ctenocolletes tigris Houston (No. 307). UCR: one slide (JP Coll.C). C1: AUSTRALIA: Western Australia, East Yuna Reserve, 34 km WNW, Mullewa, VIII-28-1984, T.F. Houston 522.1 & B.P. Hanich, colls. One larva attached to hair of adult bee Ctenocolletes nigricans Houston. CMB: vial 311, Slide M454. - AUSTRALIA: Western Australia, East Yuna Reserve, 34 km WNW, Mullewa, VIII-28-1984, T.F. Houston 522.1 & B.P. Hanich, colls; one larva attached to hair of adult bee Ctenocolletes albomarginatus Michener (No. 312). UCR: (JP Coll. B). C2: AUSTRALIA: 390 km S Carnarvon, W. A. IX-7-1981, L.P. Kelsey, coll. sweeping heath: one larva attached to posterior leg of ‘Zonitis purpureipennis’ Waterhouse, 1875. CMB: vial 494, Slide M455. C3: AUSTRALIA: Western Australia, Wiluna, 17 km W, VII-28-1983, T.F. Houston 522.1 & R.P. McMillan, colls; one larva attached to hair of adult bee Ctenocolletes centralis Houston. CMB: Slide M331. C4: AUSTRALIA: Western Australia, East Yuna Reserve, 34 km WNW, Mullewa IX-13/16-1984, T.F. Houston 522.1 & B.P. Hanich, colls; one larva attached to hair of adult bee Ctenocolletes centralis. CMB: Slide M272. D1: AUSTRALIA: Northern Territory, 15.58S 129.02E, GPS Bail Me Up Ck., 26.5 km S of Jarrnarm, Keep River Nat’l Pk., VI-9-2001, A. Calder (ex Malaise trap); one larva attached on mouthparts of Zonitis sp. CMB: vial 491, slide M456. D2: AUSTRALIA: Data as for D1. CMB: Vial 492, Slide M457. D3: AUSTRALIA: Data as for D1. CMB: Vial 493, Slide M458.

All larvae listed above (except several P. rufipennis remaining in 70% ethanol) were mounted on slides in Canada balsam. Morphological analysis and drawings were performed with a light microscope Olympus BX51 equipped with drawing tube. Some P. rufipennis were mounted on stubs, and after critical point dehydration and gold sputtering, were examined at a scanning electron microscope Philips XL30 (Interdepartmental Laboratory of Electron Microscopy, L.I.M.E., University ‘Roma Tre’, Roma, Italy). Measurements of larvae in the descriptions are means based on the specimens of each taxon mounted on slides. The nomenclature employed for larval structures follows MacSwain (1956) and Bologna and Pinto (2001). Notational conventions suggested by Selander (1990) are adopted for certain characters of larval chaetotaxy.

Results

Descriptions of the first-instar larvae

All larvae described below currently are assignable to the tribe Nemognathini. The following are reported below: (1) diagnoses of groups of species; (2) diagnoses of morphotypes; (3) complete description of P. rufipennis; and (4) selected characters (Appendix I) for triungulins of unidentified species.

GROUP 1. Included here are morphotypes A and B.

Diagnosis. Head without strongly sclerotised tentorium; epi- cranial suture present, well developed; longest basal seta of claw elongate, extending beyond half claw length; line of dehiscence present on pro- and mesonotum; spiracles on abdominal segment VIII annular, simple, not differing substantially from those on other segments; tergal setae short but not minute, present along posterior tergal margin.

Morphotype A. Included here are P. rufipennis (Figs 2a–h,3a,5) and species A1 (Figs 1a,4a,5).

Diagnosis. Body elongate, subnavigular, similar to first-instar larvae of Horiini (Bologna & Laurenzi 1994; Bologna & Pinto 2001). Head suboval or rounded, widest at middle just behind
stemmata; basal elevation present or absent; neck (portion of head posterior to basal elevation) absent or very short; gula short, V-shaped; antennomeres increasing in length from A1 to A3; sensory organ on second joint reduced to a disk-like plate placed on oblique apical platform; terminal seta of antenna about as long as head; spiracles of abdominal segment I dorsal, the remaining dorsolateral in position; spiracles on abdominal segment VIII annular, simple, similar in shape to those on segments I–VII; caudal setae elongate.

*Palaestra rufipennis* (Westwood, 1841)

**Diagnosis.** Head slightly wider than anterior part of pronotum; basal elevation present; neck short; palpomere MX2 twice as long as MX1, MX3 twice as long as MX2; ecdysial line present on pro-, meso- and metanotum.

**Description.**

Habitus and microsculpture. Triungulin elongate, about 3.7 times as long as greatest width (on pro- mesothorax), evenly narrowed posteriorly. Head, legs, terga and abdominal sterna well sclerotised. Colour light-brown. Cuticle of sclerotised areas of the body with irregular polygonal meshes, scale-like and imbricate; meshes of sterna and laterotergites with elongate, spine-like posteriorly directed protrusions giving a microserrate aspect to the posterior margins.

Head (Fig. 2b–d). Cephalic capsule transverse, sub-oval, widest just behind stemmata, broadly rounded on sides; dorsal surface regularly convex, with truncate anterior margin and thin basal elevation; cephalic capsule evenly narrowing behind basal elevation. Epicranial suture visible, stem elongate, frontal arms not reaching antennal base. Two subequal stemmata present on each side (Fig. 2b), the dorsal one more convex and slightly posterior to the ventral one. Frons fused to clypeus without apparent suture; labrum and anterolateral sides of frontoclypeus folded ventrally and partially margined anteriorly, fitting the host seta, and partially covering the mandibles. Frontoclypeal row (FCR) with three pairs of setae, the lateralmost (FCR3) nearly ventral due to folding of anterolateral frontoclypeus and slightly shorter than FCR2; FCR1 much shorter than the others; one sensory pit behind FCR3 and a larger pair of pits just behind FCR1; four pairs of frontal setae posterior to FCR: lateralmost longest, slightly anterior to antennal insertion, three shorter setae arranged longitudinally. Each epicranial plate with five short setae (including ocular seta) around each pair of stemmata (Fig. 2b); ocular seta unmodified, subequal to others, placed anterior to stemmata and to ocular sensory pit; ocular sensory pit slightly anterior to stemmata; four pairs of setae mesodorsally anterior to basal elevation, one pair of large pits displaced anteriorly of medial pair; three minute setae and one small pit posterior to basal elevation. Labrum with six pairs of setae and four pits; epipharynx with a dense tuft of long thick setae, appearing as a tangled assemblage under the light microscope. Mandibles ventral in position, short, falcate (Fig. 2c,e), moving anteriorly in a slightly oblique plane; base of mandibles broad, with a large ventral condyle; dorsal ental surface comb-like, produced into seven long, apically blunt, parallel, finger-like ridges; lateral margin with two setae on basal half and one large pit mesodorsally. Maxillae (Fig. 2b–d) with stipes very short, with two rows of setae: apical row (first row) with two setae, lateral seta short, medial seta extremely long, slightly longer than head capsule, spatulate at apex; basal row (second row) with two short setae and two pits; cardo unsclerotised, cardinal seta present; mala simple, lobiform, with five–six moderately long spiniform apical setae; maxillary palpi long, three-jointed; palpomere I short, II twice as long as I, III twice as long as II, with a small apical sensory area bearing a crown of seven–nine conical papillae and a medial conspicuous stick-like sensory appendix three times as long as others; segment I with one ventral pit; segment II with two ventrolateral subequal setae (one lateral and one medial); segment III with two mesoventral setae and one slender, elongate, lateral digitiform sensillum. Antennae (Fig. 2f) about half as long as head, anterolaterally directed; segment I short, ring-like, with one dorsal and one lateral sensory pits; segment II subcylindrical, about twice as long as I, slightly asymmetrical with four short spine-like apical setae (two dorsolateral, two ventral), and one dorsal pit; sensory appendix on second joint reduced to a disk-like plate laying obliquely at ventrolateral apex; segment III slender, cylindrical, about twice as long as II, with a long apical seta (antennal seta) about as long as head, and four short
subapical spine-like setae, three of these dorsolateral and one medial in position, also with one basolateral pit. Labium with gula fused to submentum forming a V-shaped gulamentum, weakly sclerotised, without setae; mentum with two pairs of small setae and one pair of pits basally; prementum ventrally sclerotised, membranous dorsally, with three pairs of setae: two short ventral pairs, and one short spindiform pair (ligular setae) dorsal to the insertion of palpi; ligula absent; hypopharyngeal bracon absent; labial palp small (Fig. 2c) with joints very short, cylindrical; segment II about twice as long as I, with one elongate apical sensory appendix surrounded by six smaller papillae.

Thorax (Fig. 2a,b). Segments transverse, slightly broader than head, with terga well sclerotised, subequal in width, slightly decreasing in length from pro- to metanotum; pronotum subtrapezoidal with sides diverging slightly posteriorly; meso- and metanotum subrectangular, slightly decreased in length above, with sides straight; ecdysial line very thin, complete on pro-, meso- and metanotum. Pronotum twice as wide as long; each half of pronotum with 16 minute setae and four pits placed approximately along three transverse, subparallel rows; anterior row (AR) with six setae and two pits; middle row (MR) with three small setae; posterior row (PR) with seven setae and two pits; prosternum not sclerotised, sterna of meso- and metathorax slightly sclerotised medially; prosternum with nine pairs of small setae: three pairs longitudinally arranged medially (two anterior and one long between the procoxae) and six around base of coxae. Mesonotum 2.5x as wide as long; AR with five setae and one medial pit; MR with five minute setae; PR with six minute setae and two pits; mesosternum with similar setal pattern as prosternum. Setae of metathorax similar in number, position and relative size as those on mesothorax.

Fig. 2. *Palaestra rufipennis* first-instar larva: (a) habitus, right lateral view; (b) head and pronotum, right lateral view; (c) head, ventral view; (d) head, frontal view; (e) left mandible, dorsal view; (f) right antenna, anterior view; (g) fore leg, posterior view; (h) abdominal spiracle II. Scale bars: 200 µm (a); 50 µm (b–d,g); 20 µm (e,f); 5 µm (h).
Legs (Fig. 2a,g). Coxae short and broad, subtriangular, obliquely truncate and unsclerotised at apex, with six spine-like, subapical setae; seven minute setae and one basal pit; trochanters without setae basally but with medial belt of six–seven pits and four setae: the medial, subapical seta on pro- and mesotrochanters long, slightly longer than tibiotarsus, the equivalent seta on metatrochanter shorter than tibiotarsus and spine-like; femora slightly enlarged from base to apex, slightly compressed laterally; profemur shorter than the others, meso- and metafemora similar in length; femora each with six setae and two pits, femoral seta II extremely elongate, much longer than femur itself and apically spatulate, this seta increasing in length from pro- to metafemora; femoral seta I much shorter than II; tibiotarsi cylindrical, increasing in length and narrowing from pro- to metathorax, with one ventral longitudinal row of three–four spine-like setae and four–five shorter setae; claws (Fig. 2g) curved, most abruptly so at base, slightly decreasing in length from pro- to metathorax; two elongate pretarsal setae near base of each claw, anterior seta about half as long as claw, posterior seta about half one-third claw length.

Abdomen (Figs 2a,3a). Gradually tapering from base to apex, maximum width at segment I; terga rectangular with entire posterior margins; laterotergites completely fused with medial terga; terga of segments I–VIII with three transverse rows of setae, anterior (AR), medial (MR) and posterior (PR); each lateral half of tergum I–VII with the following setation: AR with two small setae (three on tergum I) and one pit, MR with four short setae, PR with six short setae; tergum IX with two very elongate caudal setae on PR which are about as long as the last five abdominal segments. Sterna well sclerotised, entire, subrectangular; setation of sterna as follows: AR with two pairs of minute setae obliquely lined medially, PR with four pairs of spine-like, equally spaced setae (from medial to lateral pairs 1–4) to form a row along posterior margin of sclerites: pair 4 shortest, 3 longest, 1 slightly longer than 2; PR of sternum IX with 3 pairs of short setae. Abdominal apex (segment X or pygopod) membranous (Fig. 3a).

Spiracles. All spiracles consisting of a rounded or suboval plate of thin, smooth and flat cuticle that overlays a wide atrium, with the peritreme reduced to a very small hole; peritreme of mesothorax slightly wider than that on abdominal segments; abdominal peritremes I–VIII (VIII not modified) open, similar in size and shape. Mesothoracic spiracle ventrolateral in position; abdominal spiracle I (Fig. 2h) slightly bulged, dorsolaterally placed on posterior part of laterotergites; spiracles II–VIII lateral.

Species A1 (see Figs 1a,4a,5 and Appendix I).

Morphotype B. Included here is species B1 (Figs 1b,4b,5).

Diagnosis. Body short, navicular; head subtriangular or trap- ezoidal, anteriorly truncate, with maximum width at base just anterior to basal elevation; basal elevation present; neck short; gula short, V-shaped; antennomere relative lengths: A2 longer than A1 and A3; sensory organ inconspicuous on ventrolateral side of antennomere II; terminal seta of antenna shorter than head; maxillary palpomeres gradually increasing in length from MX1 to MX3; line of dehiscence present on pro-, meso- and metanotum; spiracles of all abdominal segments dorsolateral in position; caudal setae short.

Species B1 (see Figs 1b,4b,5 and Appendix I).

GROUP 2. Included here are morphotypes C and D.

Diagnosis. Head with strongly sclerotised, complex tento- rium; epicranial suture absent except basal stem vestigial in some; basal elevation present; antennomere relative lengths: A2 longer than A1 and A3; sensory organ of antenna inconspicuous on ventrolateral side of antennomere II; line of dehis- cence absent on pronotum; longest basal seta of claw short, not extending to half claw length; spiracles of all abdominal segments dorsolateral in position; spiracles on abdominal segment VIII placed at apex of a cone-shaped protuberance, very different from those on segments I–VII; tergal setae minute, posterior row along the tergal margin lacking.
Morphotype C. Included here are species C1, C2, C3, C4 (Figs 1c, 4c, 5).

Diagnosis. Body short, navicular; head subtriangular, anteriorly pointed, with maximum width at base just anterior to basal elevation; neck long; gula elongate and subparallel; terminal seta of antenna subequal or slightly longer than head; maxillary palpomere relative lengths: MX2 twice as long as MX1, MX3 twice as long as MX2; caudal setae very short.

Species C1, C2, C3, C4 (see Fig. 5 and Appendix I).

Morphotype D. Included here are species D1, D2, D3 (Figs 1d, 4d, 5).

Diagnosis. Body thin and elongate, subnavicular; head elongate and slender with maximum width at base; neck long; gula extremely long and narrow, almost reduced to a suture; terminal seta of antenna shorter than head; maxillary palpomere relative lengths: MX2 longer than MX1 and MX3; caudal setae elongate.

Species D1, D2, D3 (Fig. 5 and Appendix I).

DISCUSSION

Two larval groups, possibly representing two lineages, are recognised (Fig. 5). The first (Group 1), characterised by pleiomorphic traits, includes two morphotypes: morphotype A (with the genus *Palaestra* and species A1) and morphotype B, with a single species (B1). It is likely that one or more genera in addition to *Palaestra* are included. The second assemblage (Group 2), characterised by more derived features, includes two distinct morphotypes, C apparently with four species, and D with three. Morphological differences suggest that at least two taxa are represented.

The prominent tooth-like transverse ridges of the mandibles and two pairs of ocelli clearly assign Group 1 larvae to the Nemognathinae as characterised by MacSwain (1956). However, assignment to the tribe Nemognathini remains tentative. These larvae differ from all known Nemognathini in lacking modified spiracles on abdominal segment VIII and from most in having hair-like caudal setae (Fig. 3a). Both features are believed to be primitive for the subfamily. Other primitive traits, the presence of a well-developed epicranial suture and a line of dehiscence on the pronotum (Fig. 1a,b), also occur in several genera in the subfamily. Group 1 larvae share these traits with the Horini, considered a subfamily by MacSwain (1956) and only a tribe in the more recent literature, but they lack toothed tarsal claws, the only clearly derived larval feature of horiines. Bologna and Pinto (2001) placed clade L, which included two of the group species studied here (A1, B1), in the Nemognathini based on the presence of a dense tuft of setae on the epipharynx (char. 20), a feature absent in the Horini. However, the monophyly of Group 1 is inadequately supported. The only character believed to be

![Fig. 4. Head, ventral view: (a) morphotype A; (b) morphotype B; (c) morphotype C; (d) morphotype D. Scale bars: 0.1 mm.](image-url)
derived is the dorsal position of abdominal spiracle I. This condition, known to occur in several genera of Meloinae, has not been reported in other nemognathines. Other features supporting monophyly of clade L (which would now also include Palaestra) in Bologna and Pinto (2001) either are reversals (chars. 17, 46, 49) or now are known in other nemognathine genera (char. 85). The study of adult traits and additional larvae should assist in the taxonomic positioning of this assemblage. What is clear is that the larvae of Group 1 species are thus far unique to Australia.

Group 2 larvae are more consistent with known Nemognathini. As in all genera described thus far the spiracles of abdominal segment VIII are placed on projecting horn-like evaginations (Fig. 3b) (MacSwain 1956; Bologna & Pinto 2001). Within the tribe, Group 2 appears to be most similar to genera which MacSwain placed in the Zonitides (Zonitis, Gnathium Kirby, 1818, Leptopalpus Guérin-Méneville, 1834, and Pseudozonitis Dillon, 1950), and Bologna and Pinto in clade K. In this assemblage, as in all Group 2 representatives, the epicranial suture is absent as is the line of dehiscence on the pronotum (Fig. 1c,d). The number of tooth-like transverse ridges on the mandibles also is reduced (<5) (Fig. 4c,d). The distinct caudal setae of species of Group 2 (Figs 1d,5) however separates it from larvae thus far described in these other genera (Fig. 3b). This character may represent a primitive condition in these Australian Nemognathini of clade K that also occurs in some Palaeartic genera such as Sitaris Latreille, 1802 and Apalus Fabricius, 1775.

Among the larvae studied here only those of Palaestra are identified to genus. The only other genera reported for Australia thus far are Horia (Horini), Palaestrula and Zonitis (Nemognathini), with most Australian species placed in the latter

Fig. 5. Summarising plate of Australian nemognathine larvae (mounted on slides), representative of the recognised morphotypes A–D, including Palaestra rufipennis and undetermined morphospecies.
genus. Ongoing studies of adults (A Bologna, JD Pinto and F Turco unpubl. data 2007–2010) document the presence in Australia also of Synhoria Kolbe, 1897 (Horiini) and Zonitoschema Péringuey, 1909 (Nemognathini). They show clearly that many of these species (Z. purpureipennis, Z. violacea Hope, 1842, Z. violaceipennis Waterhouse, 1875, and many others) are placed inappropriately in Zonitis and instead are allied more closely to Palaestra. Morphotypes A and B (Group 1) probably represent this lineage which is known currently only from Australia, New Guinea, Micronesia, Sri Lanka and East Africa. Morphotypes C and D (Group 2) are more cosmopolitan, with basic features characterising Nemognathini from other parts of the world. They are probably assignable to Zonitis and/or Zonitoschema or possibly to undescribed genera.

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### APPENDIX I

**Comparative analysis of characters of morphospecies**

|    | Palaestra | A1 | B1 | C1 | C2 | C3 | C4 | D1 | D2 | D3 |
|----|-----------|----|----|----|----|----|----|----|----|----|
| 1  | 0         | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 2  | 2  |
| 2  | 0         | 0  | 1  | 1  | 1  | 1  | 1  | 2  | 2  | 2  |
| 3  | 0         | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |
| 4  | 0         | 0  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  |
| 5  | 0         | 0  | 1  | 1  | 2  | 2  | 2  | 2  | 2  | 2  |
| 6  | 1         | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |
| 7  | 1         | 0  | 1  | 1  | 2  | 2  | 2  | 2  | 2  | 2  |
| 8  | 0         | 0  | 0  | 0  | 1  | 1  | 1  | 1  | 2  | 2  |
| 9  | 0         | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |
| 10 | 0         | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |
| 11 | 0         | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 1  |
| 12 | 0         | 1  | 2  | 0  | 0  | 0  | 0  | ?  | 3  | 3  |
| 13 | 0         | 1  | 0  | 2  | 2  | 2  | 2  | 2  | 2  | 2  |
| 14 | 0         | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |
| 15 | 0         | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  |
| 16 | 0         | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 0  |
| 17 | 0         | 0  | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  |

1. **G.** General body shape: elongate, subparallel (0); short, navicular (1); thin and elongate, subnavicular (2).
2. **H.** Head shape: rounded with maximum width at middle (0); subtriangular with maximum width at base (1); elongate and slender with maximum width at base (2).
3. **H.** Strongly sclerotised and complex tentorium: absent (0); present (1).
4. **H.** Frontal suture: present (0); absent (1).
5. **H.** Basal stem of frontal suture: normal (0); elongate (1); vestigial or absent (2).
6. **H.** Basal elevation: absent (0); present (1).
7. **H.** Length of neck: inconspicuous (0); short (1); long (2).
8. **H.** Shape of gula: short, V-shaped (0); elongate and subparallel (1); extremely long and thin, almost reduced to a suture (2).
9. **H.M.** Antennomers relative length: antennomers increasing in length from A1 to A3 (0); A2 longer than A1 and A3 (1).
10. **H.M.** Hyaline vesicle on second joint: reduced to a disk-like plate laying on oblique platform (0); inconspicuous on antennomere ventrolateral side (1).
11. **H.M.** Length of antennal setae: as long or slightly longer than head (0); shorter than head (1).
12. **H.M.** Maxillary palpomeres relative length: MX2 twice as long as MX1, MX3 twice as long as MX2 (0); MX1 about as long as MX2, MX3 about as long as MX1+MX2 (1); maxillary palpomeres gradually increasing in length from MX1 to MX3 (2); MX2 longer than MX1 and MX3 (3).
13. **T.** Ecdysial line on thorax: present on pro-, meso- and metanotum (0); present on pro- and mesonotum and absent on metanotum (1); present on meso- and metanotum and absent on pronotum (2).
14. **T.L.** Pretarsal setae: elongate (0); very short (1).
15. **A.** Type of spiracles at abdominal segment VIII: annular, simple (0); at apex of cone-shaped protuberance (1).
16. **A.** Caudal setae: elongate (0); short (1).
17. **A.** Tergal setae: short (0); minute (1).