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The Meloidae (Coleoptera) of Australasia: a generic review, descriptions of new taxa, and a challenge to the current definition of subfamilies posed by exceptional variation in male genitalia

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Abstract. The seven Australasian genera of blister beetles (Coleoptera : Meloidae : Nemognathinae) are reviewed. Included are a key to genera, generic synopses and descriptions of two new genera of Nemognathini, *Australozonitis* and *Pulchrazonitis*, as well as a new monotypic tribe Palaestrini, which features a bauplan of male genitalia unique not only to the subfamily Nemognathinae but to the entire family. The genus *Palaestra* is redefined to include several Australasian, Asian and African species previously assigned to *Zonitis*. Exceptional variation of male genitalia encountered in the Palaestrini challenges current subfamily definitions, which are partly based on male genitalic structure and correlated sexual behaviour. Generic synopses include synonyms, type species, number of species, geographic distribution, significant references on taxonomy, life history and morphology, and additional notes. Forty-six new combinations are proposed for species previously in *Zonitis*. Distribution and relationship of tribes within the Nemognathinae, as well as the biogeography of the Australasian Meloidae are outlined and discussed.

Additional keywords: biogeography, taxonomy, new tribe, new genera, key to genera, Australia, New Guinea, New Caledonia, Pacific Islands.

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Introduction

This paper reviews the genera of Australasian Meloidae. Preceded by similar studies of New and Old World taxa (Pinto and Bologna 1999; Bologna and Pinto 2002), this is the third and final contribution treating the genera in the family. The area covered includes landmasses and islands east and south of Weber's Line, a boundary used, among others, to divide Oriental from Australasian faunal elements (Mayr 1944; Simpson 1977). Micronesia, Melanesia, Polynesia and islands of Wallacea east of Weber's Line are included. Although the various regional boundary lines proposed to delineate Oriental and Australasian regions do not necessarily correspond well to the separation of distinctive faunas (Simpson 1977; Cranston 2010), Weber's Line is not without heuristic value for Meloidae.

In the vast area covered here, east and south of Weber's Line, all recorded blister beetles belong to the subfamily Nemognathinae, a group whose first instar larvae are primarily phoretic on bees (Bologna and Pinto 2001). Of the two other subfamilies recognised (Bologna *et al*. 2008), the Meloinae, distributed throughout the world except Australasia, approach Weber's Line in western Wallacea but extend no further east than Timor where two genera occur, *Hycleus* Latreille and *Epicauta* Dejean. The third subfamily, Eleticinae, distributed in the Neotropical, Afrotropical and Oriental regions, has not been recorded beyond the Malay Peninsula where it is represented by *Eletica* Lacordaire. Although nemognathine Meloidae occur throughout most of Australasia, the family has never been reported from New Zealand or the eastern Polynesian Islands. The New World *Cissites auriculata* (Champion, 1892) was introduced to Hawaii in 1936 but did not survive (Bianchi 1962; Barrows 1980).

There are 90 described species of Australasian blister beetles (Appendix 1), the majority (70) occurring in Australia. In spite of this considerable diversity, taxonomic studies are few and dated, with ~60 contributions from the late 19th to early 20th century. The first meloid described from the region is a Polynesian species collected during one of the first European expeditions in this part of the world (*Zonitis angulata* Fabricius, 1787 see note in

Appendix 1). Subsequent works largely dealt with the description of new species (e.g. Fairmaire 1887; Blackburn 1892; Lea 1917, 1929); comprehensive papers are scarce (Fairmaire 1880; Blackburn 1899; Lea 1914). Generic concepts were last reviewed by Blair (1920). In the past 70 years very few studies focusing on Australasian meloids have appeared. These include descriptions of new species (Borchmann 1937; Blair 1940; Mohamedsaid 1981) and recent studies on first instar larvae (Bologna and Pinto 2001; Di Giulio *et al*. 2010*a*, 2010*b*), the only works on Australasian blister beetle larvae since a short note by Silvestri (1920) reported one unidentified nemognathine triungulin on a specimen of *Trinemura* Silvestri (Thysanura: Nicoletiidae).

Three tribes of Nemognathinae were recognised by Bologna *et al*. (2008): Stenoderini[1], Horiini and Nemognathini. The last two occur in Australasia as well as all other biogeographic regions, whereas the Stenoderini are restricted to the Palaearctic and the transitional Chinese zone (Bologna *et al*. 2002). Australasian species historically have been placed in six genera, two in the Horiini (*Horia* Fabricius, 1787 and *Synhoria* Kolbe, 1897) and four in the Nemognathini (*Palaestra* Laporte de Castelnau, 1840, *Palaestrida* White, 1846, *Zonitis* Fabricius, 1775 and *Zonitoschema* Péringuey, 1909) (Di Giulio *et al*. 2010*b*). The two horiine genera occur in Asia, Africa and Australasia. A similar but broader distribution characterises *Zonitoschema*, which also occurs in the southern Palaearctic from Morocco to China and into Japan. *Palaestra* and *Palaestrida* have been considered endemic to Australia, with *Zonitis* widespread, occurring throughout the New and Old worlds. Two additional nominal genera, *Sitarida* White, 1846 and its synonym *Goetymes* Pascoe, 1863, referred to Meloidae in the early literature (e.g. Borchmann 1917), were correctly transferred to Ripiphoridae by Selander (1957). Fairmaire (1879) described one species from Queensland in *Cantharis* (*C. posticalis*), but it was transferred to *Zonitis* (Borchmann 1917).

The earlier reviews of New and Old World Meloidae genera (Pinto and Bologna 1999; Bologna and Pinto 2002) focused on generic synopses and identification. Taxonomic problems were noted but formal changes were minimal. A similar approach was projected for Australasia until it became evident that its fauna was considerably more complex than anticipated and required significant taxonomic rearrangement at generic and tribal levels.

Taxonomic changes concern groups previously placed in the Nemognathini. At the generic level, it is clear that Australasian species heretofore placed in *Zonitis* (e.g. see Borchmann 1917) require reassignment. Several are transferred to *Palaestra* and others are closest to *Zonitoschema* and placed in the new genus *Australozonitis*. One distinctive species is treated as the only member of the new genus *Pulchrazonitis*. Although we could not examine all species known from the area, we do not believe that *Zonitis*, as currently defined (MacSwain 1952, 1956; Bologna 1991), occurs in Australasia. For the interim we retain in *Zonitis* as *incertae sedis* species that we have not studied and whose generic assignments are not clear from original descriptions, as well as two examined species tentatively referred to as the '*Zonitis*' *brevicornis* Group ('*Z.*' *brevicornis* Blackburn, 1889 and '*Z.*' *murrayi* Blackburn, 1889) that we are unable to place to genus (Appendix 1). Also transferred to *Palaestra* are some eastern African, south-eastern Asian and one southern Palaearctic species (*Z. bytinskii* Kaszab, 1957) all described as *Zonitis*. The current geographic distribution of *Palaestra* is somewhat similar to that of *Zonitoschema* (Bologna and Pinto 2002). We also are aware of one species of *Australozonitis* from eastern Africa (Malawi) in the Natural History Museum UK identified as *Zonitis latipennis* (Pic, 1909). This leaves only two monotypic genera, *Palaestrida* and *Pulchrazonitis*, as endemic to Australia.

Palaestra, as now defined, is considerably expanded. In the early literature (e.g. Wellman 1910; Blair 1920) the genus was restricted to a small number of blister beetles belonging to a lycid-based mimicry ring (see 'Discussion'). This masked their relationship to species unassociated with this complex, but which is now obvious based on similarities of male genitalia, legs and antennae. *Palaestrida* and certain species of *Australozonitis* also have converged on a lycoid phenotype.

Finally, the distinctiveness of *Palaestra* from other Nemognathinae prompts assignment to its own new tribe, Palaestrini. Separation from Nemognathini is based on adult and larval features. Male genitalia of Nemognathinae have been described as relatively simple and uniform (Selander 1964). *Palaestra* is a remarkable exception. The basic structure of the aedeagus differs from that found not only in other nemognathines but in all other Meloidae. In addition, the level of interspecific variation in aedeagus structure is enormous, far surpassing anything thus far described in other meloid genera. This range of variation is illustrated (Figs 3–7, 11–21). Modification of antennae and legs also occurs in males of several species of *Palaestra.* Such sexual dimorphism, common in genera of Meloinae, has not been reported previously in the Nemognathinae. Tribal recognition also is supported by features of first instar larval morphology, which thus far are unique to *Palaestra* (Di Giulio *et al*. 2010*a*, 2010*b*).

The genera of Meloidae now recognised in Australasia include *Palaestra* in the monotypic tribe Palaestrini, *Horia* and *Synhoria* in the Horiini, *Australozonitis*, *Palaestrida*, *Pulchrazonitis* and *Zonitoschema* in the Nemognathini. This work provides keys to the tribes of Nemognathinae and to the Australasian genera, justifications for taxonomic changes and generic synopses.

Materials and methods

Collections from numerous institutions, listed in the 'Acknowledgements', were studied for this project. Those specifically cited in the text and appendices are indicated by acronyms, also given in the 'Acknowledgements', which follow the Bishop Museum's Insect and Spider Collections of the World list. Additional material was collected by colleagues or us and includes specimens from our home institutions (Università 'Roma Tre', Rome, Italy – CB; Queensland Museum, Brisbane, Australia – QMBA; and University of California, Riverside). Type specimens of several Australasian species were examined;

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[1] Stenoderini Selander (1991) is used here provisionally. The name Stenoderinae (Coleoptera, Cerambycidae) was proposed earlier by Pascoe (1867). The case must be referred to the International Commission of Zoological Nomenclature to remove family-group homonymy (Article 55.3.1).

these are indicated in Appendix 1. Several years before our study began another entomologist borrowed a large number of Australian Meloidae from various museums and collections in Europe and Australia. Unfortunately much of this material, including types, was never returned and apparently is lost. Attempts to locate these specimens were unsuccessful.

To assess the position of Australasian taxa within the Nemognathinae we took into account all world genera of the subfamily, except *Ctenopus*, *Onyctenus* and *Sitaromorpha*, which were unavailable. A survey of genus morphology included the dissection of male and female genitalia from exemplar species. In particular we focused on those genera from Africa and south-eastern Asia which also occur in Australasia. From these regions we examined the following genera (number of species studied in parentheses): *Horia* (3), *Synhoria* (3), *Palaestra* (7), *Australozonitis* (1) and *Zonitoschema* (13). For Australasian groups we examined the following: *Palaestra* (35), *Zonitoschema* (4), *Palaestrida* (1), *Australozonitis* (13) and *Pulchrazonitis* (1). Male genitalia were examined in most species (Appendix 1).

To examine male and female genitalia, the last visible urite was removed and placed in 10% KOH for clearing. After clearing, genitalic parts were separated and placed in glycerine. Placement in glycerine is important for optimum viewing, especially of the sperm duct and ventral lobes of the aedeagus in males. Terms applied to male and female genitalic structures in Meloidae follow Selander (1964, 1966). The orientation of male genitalic structures follows Gerber *et al.* (1972).

Figures of morphological details were made using a stereomicroscope Olympus SZX12 equipped with a camera lucida (Olympus, Shinjuku, Japan). Photographs of genitalia were made using a stereomicroscope Leica Z16APO, equipped with a camera Leica DFC420 and Leica application suite 3.7 (Leica, Wetzlar, Germany). Photographs of entire insects were made using a Visionary Digital BK-Plus System (http://visionarydigital.com/index.html); source images were then aligned and stacked using Zerene Stacker (2011: v.102, see References) to obtain a fully sharpened image (PMax option).

Taxonomic revision

Key to the tribes of Nemognathinae

1. Adult: Maxillary palpifer separated from stipes by a distinct suture. Male with last ventrite (VI) emarginate but not divided for more than half its length; gonostyli divided in entire apical half. First instar larva: Non-phoretic. Head with 1 c-shaped stemma on each side. Mandibles directed forward, parallel to frontal plane of head, with ental surface lacking prominent tooth-like transverse ridges. Distribution: Palaearctic Region .... **Stenoderini**

   Adult: Maxilla without distinct suture separating stipes from maxillary palpifer. Male with last ventrite (VI) divided well beyond half its length, often completely so; gonostyli only divided near apex (Fig. 3*c, g*) or completely fused (Fig. 8*b*). First instar larva: Phoretic. Head with one or two circular stemmata on each side. Mandibles directed ventrally, at approximate right angles to frontal plane of head, with ental surface bearing distinct tooth-like transverse ridges. Distribution: Widespread, including Australasia...2

2. Adult: Colour uniformly orange or orange-brown (Australasian genera) or with wide black spots on elytra; surface often laquered in appearance. Labrum extremely short, not extending beyond basal third of mandibles (Fig. 26). Large beetles, exceeding 15 mm and usually attaining 30–50 mm in length. First instar larva: Head with one or two circular stemmata on each side. Epipharynx without a dense tuft of thick setae. Tarsal claws toothed, one basal seta on tarsungulus. Spiracles on abdominal segment VIII flush with surface, not modified. Caudal setae present. Distribution: All biogeographic regions, but marginal in Palaearctic (Egypt and Arabian Peninsula) ....**Horiini**

   Adult: Colour variable; surface rarely lacquered in appearance. Labrum longer, attaining at least middle of mandibles (Fig. 18*b*). Smaller beetles, usually less than 20 mm, rarely attaining 30 mm in length. First instar larva: Head with two circular stemmata on each side. Epipharynx with a dense tuft of thick setae. Tarsal claws not toothed, two basal setae on tarsungulus. Spiracles on abdominal segment VIII modified or not. Caudal setae present or not. Distribution: Widespread including Australasia 3

3. Adult: Aedeagus dorsoventrally compressed, concave dorsoapically; with lateral or dorsal hooks near apex (e.g. Figs 15*f–h*, 16*e–g*, 17*f–h*), less commonly unarmed; ventroapically with two externally visible spiculate lobes which are capable of inflation (e.g. Fig. 3*b, f*); sperm duct not obviously sclerotised anywhere along its length. Gonostyli at least slightly divided apically; gonocoxal plate not gibbose, relatively flat, more or less in same plane as gonostyli. Aedeagus variable but usually considerably (0.2–0.8×) longer than gonoforceps. Antennae with antennomere II considerably shorter than III in both sexes ($\leq$0.5× as long); middle antennomeres in male with or without a smooth, longitudinal glabrous area. Male profemora with (Fig. 12*f*) or without a dorsal notch near apex. First instar larva: Abdominal spiracle I dorsal in position; spiracle VIII with opening flush with surface; caudal setae present. Distribution: Afrotropical, Oriental and Australasian regions, marginal in Palaearctic (Israel) .... **Palaestrini, new tribe**

   Adult: Aedeagus subcylindrical and unarmed; with or without two ventroapical lobes; sperm duct sclerotised or not along its length. Gonostyli totally fused or slightly divided apically; gonocoxal plate gibbose. Aedeagus usually subequal in length to gonoforceps. Antennomere II length relative to that of III variable; male antennomeres uniformly setose and profemora without a dorsal notch near apex. First instar larva: Abdominal spiracle I sublateral in position; spiracle VIII placed at apex of a projecting evagination and with an associated spine; caudal setae present (Australasia) or not. Distribution: Widespread, including Australasia ....
   ....**Nemognathini**

Key to the Australasian genera of Meloidae (adults)

1. Colour uniformly orange or orange-brown; surface often laquered in appearance. Labrum extremely short, not extending beyond basal third of mandibles (Fig. 26). Large beetles, exceeding 15 mm and usually attaining 30–50 mm in length 2

   Colour variable; surface rarely lacquered in appearance. Labrum longer, attaining at least middle of mandibles. Smaller beetles, usually less than 20 mm, rarely attaining 30 mm in length 3

2. Male metafemora inflated, noticeably broader than mesofemora (Fig. 1*d*). Males with mandibles short, their length less than half that of head and with head widest at eyes (Fig. 26*a*). Pronotum length usually greater than head length to apex of mandibles. Eastern Wallacea, New Guinea, northern and eastern Australia .... ***Horia***

   Male metafemora not inflated, subequal in width to mesofemora. Males with mandibles long, their length subequal to or greater than half the length of head and with head clearly widest at temples (Fig. 26*b*). Pronotum length equal to or less than head length to apex of mandibles. Eastern Wallacea, New Guinea, northern and eastern Australia ....
   ....***Synhoria***

3. Antennomeres III–VIII compressed and distinctly widened, at least III–VI symmetrical in shape (Fig. 25*b*). Elytra costate and setose. Head with temples strongly recessed relative to medial region of vertex (Fig. 2*a*). Gonostyli of male genitalia completely fused (Fig. 8*b*). Australia .... ***Palaestrida***

   Antennomeres III–VIII usually subcylindrical (Fig. 25*a*), if compressed then segments asymmetrical in shape. Elytra rarely costate, setose or not. Head without strongly recessed temples. Gonostyli of male genitalia divided apically (Fig. 8*g*) 4

4. Antennomere II less than 2/3 as long as III (Figs 1*a–c*, 12*g*, 13*b*, 21*g*). Aedeagus dorsoventrally compressed with dorsoapical surface concave, usually with hooks in apical half (Figs 3*b, f*, 4*b*, *e*, 16*g*, 17*f–h*). Gonocoxal plate relatively flat in lateral view (Fig. 3*d*). Male of several species with middle antennomeres with a glabrous and smooth longitudinal line or keel, and/or profemora with a notch or depression near apex (Fig. 12*f–g*). Micronesia, New Guinea, Melanesia, Australia .... ***Palaestra***

   Antennomere II at least 2/3 as long as III (Fig. 2*b–d*). Aedeagus subcylindrical and unarmed (Figs 8*f, h*, 9*b*). Gonocoxal plate distinctly gibbose in lateral view (Fig. 9*d, f*). Male antennomeres and profemora not so modified 5

5. Eyes very large (Fig. 2*c*), extending beyond inner margin of maxillae and approaching one another on underside of head. Antennae extremely long, antennomere VIII usually at least 6× as long as wide. Eastern Wallacea, New Guinea, Melanesia, northern Australia ....***Zonitoschema***

   Eyes smaller, at most extending to inner margin of maxillae on underside of head. Antennae not as long, antennomere VIII less than 6× as long as wide 6

6. Elytra metallic blue-green with a violet luster, glabrous (Fig. 2*d*). Male gonostyli unique, with a pair of subapical dorsal protuberances and angulate posteriorly at apex (Fig. 23*g*). Western and southern Australia ....***Pulchrazonitis*, gen. nov.**

   Elytra variously coloured but never as above, setose or glabrous. Male gonostyli not so modified.. 7

7. Aedeagus with distinct ventral lobes (Fig. 9*b*) and sperm duct bearing concentric sclerotised rings near apex (Fig. 10*c*). New Guinea, Melanesia, Australia..................................***Australozonitis*, gen. nov.**

   Aedeagus without distinct ventral lobes and sperm duct lacking sclerotised rings (Fig. 8*f*). Australia.. ....*brevicornis* group, *incertae sedis* (see Nemognathini below)

New taxa and a redefinition of *Palaestra*

PALAESTRINI Bologna, Turco & Pinto, new tribe

Type genus: *Palaestra* Laporte de Castelnau, 1840: 251.

Distinguished from other Nemognathinae by adult and larval characters indicated in the key to tribes. Monotypic.

Kaszab (1969), in his treatment of the family Meloidae, listed the subtribe Palaestrina Kaszab, 1959 within the Nemognathini. However, as pointed out by Selander (1991), because the name does not appear in Kaszab's 1959 work, Palaestrina Kaszab, 1969 is a *nomen nudum* and unavailable.

The new tribe Palaestrini includes only *Palaestra*. Blair (1920) considered this genus endemic to Australia with only three species. As defined here the genus is very heterogeneous and speciose with at least 34 named species (see synopsis for additional comments). It is widely distributed from eastern Africa (and possibly Madagascar), to the Negev, through south-eastern Asia to New Guinea, Australia (Tasmania included) and on certain Pacific archipelagos (see synopsis).

First instar larva

The first instar larva of *Palaestra* was described by Di Giulio *et al.* (2010*a*, 2010*b*). These authors also described similar larvae of two other species unassociated with adults and unassigned to genus that they placed with *Palaestra* in Group 1. We now feel it likely that all Group 1 larvae represent *Palaestra.* As the Horiini, these larvae are intermediate in morphology between those of the Stenoderini (Bologna *et al*. 2002) and the more derived Nemognathini (Bologna and Pinto 2001, 2002). Unlike the Stenoderini they are clearly phoretic as are the other nemognathine tribes. Two probable plesiomorphies shared with Horiini are the unmodified abdominal spiracle VIII and the hair-like caudal setae. The derived state of both characters occurs in Nemognathini (Di Giulio *et al*. 2010*a*). The primary differences between horiine and palaestrine larvae are claw and epipharynx structure (see key to tribes). Other primitive traits of Palaestrini, the presence of a well-developed epicranial suture and a line of dehiscence on the pronotum, also occur in several genera in the subfamily (MacSwain 1956). The only larval apomorphy of Palaestrini is the dorsal position of abdominal spiracle I, a condition found in several genera of Meloinae, but not reported in other Nemognathinae.

Adults

Male aedeagal structure separates the Palaestrini from other Nemognathinae. The aedeagus is dorsoventrally compressed, concave apically, and, in most species, either bears hooks (laterally or dorsally) or a sclerotised dorsoapical horizontal bar. Aedeagal hooks, when present, are either laterally paired (Figs 3*f*, 4*a*, *b*, 12*d*, 15*f*) or, less commonly, unpaired (Fig. 17*f*, *h*). Other traits, almost certainly primitive and varying in the subfamily, include the apically divided male gonostyli (Figs 3*c*, *g*, 5*c*, *g*, 6*b*), the presence of tergum IX, and the short antennomere II relative to III (Figs 1*a–c*, 12*g*, 13*b*, 21*g*).

In all nemognathine tribes except Palaestrini, the aedeagus is subcylindrical and unarmed (Figs 8*a*, *f*, *h*, 24*a*) (Escherich 1891; Selander 1964). Only in the Stenoderini and in *Zonitodema* Péringuey (Nemognathini) it is slightly compressed dorsoventrally. The presence of dorsal hooks on a laterally compressed aedeagus is typical of the subfamily Meloinae (usually two hooks; only one in Epicautini and a few Mylabrini and Lyttini) and uncommon in the Eleticinae. Paired hooks, when present in these subfamilies, are always longitudinally arranged, never laterally so as in the Palaestrini. The aedeagal structure of Palaestrini is unique in the Meloidae and, together with the male antennal and leg modifications found in several species, is likely associated with a similarly distinct form of sexual behaviour. The divided apex of the gonostyli is a plesiomorphy shared with Stenoderini (Bologna *et al*. 2002) and certain Nemognathini. The shortened second antennomere, also presumably plesiomorphic, occurs in the Stenoderini, several genera of Nemognathini (e.g. *Zonitomorpha*, *Megatrachelus*, *Tricrania* and the Australian *Palaestrida*) as well as in certain species of *Zonitis* and *Nemognatha.* Both characters (gonostyli apically divided and short antennomere II) are symplesiomorphic states within the family, being typical of Eleticinae, Meloinae and

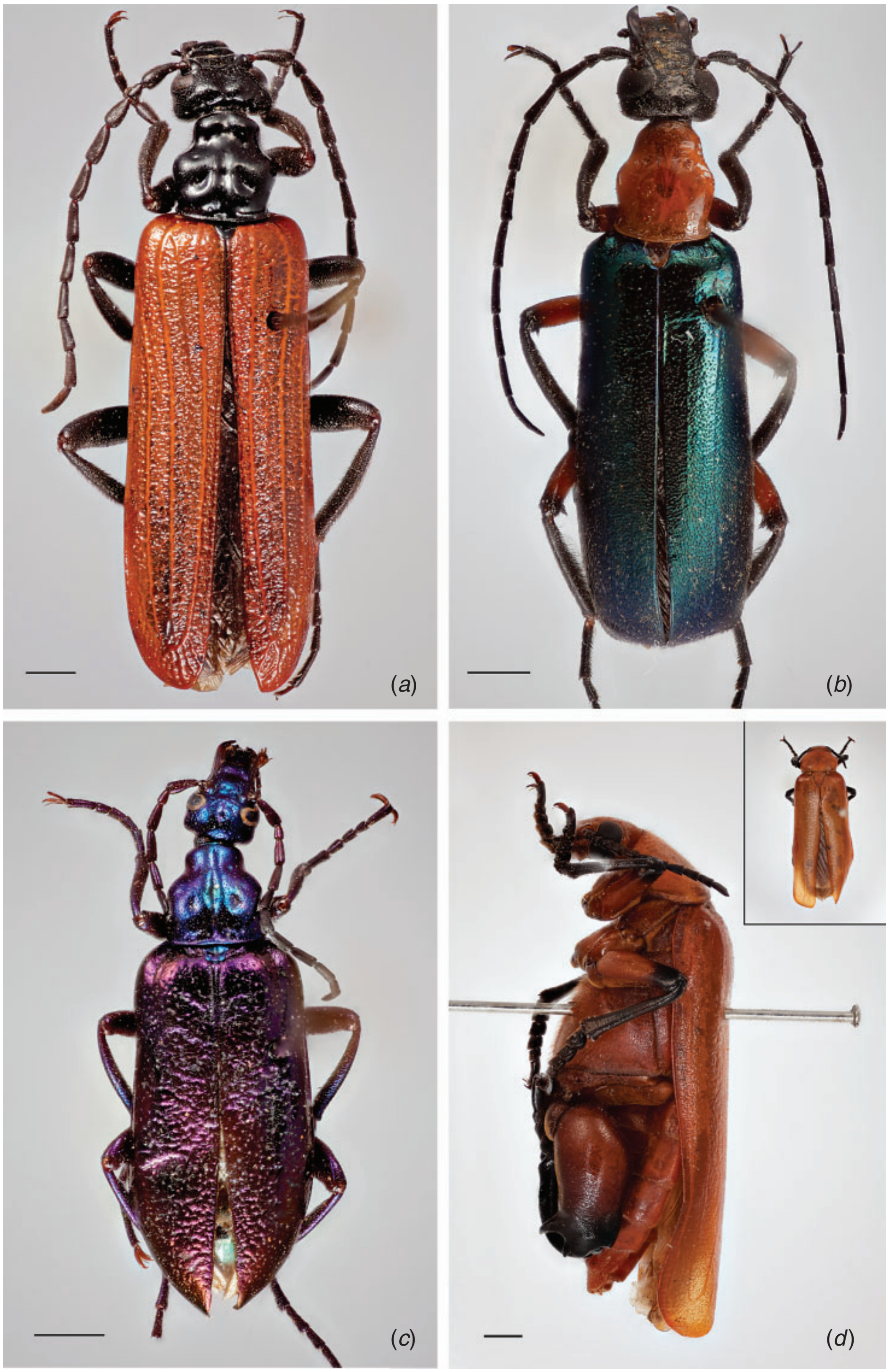

Fig. 1. Habitus, dorsal view (*Palaestra* and *Horia*: (*a*) *P. rufipennis* (Group I) (QLD, Kroombit Tops); (*b*) *P.* sp. (Group VIe) (QLD, Auburn River NP); (*c*) *Palaestra* sp. near *purpureipennis* (Group IIb) (WA, Shark Bay); (*d*) *H. blairi* (QLD, Carmila), lateral (inset: dorsal). Scale bars: 2 mm.

basal Nemognathinae (Bologna 1991; *hoc opus*). Sclerotisation of tergum IX also is characteristic of primitive nemognathines. Gupta (1971) reported it in *Stenodera* and *Horia* but absent in Nemognathini. We find it in *Palaestra* but also in at least some species of Australasian Nemognathini (see below). As in other nemognathine tribes, a sclerous aedeagal rod is absent, but externally visible membranous ventral lobes do occur (Figs 3*b*, *f*, 5*b*, 6*d*, 7*b*).

Fig. 2. Habitus, dorsal view. (*a*) *Palaestrida assimilis* (QLD, Mt Moffat NP); (*b*) *Australozonitis tricolor* (QLD, Mt Moffat NP); (*c*) *Zonitoschema* sp. (QLD, Garradunga); (*d*) *Pulchrazonitis splendida* (WA, Wilga). Scale bars: 2 mm.

Museum and personal records indicate that *Palaestra* adults are polyphagous and anthophilous. As in Horiini and Nemognathini, *Palaestra* larvae are known to be phoretic on bees and presumably develop on their provisions and larvae (Di Giulio *et al*. 2010*b*). No definite larval host association has ever been made, however. Hosts of the non-phoretic Stenoderini also are unknown.

It is likely that sexual behaviour in the Palaestrini is a marked departure from that found in other Nemognathinae. The presence

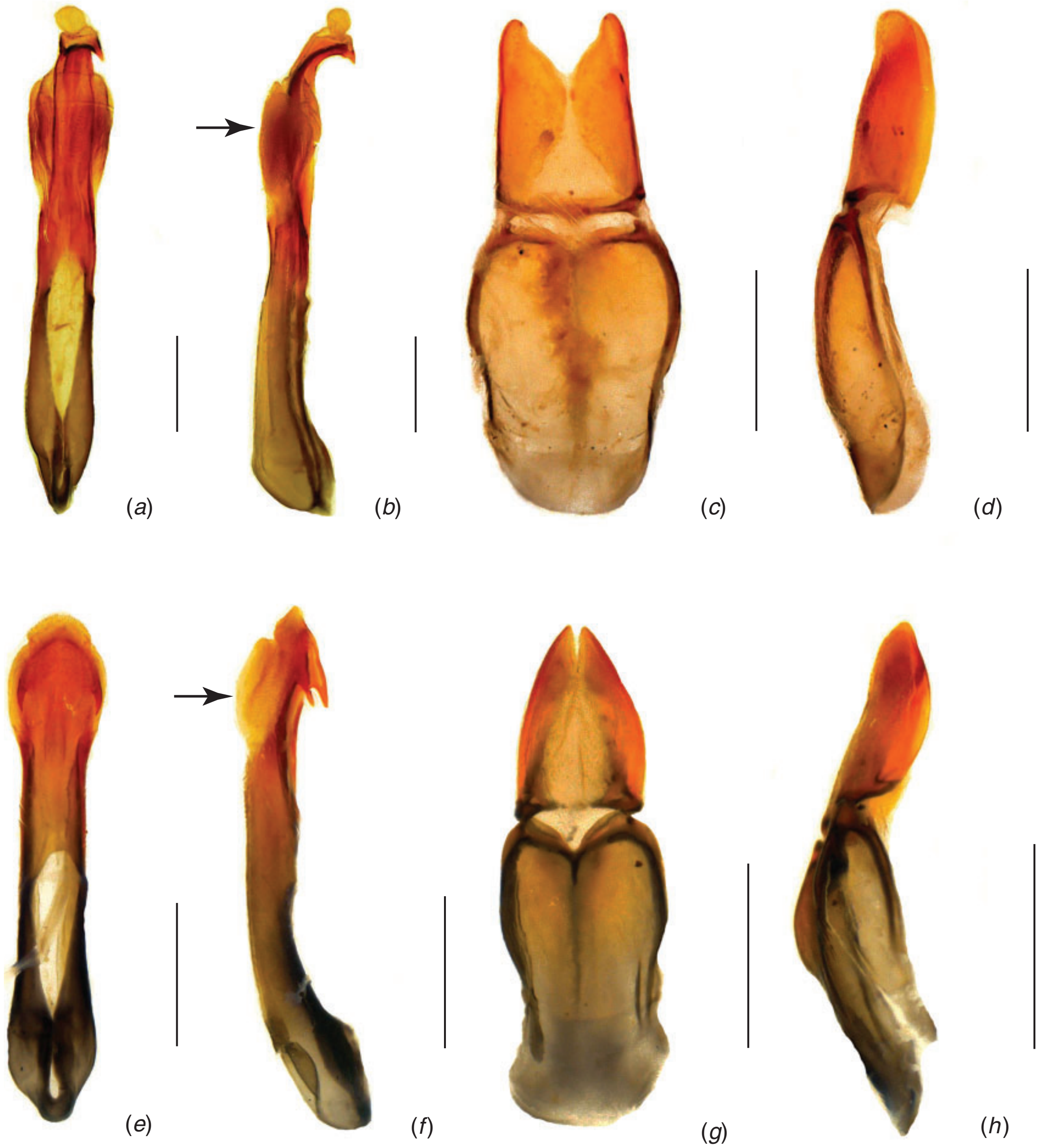

Fig. 3. Male genitalia. *Palaestra queenslandica* (Group IIa) (QLD, Dimbulah): (*a*) aedeagus, dorsal; (*b*) aedeagus, lateral (arrow pointing at ventral lobes); (*c*) tegmen, ventral; (*d*) tegmen, lateral. *Palaestra* sp. (Group IIa) (SA, Old Gerabullan Well): (*e*) aedeagus, dorsal; (*f*) aedeagus, lateral (arrow pointing at ventral lobes); (*g*) tegmen, ventral; (*h*) tegmen, lateral. Scale bars: 0.5 mm.

of aedeagal hooks and modified male antennae, profemora and other leg structures in *Palaestra* suggest behavioural parallels with Meloinae (see 'Discussion').

Palaestra Laporte de Castelnau, 1840, redefined

The study of a large number of Australasian and Palaeotropical species referred to *Zonitis* supported our previous suspicion (Pinto and Bologna 1999; Bologna and Pinto 2002) that this genus has been used as a reservoir for unrelated species. We have yet to encounter an Australasian species assignable to *Zonitis* as currently defined (Bologna and Pinto 2002). A large number of those species described as *Zonitis* clearly belong to *Palaestra*, which until now was restricted to a few Australian species of phenetically similar lycid mimics with costate elytra (Fairmaire 1880; Blackburn 1899; Lea 1914; Blair 1920). We herein recognise ~60 species of *Palaestra*; at least 34 are described. Most are Australasian but certain eastern African, south-eastern Asian and one southern Palaearctic species are included (see synopsis and appendices). Consequently *Palaestra* can no longer be considered endemic to Australia.

Palaestra is defined by the unique structure of the aedeagus. The genus is further distinguished by the much shorter second antennal segment relative to the third, a feature which, alone,

Fig. 4. Male genitalia. *Palaestra* sp. (Group IIa) (SA, Mudla Miracka): (*a*) aedeagus, dorsal; (*b*) aedeagus, lateral (arrow pointing at ventral lobes); (*c*) tegmen, ventral. *Palaestra* sp. (Group IIa) (QLD, Mt White): (*d*) aedeagus, dorsolateral; (*e*) aedeagus, lateral (arrow pointing at ventral lobes); (*f*) tegmen, ventral; (*g*) tegmen, lateral. Scale bars: 0.5 mm.

allows separation from all other Australasian genera except *Palaestrida*. However, within *Palaestra* we find vast variation in several male characters. Species differ most in aedeagal structure. Differences include the presence or absence of aedeagal hooks and, where hooks are present, variation in number, size, position and shape. The ventroapical surface of the aedeagus, the area associated with the phallotreme, is membranous and harbours paired spiculate lobes or flaps of varying size and shape. In at least some species these structures are capable of inflation and may function as does the everted endophallus in other Coleoptera (e.g. Düngelhoff and Schmitt 2006). Males of several species also have variously modified antennae, profemora, and tarsi. We originally assumed that such vast variation would allow recognition of distinct lineages. However, our inability to homologise the different states of these features and the absence of character correlation preclude formal grouping beyond genus at this time. Instead *Palaestra* is divided below into phenetic groups in an attempt to provide an ordered summary of intrageneric variation. An in-depth study of character variation using molecular and larval features could help unravel phylogenetic relationships in the genus. It also would be helpful to know the function of the puzzling array of presumably epigamic traits found in the group. Sexual behaviour has not been described for any Australasian species of Meloidae.

Appendices 1 and 3 list all species currently assigned to *Palaestra*. In addition, we are aware of several new species (Appendix 2), primarily from Australia but also from

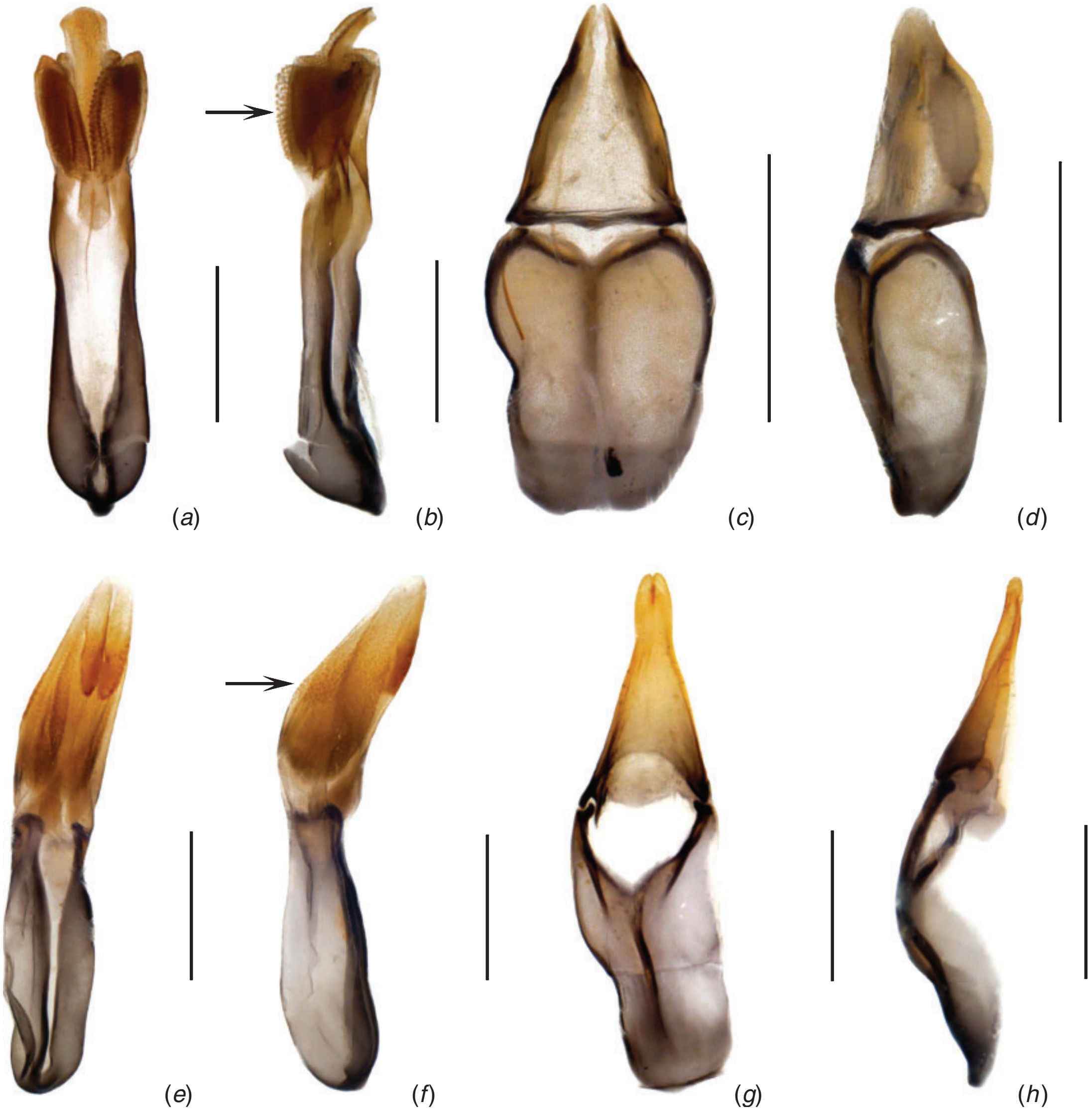

Fig. 5. Male genitalia. *Palaestra helmsi* (Group IIb) (WA, Yuinmery): (*a*) aedeagus, dorsal; (*b*) aedeagus, lateral (arrow pointing at ventral lobes); (*c*) tegmen, ventral; (*d*) tegmen, lateral. *Palaestra* sp. (Group IIIa) (Sri Lanka): (*e*) aedeagus, dorsolateral; (*f*) aedeagus, lateral (arrow pointing at ventral lobes); (*g*) tegmen, ventrolateral; (*h*) tegmen, lateral. Scale bars: 0.5 mm.

Melanesia, which will be described in the future. It also is likely that some of the ~30 described Australasian species unknown to us (Appendix 1, *incertae sedis*) belong here, as do species from elsewhere referred to as *Zonitis* that we have not examined. Based on the description of antennal structure, we suspect that some 15 additional African, Malagasy (e.g. Kaszab 1954, 1965) and Asian species (e.g. Pic 1911) ultimately will be transferred when they are adequately studied. A case in point is the unexpected discovery that *Palaestra* occurs in the southern Palaearctic (Israeli Negev) upon examining the type of *P. bytinskii* (Kaszab, 1957).

Below are six phenetic groups of *Palaestra* based on three features: presence or absence of modified profemora and antennae in males, and elytral structure. Group numbers tagged with lower case letters indicate species assemblages within groups where significant variation occurs. A key to groups follows.

Key to the phenetic groups of *Palaestra* (males)

1. Profemoral notch present (Fig. 12*f*)..2
   Profemoral notch absent..4
2. Elytra costate and glabrous (Fig. 1*a*)..Group I
   Elytra not costate, glabrous or not..3
3. Several antennomeres with a longitudinal glabrous line or keel (Fig. 12*g*)
   ....Group II
   Antennomeres without a longitudinal glabrous line or keel.......Group III
4. Antennomeres III–VI with anterior surface subglabrous and concave.....
   ....Group IV
   Antennomeres not so modified..5
5. Elytra costate and glabrous (as in Fig. 1*a*)..Group V
   Elytra without costae, glabrous or setose..Group VI

Fig. 6. Male genitalia. *Palaestra* sp. (Group IIIb) (NT, Timber Creek): (*a*) aedeagus, dorsal; (*b*) tegmen, ventral. *Palaestra* sp. (Group VIc) (WA, Tangadee): (*c*) aedeagus, dorsal; (*d*) aedeagus, lateral (arrow pointing at ventral lobes); (*e*) tegmen, ventral; (*f*) tegmen, lateral. Scale bars: 0.5 mm.

Phenetic groups of *Palaestra*

I. Male with both profemoral notch (Fig. 12*f*) and longitudinal glabrous line or keel on several antennomeres (Fig. 12*g*). Elytra costate, glabrous (Fig. 1*a*).

Frons depressed. Antennae subfiliform or with middle segments produced ventrally. Pronotum abruptly constricted in apical half. Elytra non-metallic. Mesotarsi swollen and subglabrous. Aedeagus armed with one pair of dorsolateral hooks.

This group is known only from Australia including Tasmania. It contains two species of lycid mimics traditionally placed in *Palaestra* (Blair 1920): *P. rufipennis* Westwood, 1841; *P. quadrifoveata* Fairmaire, 1880; and an undescribed species from New South Wales (Waterfall, Sydney Nat. Park: ANIC). Other lycoid species historically treated as *Palaestra* are included in Group V.

II. Male with both profemoral notch (Fig. 12*f*) and longitudinal glabrous line or keel on several antennomeres (Fig. 12*g*). Elytra not costate, glabrous or not (Fig. 1*c*).

This group is subdivided into two assemblages based on aedeagal structure.

IIa. Aedeagus (Figs 3, 4, 11*e, f*) armed subapically with 1–2 pairs of lateral hooks which vary considerably in size.

Frons depressed. Antennae subfiliform. Elytra subglabrous, slightly to moderately rugose, metallic (green, blue, violet, purple, etc.) or shiny black in most species. Pronotum usually abruptly constricted in apical half. Mesotarsi swollen and

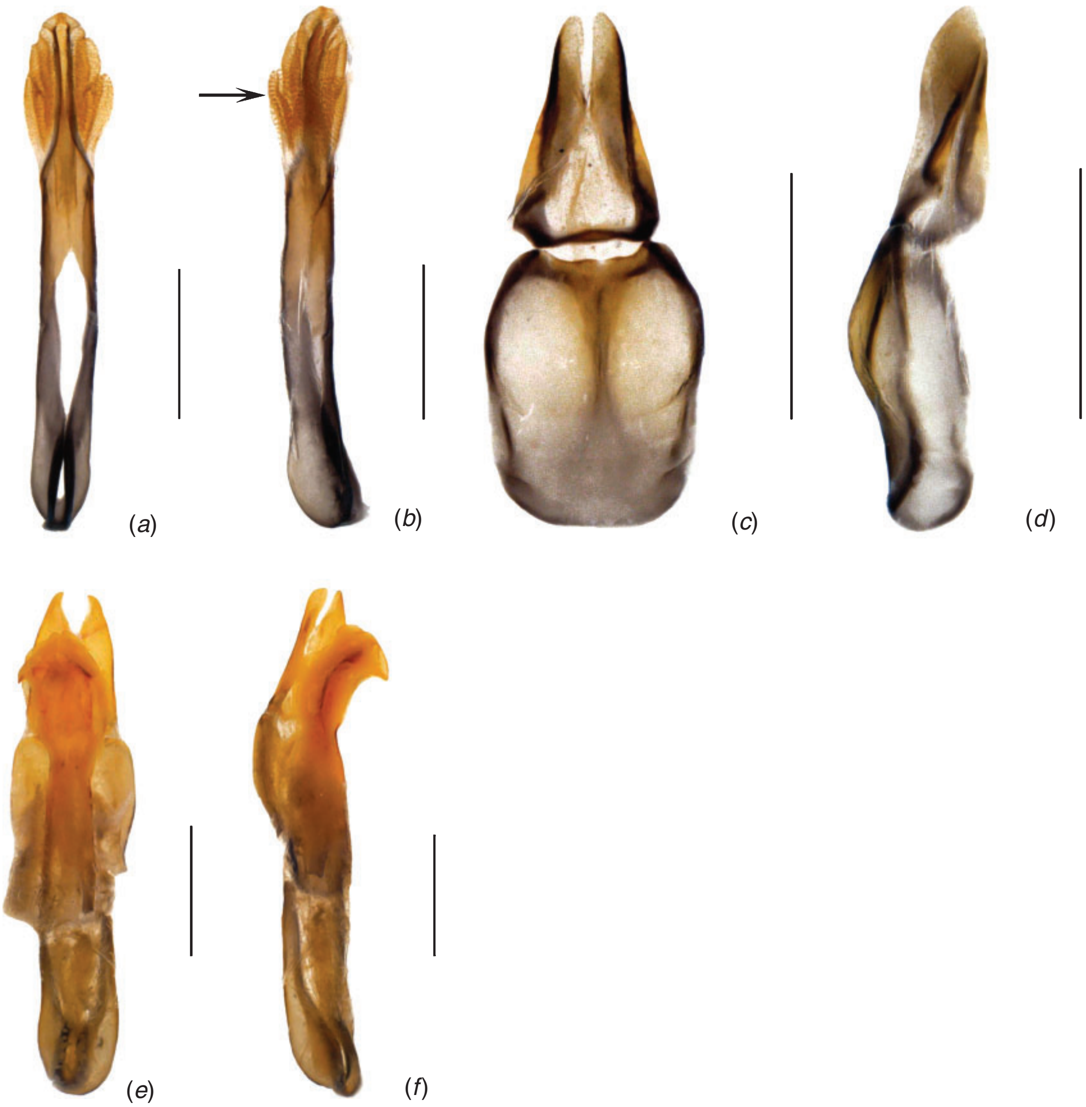

Fig. 7. Male genitalia. *Palaestra* sp. (Group VIg) (QLD, Cooper Creek): (*a*) aedeagus, dorsal; (*b*) aedeagus, lateral (arrow pointing at ventral lobes); (*c*) tegmen, ventral; (*d*) tegmen, lateral. *Palaestra carpentariae* (group not defined) (Holotype: 'N. Ql.T.'): (*e*) aedeagus and tegmen, dorsal; (*f*) aedeagus and tegmen, lateral. Scale bars: 0.5 mm.

subglabrous in some species. Male last abdominal ventrite with hemisternites elongate, apically narrowed (Fig. 11*b*).

This assemblage includes at least 19 species (all named species previously in *Zonitis*). Included are: *P. aspericeps* (Blackburn, 1899), *P. bipartita* (Fairmaire, 1879), *P. cyanipennis* (Pascoe, 1862), *P. flavicrus* (Fairmaire, 1879), *P. hakeae* (Lea, 1914), *P. indigacea* (Fairmaire, 1880), *P. janthinipennis* (Fairmaire, 1880), *P. nigroaenea* (Fairmaire, 1879), *P. purpureipennis* (Waterhouse, 1875) (Fig. 12), *P. queenslandica* (Blackburn, 1899) (Fig. 3*a–d*), *P. rostrata* (Blessig, 1861), *P. rubricollis* (Hope, 1842), *P. rugata* (Fairmaire, 1880) (possible synonym of *P. rubricollis*), *P. rugosipennis* (Fairmaire, 1879), *P. sedilloti* (Fairmaire, 1880), *P. semirufa* (Fairmaire, 1880) (possible synonym of *P. rostrata*), *P. violacea* (Hope, 1842), *P. violaceipennis* (Waterhouse, 1875) and four undescribed species (one from several localities in Western Australia (ANIC, BMNH, QMBA; Fig. 1*c*, as *P.* sp. near *purpureipennis*), one from Queensland (Mt White: ANIC) (Fig. 4*d–g*), one with a very elongate head from South Australia (Mudla Miracka: ANIC) (Fig. 4*a–c*), and another from the same state (Old Gerabullan Well, 29.00 S- 135.41 E: ANIC) (Fig. 3*e–h*)).

The elytra are unicolorous except in *P. bipartita* and *P. queenslandica* in which they are brown and black.

IIb. As in IIa except aedeagus unarmed, having only a narrow transverse sclerotised bar dorsoapically (Fig. 5*a, b*).

The only species here are *P. helmsi* (Blackburn, 1892), previously placed in *Zonitis*, and an undescribed species from Northern Territory (41 km N Barrow Creek: LACM). The elytra are setose in *P. helmsi* and glabrous in the unnamed species. The mesotarsi are unmodified in both.

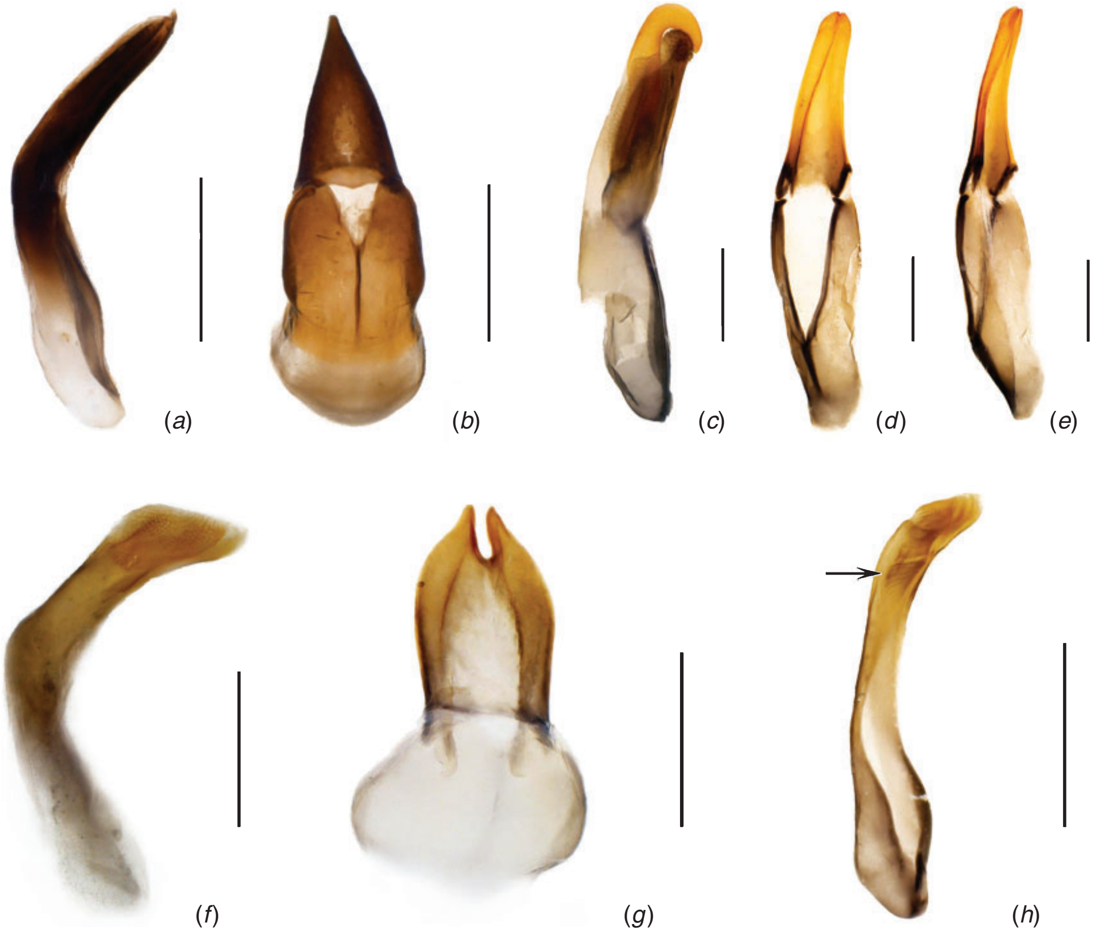

Fig. 8. Male genitalia. *Palaestrida assimilis* (QLD, Bundaberg): (*a*) aedeagus, lateral; (*b*) tegmen, ventral. '*Zonitoschema*' *posticalis* (South Africa, Kwa Zulu-Natal, Sodwana Bay): (*c*) aedeagus, lateral; (*d*) tegmen, ventrolateral; (*e*) tegmen, lateral. '*Zonitis*' sp. cfr. *brevicornis* (WA, Cunderdin): (*f*) aedeagus, lateral; (*g*) tegmen, ventral. *Zonitoschema nigroapicata* (QLD, Cape York Peninsula): (*h*) aedeagus, lateral (arrow pointing at sclerotised rings of the sperm duct). Scale bars: 0.5 mm.

P. bytinskii (Kaszab, 1957) from Israel seems to be referable here.

III. Males with a profemoral notch (Fig. 12*f*) but without a glabrous line or keel on antennomeres. Elytra not costate, setose.

This group is divided into two assemblages based on antennal structure.

IIIa. Antenna filiform in both sexes.

This assemblage is unknown from Australasia. It includes three eastern African species – *P. kittenbergeri* (Kaszab, 1954), *P. sternalis* (Kaszab, 1954) and *P. woodi* (Pic, 1926), all described as *Zonitis* – two undescribed species, one from Ethiopia (CB, coll. François), the other from Sri Lanka (BMNH) (Fig. 5*e–h*), and *P. subviridipes* (Pic, 1926), also described as *Zonitis*, from Indochina (Vietnam and Laos). With the exception of *P. subviridipes*, these species have a well-developed profemoral notch. In *P. subviridipes* the apex of the profemur has a small pointed protrusion, not a distinct notch. Meso- and metatarsomeres not modified, but in *P. subviridipes* protarsomeres I–III and mesotarsomeres I–IV are wider than V. The aedeagus bears a small pair of lateral hooks at its apex in *P. woodi* and *P. subviridipes*; it is completely unarmed and lacking all apical sclerotisation in *P. kittenbergeri*, *P. sternalis* and in the undescribed species from Sri Lanka (Fig. 5*e, f*). The aedeagus in *P. woodi* is very similar to that in certain species in IIa (e.g. *P. bipartita*; Fig. 11*e, f*).

IIIb. Antennomeres V–VIII widened and subtrapezoidal, particularly in males (Fig. 13*b*).

This assemblage includes *P. guerini* from New Caledonia, two undescribed Australian species, respectively, from Queensland (Desailly: BMNH, ANIC) and Northern Territory (Timber Creek: MRSN) (Figs 6*a*, *b*, 13), and a third undescribed species from Fiji (BMNH). Leg and aedeagal structures vary in these species. Male mesotarsomere II unmodified, or flattened, glabrous and with a shagreened surface anteriorly (meso- and metatarsomeres III and IV may be similarly modified). Aedeagus unarmed and lacking all dorsoapical sclerotisation (Fiji species), unarmed but partially sclerotised dorsoapically (NT species) (Figs 6*a*, 13*e, f*), or armed with two very short dorsoapical hooks (Queensland species).

IV. Male without profemoral notch but antennomeres with longitudinal subglabrous area (Fig. 12*g*). Elytra not costate, setose.

Fig. 9. Male genitalia. *Australozonitis opacorufa* (NSW, Caparra): (*a*) aedeagus, dorsal; (*b*) aedeagus, lateral (arrow pointing at ventral lobes); (*c*) tegmen, ventrolateral; (*d*) tegmen, lateral. *Australozonitis* sp. (QLD, Hughenden): (*e*) tegmen, ventral; (*f*) tegmen, lateral. Scale bars: 0.5 mm.

A single undescribed species from Western Australia (Newman; Nyang: WAM) (Fig. 14), Queensland (Rokeby: WAM; Mt Garnet: BMNH) and New South Wales (Fowlers Gap Res. Station: WAM; Cobar: BMNH) is assigned here. In this species the subglabrous anterior surface of antennomeres III–VI in males is distinctly concave, a unique modification. Also, the frons and vertex are concave in both sexes, a modification occurring in certain other *Palaestra* (e.g. *queenslandica* in Group IIa and some undescribed species in Group VI). The hind legs of males are modified with elongate hairs at the basal half of the femora and a fringe on the apical half of tibiae. The aedeagus bears a lateral pair of small, obsolescent dorsoapical extensions (Fig. 14*e*, *f*).

V. Male without profemoral modification and antennomeres without glabrous line or keel. Elytra costate or subcostate, glabrous.

Species placed here are phenetically similar to those in Group I except males lack leg and antennal modifications. The aedeagus is armed with two pairs of relatively small lateral or dorsal hooks.

This group includes: *P. rubripennis* Laporte, 1840; *P. rufocincta* Fairmaire, 1880; *P. foveicollis* Blair, 1920; and one undescribed species from New South Wales (Armendale; and Ebor: ANIC) with relatively weak elytral costae. The described species were originally placed in *Palaestra* based on what now appears to be convergent lycoid features that also characterise Group I.

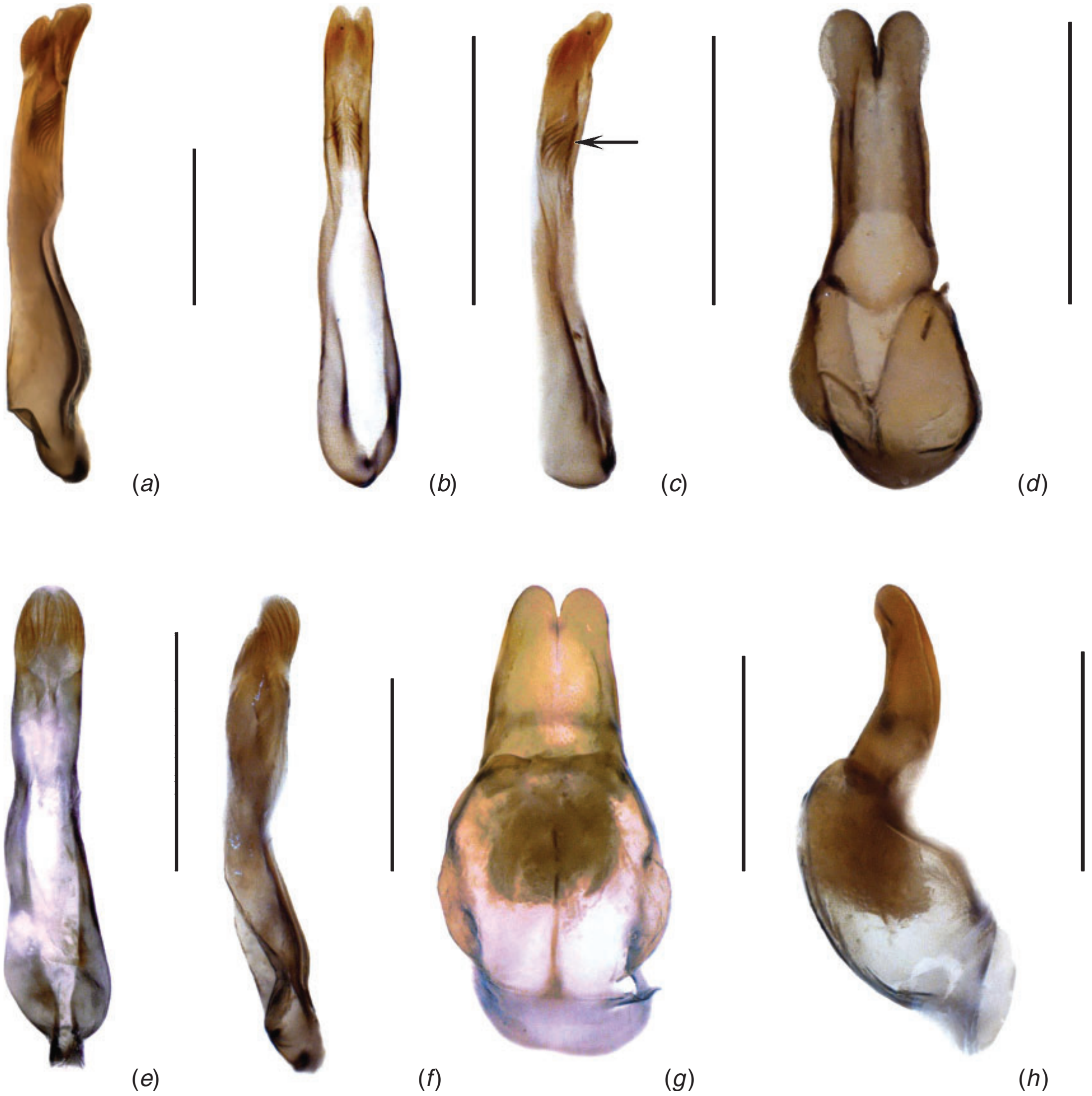

Fig. 10. Male genitalia. *Zonitoschema nigroapicata* (QLD, Cape York Peninsula): (*a*) aedeagus, lateral. *Australozonitis* sp. (QLD, Millstream Falls): (*b*) aedeagus, dorsal; (*c*) aedeagus, lateral (arrow pointing at sclerotised rings of the sperm duct); (*d*) tegmen, ventral. *Australozonitis handschini* (QLD, Holts Creek): (*e*) aedeagus, dorsal; (*f*) aedeagus, lateral; (*g*) tegmen, ventral; (*h*) tegmen, lateral. Scale bars: 0.5 mm.

VI. Males without profemoral modifications; antennomeres without a glabrous line or keel. Elytra not costate, glabrous or setose.

This heterogeneous group includes seven subgroups; all except VIg are characterised by at least one unique modification. These are stated in the first paragraph of each treatment.

VIa. Labrum short, not extending beyond half the mandibular length. Aedeagus with three pairs of dorsolateral hooks (Fig. 15*f*–*h*).

Elytra setose, colour varying from black and brown to completely black. The male tarsi are unmodified in these species. Included here are: *P. blairi* (**new name** for *Zonitis oceanica* Blair, 1940, preoccupied by *Z. oceanica* Pic, 1915), known from Micronesia (the Caroline Islands and Guam); and four undescribed species, three from Fiji (Vanua Balava: BMNH; Kadavu Island BPBM) and New Caledonia (BMNH), and one from New Guinea (Madang District, Finistere Mts: BMNH) (Fig. 15).

VIb. Aedeagus unique, with three hooks, one dorsoapically and a more basal lateral pair (Figs 16*e*–*g*, 17*f*–*h*).

In one species the male mesotarsomeres I–IV are slightly inflated with the anterior surface glabrous and shagreen. The elytra are glabrous in both species. Gonostyli as in Figs 16*c*–*d*, 17*d*–*e*. Included are two undescribed species, one from Western Australia (Bullfinch: WAM), the other from Northern Territory (Alice Springs: ANIC).

VIc. Protibia with setae short and spiniform (Fig. 18*d*).

Aedeagus with one or two short dorsoapical hooks visible in lateral view (Figs 6*c*–*f*, 18*h*–*j*). Included here are two or possibly

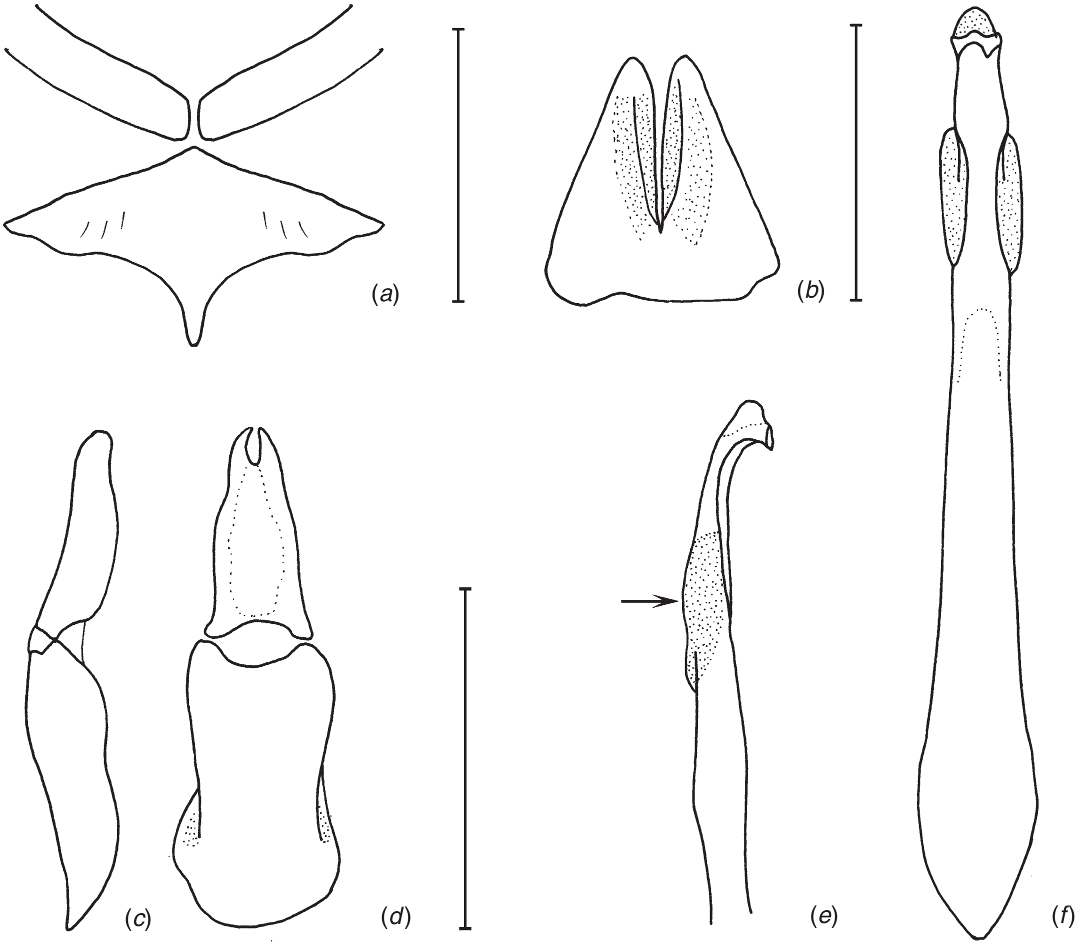

Fig. 11. *Palaestra bipartita* (Group IIa) (NSW, Heathcote): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) tegmen, lateral; (*d*) tegmen, ventral; (*e*) aedeagus, lateral (apical half; arrow pointing at ventral lobes); (*f*) aedeagus, dorsal. Scale bars: 1 mm.

three undescribed species from Western Australia (Tangadee; Lake Cohen; Mt Jackson: WAM). In the last two the head is elongate, very narrow with frons and vertex depressed (Fig. 18*b*). The elytra are glabrous in all three.

VId. Gonostyli widely separated (Fig. 19*g–h*).

Aedeagus unarmed, with only an arcuate sclerotised bar at apex (Fig. 19*d–f*); distinctly longer than tegmen. Mesotarsomere II modified in male, with anterior surface concave, glabrous (Fig. 19*c*). A single pallid yellow species with glabrous elytra from Western Australia (Nyang; Carnarvon: ANIC) is placed here.

VIe. Male legs unique. Meso- and metafemora with a line of spiniform microsetae on ventral surface; metafemora additionally with a tuft of setae at middle and at apex; metatibiae fringed with dense, long setae (Fig. 20*h*). Last ventrite of male with elongate setae at apex (Fig. 20*b, i*).

Aedeagus unarmed, with dorsoapical surface noticeably emarginate in lateral view (Fig. 20*e–g*); gonoforceps as in Fig. 20*c, d*. The elytra are shiny blue metallic and setose. One undescribed species is placed here. It occurs in New South Wales (Pentland: BMNH), Queensland (Daintree; Hughenden; Cape York: BMNH), Northern Territory (Katharine: MRSN) and Western Australia (Margaret River: WAM).

VIf. Male antennae unique with segments VIII and X much shorter than their preceding segment (VII and IX, respectively) (Fig. 21*g*). Gonostyli abruptly bent dorsally and setose at apex (Fig. 21*d, e*).

Meso- and metatarsi modified; mesotarsal segments II–IV subglabrous, slightly swollen; metatarsal segments II–IV glabrous and flattened (Fig. 21*h*). Aedeagus unarmed; also lacking an apical sclerotised bar (Fig. 21*a–c*). A single species from Queensland (65 miles N Mareeba: CMNC; Desailly: ANIC; Mt Carbine ner Desailly: BMNH) is placed here (Fig. 21).

VIg. Male without any modifications of antennae or legs. Aedeagus unarmed; also lacking an apical sclerotised bar (Fig. 7*a, b*). Two small undescribed species from Queensland are placed here: one yellow (Tamborine: BPBM) and another bicoloured (orange with black head, apex of elytra and part of legs) from

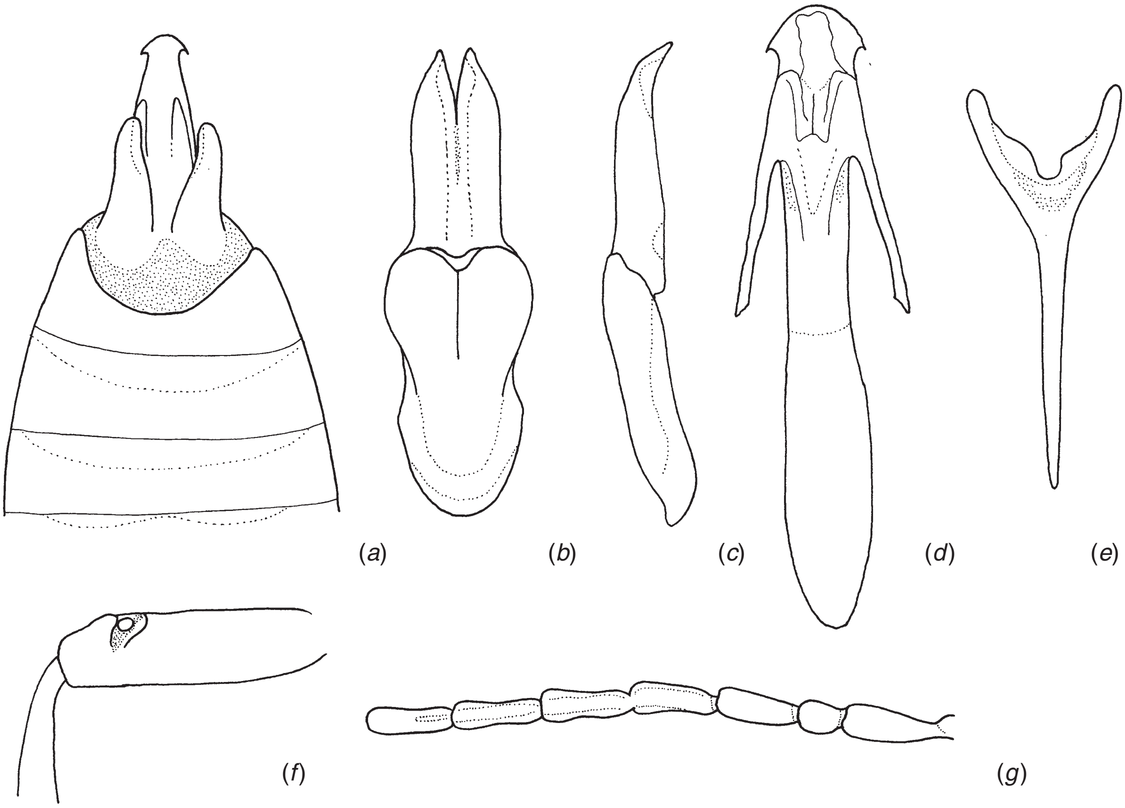

Fig. 12. *Palaestra purpureipennis* (Group IIa) (WA, Wanoo): (*a*) male last four abdominal sternites with extruded aedeagus; (*b*) tegmen, ventral; (*c*) tegmen, lateral; (*d*) aedeagus, dorsal; (*e*) spiculum gastrale; (*f*) male profemur and part of protibia, anterodorsal; (*g*) male antennomeres I–VII. Scale bars: 1 mm.

Cooper Creek (ANIC). (Fig. 7*a–d*). Although aedeagal anatomy places these species in *Palaestra* no other structural modifications occur.

Species referable to *Palaestra* but difficult to assign to group are *P. carpentariae* (Blackburn, 1899) (Fig. 7*e,f*) and *P. yorkensis* (Blackburn, 1899) from Australia, and the Ethiopian species *P. zavattarii* (Kaszab, 1949).

NEMOGNATHINI

With the exclusion of *Palaestra*, we are aware of ~40 Australasian species that remain in this tribe. They are distinguished from the Horiini by the characters listed in the first couplet of the tribal key. All except *Palaestrida* can be separated from Palaestrini by the relative length of antennomeres II and III. Features shared with all other Nemognathinae include the cylindrical and unarmed aedeagus and the unmodified antennae and legs in males.

Three Nemognathini groupings are recognisable in Australasia based primarily on aedeagal structure:

(i) A Palaeotropical–Australasian lineage, which includes *Zonitoschema* and *Australozonitis*, gen. nov. It is characterised by the paired non-sclerotised ventral aedeagal lobes, which appear to be bilobed, and 'sclerotised rings' in the terminal part of the sperm duct (Figs 8*h*, 10*c*). We are not aware of this form of duct sclerotisation in any other group of Meloidae. *Zonitoschema* and *Australozonitis* are closely related. Shape of eyes and antennae are the only clearly distinguishing features (see key). Most of the remaining Australasian species that we have studied are assigned to these genera. All were previously treated as *Zonitis*.

(ii) The second group includes only *Pulchrazonitis*, gen. nov., and is restricted to Australia. In this genus the aedeagus has two narrow and elongate ventral lobes, with the ventral surface of each lobe sclerotised. The genus is further distinguished by its highly modified gonostyli (see key).

(iii) This group is similar to other Old and New World Nemognathini such as *Nemognatha* Illiger, 1807 in that the aedeagus lacks ventral lobes. Included is the Australian endemic *Palaestrida*, characterised by its costate, setose elytra, and flat, symmetrically widened antennomeres. It also is the only Australasian member of its tribe with completely fused gonostyli. Two Australian species (tentatively = *brevicornis* group: *Z. murrayi* and *Z. brevicornis*, *incertae sedis*) also are included here (Fig. 8*f, g*). The *brevicornis* group seems closest to *Nemognatha* but lacks the modified maxillary galeae and other derived features which characterise that genus.

Australozonitis Bologna, Turco & Pinto, gen. nov.

(Figs 2*b*, 9, 10*b–h*, 22)

Type species: *Zonitis tricolor* Le Guillou, 1844, by present designation.

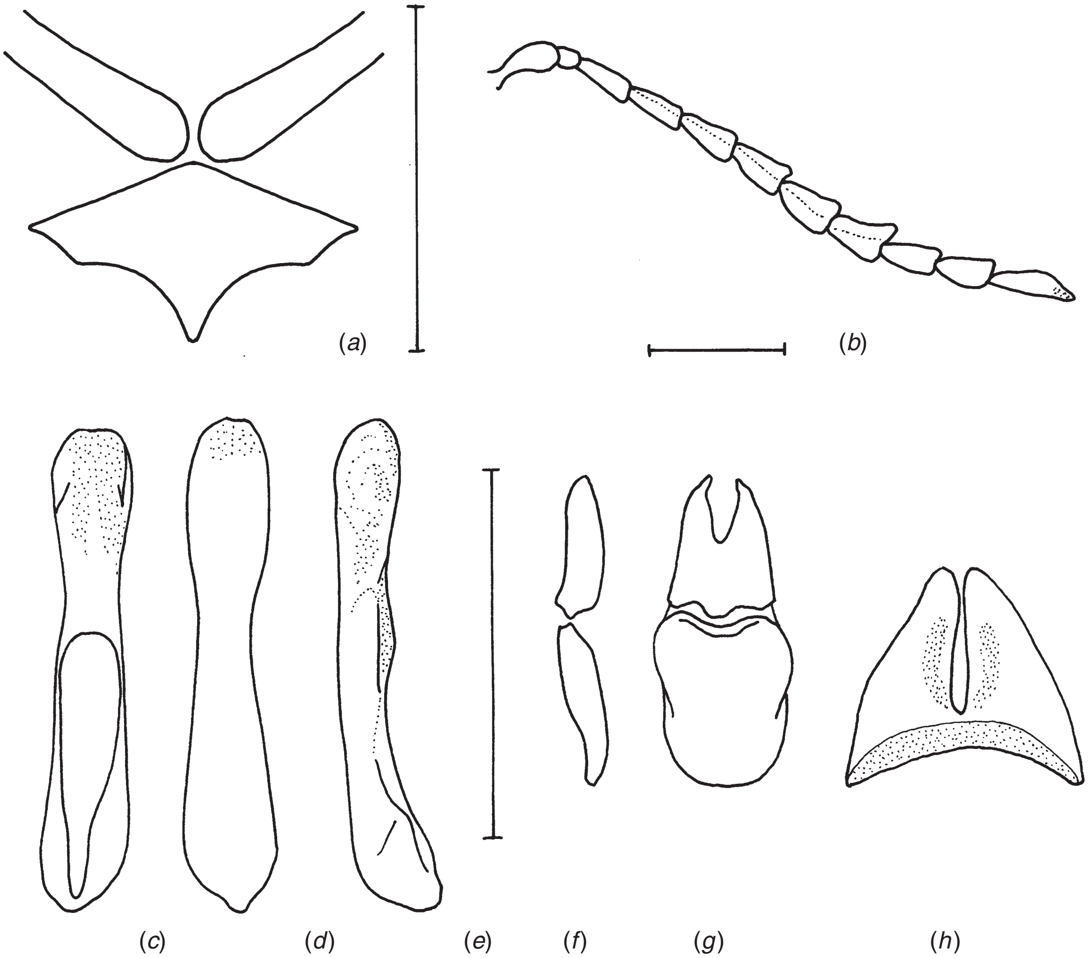

Fig. 13. *Palaestra* sp. (Group IIIb) (Timber Creek): (*a*) mesepisterna and mesosternum; (*b*) male right antenna; (*c*) aedeagus, dorsal; (*d*) aedeagus, ventral; (*e*) aedeagus, lateral; (*f*) tegmen, lateral; (*g*) tegmen, ventral; (*h*) male last abdominal sternite. Scale bars: 1 mm.

Etymology

From the Latin adjective '*australis*' meaning southern and *Zonitis*, the name of the genus to which most of the Australian species were previously referred.

Description

Variously coloured but usually not completely metallic; surface shiny or opaque; sparsely to moderately densely setose. Head with frons not distinctly depressed; eyes narrow and short, usually not extending on underside of head (except *A. lutea* and relatives); labrum apically rounded; mandibles, at most, extending slightly beyond labrum; antennae subfiliform, antennomere II about as long as III, VIII less than 6× as long as wide. Pronotum slightly longer than wide; legs simple, never sexually dimorphic; elytra not costate (except weakly so in *A. opacorufa* and another unidentified species), with short setae particularly posteriorly; both metatibial spurs narrow, inner spur pointed, outer spur rounded at apex; mesopleural marginal areas very wide. Abdominal tergum IX in both sexes present or absent; male ventrite VIII completely divided, hemisternites slightly depressed medially (Fig. 22*b*). Aedeagus cylindrical and unarmed, with distinct but poorly sclerotised ventral lobes (Figs 9*a, b*, 10*b, c, e, f*, 22*e*); sperm duct*s* with a series of sclerotised, parallel ridges or rings near apex (Fig. 10*c*); gonostyli relatively straight, slightly compressed dorsoventrally, divided near apical fifth to form two rounded lobes; gonocoxal piece longer than wide, gibbose ventrally (Figs 9*c–f*, 10*d, g, h*, 22*c, d*).

Relationships

Eighteen species from Australia, New Guinea and the Solomon Islands are removed from *Zonitis* and placed in *Australozonitis*. An African species, identified in the British Museum as *Zonitis latipennis* (see 'Introduction') also belongs here and we suspect that other Afrotropical and perhaps Asian species will require transfer when these faunas become better known. This diverse assemblage clearly is most closely related to *Zonitoschema* and not to *Zonitis*. Aedeagal structure, the same in both, is unique within the subfamily. In these genera, the ventral lobes of the aedeagus are present but poorly sclerotised and the apical portion of the sperm duct is reinforced with a series of sclerotised parallel rings or ridges. In *Zonitis* and related genera such as

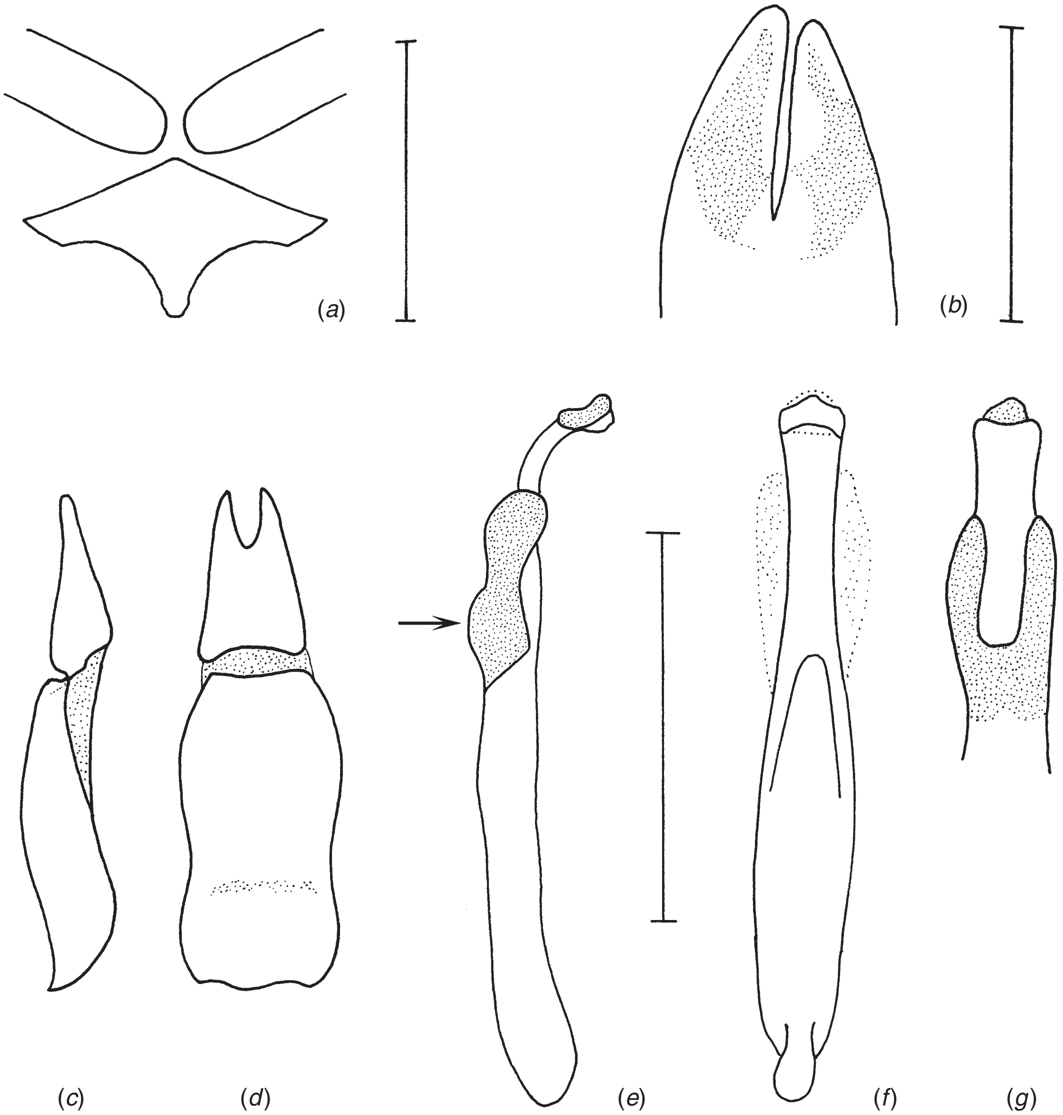

Fig. 14. *Palaestra* sp. (Group IV) (WA, Newman): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) tegmen, lateral; (*d*) tegmen, ventral; (*e*) aedeagus, lateral (arrow pointing at ventral lobes); (*f*) aedeagus, dorsal; (*g*) aedeagus, ventral (apical third). Scale bars: 1 mm.

Megatrachelus and *Euzonitis*, the two ventral lobes are considerably larger, well sclerotised and not individually bilobed, and the sperm duct is uniformly sclerotised much of its length. The sclerotised rings (Fig. 10*c*) are probably composed of micro-spicules as is the uniformly sclerotised portion of the duct in many other Meloidae (Bologna 1991). Additionally, unlike first instar larvae of species presumed to belong to *Australozonitis*, *Zonitis* lacks caudal setae (Di Giulio *et al.* 2010*b*).

Australozonitis and *Zonitoschema* are separable only by eye size and antennal length. In most species the distinction is clear. In *Australozonitis* the eyes usually are small and barely extend beneath the head, whereas in *Zonitoschema* they are bulging, extend ventrally beyond the inner margin of the maxilla and almost contact each other. Similarly, the antennae are generally quite distinct with antennomere VIII at least 6× as long as wide in *Zonitoschema* but considerably shorter in *Australozonitis*. The apparently nocturnal *A. lutea* and related species have larger eyes and longer antennae than congeners but remain distinguishable from *Zonitoschema*.

The species referred to *Australozonitis* are indicated in Appendix 1; additional information also is given in the synopsis.

Pulchrazonitis Bologna, Turco & Pinto, gen. nov.

(Figs 2*d*, 23)

Type species: *Zonitis splendida* Fairmaire, 1879, by present designation.

Etymology

From the Latin female adjective ‘*pulchra*’ meaning beautiful, and *Zonitis*.

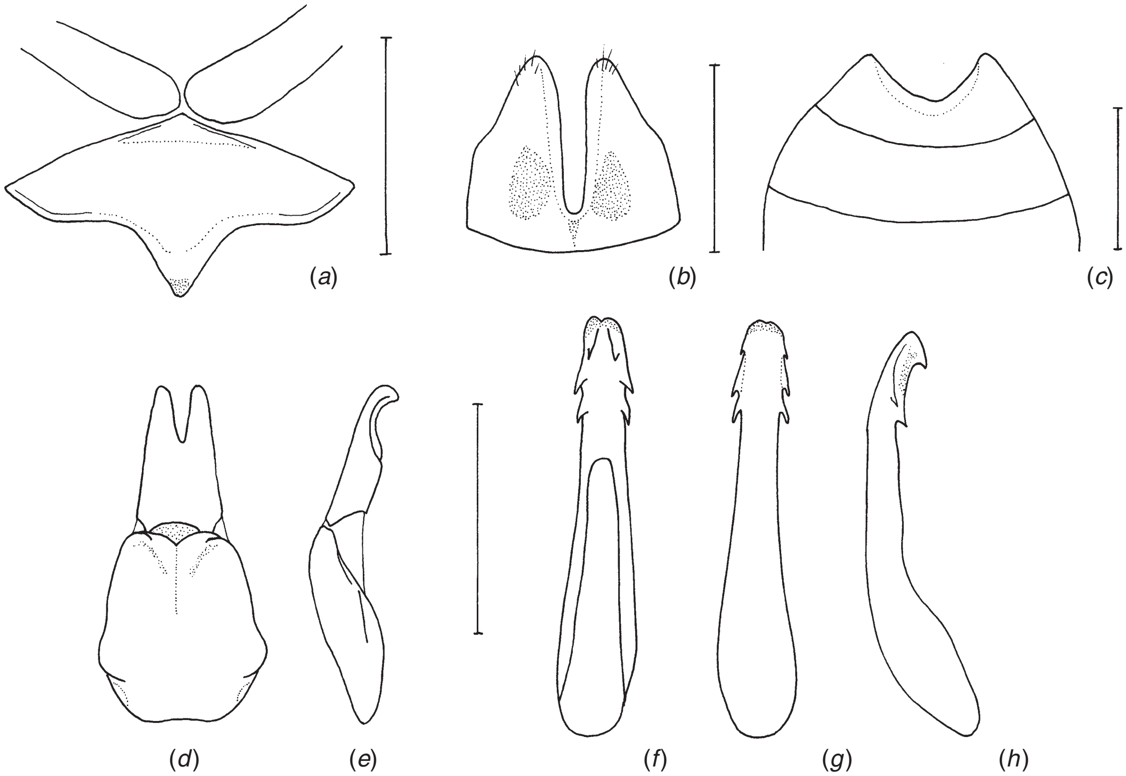

Fig. 15. *Palaestra* sp. (Group VIa) (Papua New Guinea, Madang district, Finistere Mts): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) male abdominal visible sternites III–V; (*d*) tegmen, ventral; (*e*) tegmen, lateral; (*f*) aedeagus, dorsal; (*g*) aedeagus, ventral; (*h*) aedeagus, lateral. Scale bars: 1 mm.

Description

Monotypic. Dark brown or almost black except elytra blue-green or purple-green, with a violet lustre, iridescent; surface shiny dorsally, subopaque ventrally, elytra densely micropunctate. Head smooth, short, subtriangular, frons not distinctly depressed (Fig. 23*b*); eyes large but not bulging, extending ventrally to inner margin of maxillae on underside of head, not contacting at middle; mandibles long, extending to foremargin of labrum; galeae short and fringed; antennomere II about as long as III, antennomeres cylindrical, VIII 4–5 × as long as wide, male antennomere XI abruptly narrowed in apical third. Pronotum smooth, about as wide as long; legs not modified in either sex; claws with ventral blade narrow; metatibial spurs narrow, narrowly rounded apically; elytra neither costate nor setose, almost smooth, very convex, particularly posteriorly, slightly sinuate apically in lateral view. Abdominal tergum IX present in both sexes, male ventrite VIII completely divided, each hemisternite slightly depressed medially. Aedeagus subcylindrical, unarmed, ventral lobes narrow and elongate, with ventral surface of each lobe sclerotised (Fig. 23*d, e*); sperm duct uniformly and lightly sclerotised along its apical section; gonostyli distinctly separate at apex, slender, sinuate in lateral view with a pair of beak-like ventral projections at apex, and a pair of larger, dorsal hooks subapically; gonocoxal piece longer than wide, gibbous ventrally (Fig. 23*f, g*).

Relationships

The unique features of the aedeagus and gonoforceps clearly distinguish *Pulchrazonitis* from other nemognathine genera. The presence of ventral lobes is shared with several genera including *Zonitoschema* and *Australozonitis*, but their structure in *Pulchrazonitis* also is distinctive. The uniform sclerotisation of the sperm duct is similar to *Zonitis* and other Old World nemognathine genera.

Additional information on this new genus is given in the synopsis.

Synopsis of the Australasian genera of Meloidae

Subfamily **NEMOGNATHINAE**

Tribe **PALAESTRINI** new tribe (see ‘Taxonomy’ section)

1. ***Palaestra*** Laporte de Castelnau, 1840: 251. (Fig. 1*a–c*)

Tmesidera Westwood, 1841: 1. *Type species*: *Tmesidera rufipennis* Westwood, 1841, by monotypy.

Type species: *Palaestra rubripennis* Laporte de Castelnau, 1840: 251, by monotypy. Ca 34 spp. (29 described and several undescribed from Australasia, see appendices I and II). Based on descriptions, certain

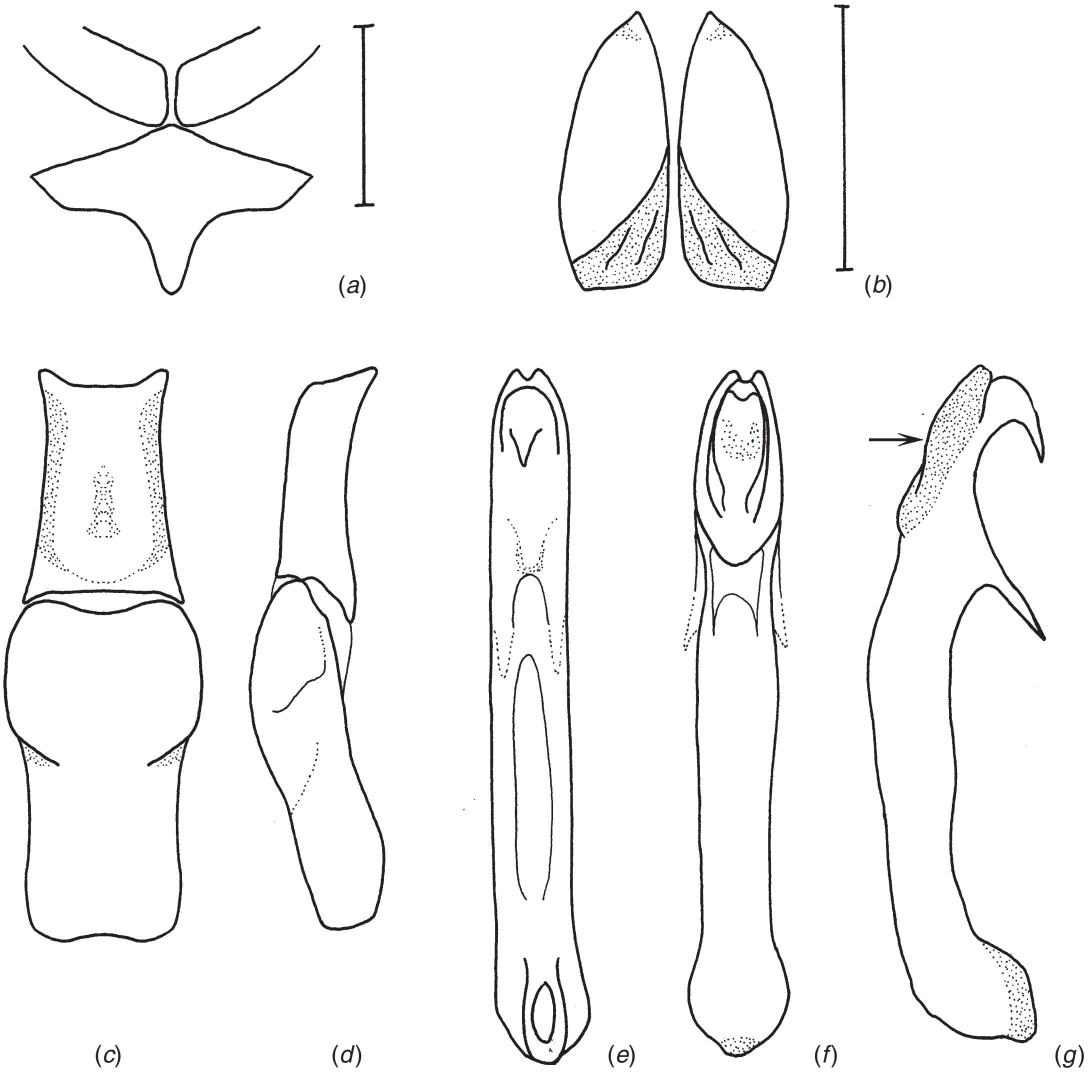

Fig. 16. *Palaestra* sp. (Group VIb) (NT, Alice Springs): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) tegmen, ventral; (*d*) tegmen, lateral; (*e*) aedeagus, dorsal; (*f*) aedeagus, ventral; (*g*) aedeagus, lateral (arrow pointing at ventral lobes). Scale bars: 1 mm.

unexamined '*Zonitis*' species from Australasia, south-eastern Asia, Africa and Madagascar could belong to *Palaestra*.

Geographic distribution

Eastern Africa (from Ethiopia south to Zambia); southern Israel, Sri Lanka, Indochina, Australasia (Micronesia, New Guinea, Melanesia, Australia and western Polynesia).

References

Taxonomy. Westwood 1841; Fairmaire 1880; Blackburn 1889, 1899 (partial key); Lea 1914, 1916, 1917; Blair 1920 (key to the lycid mimicking species). Several species are treated as *Zonitis* by these authors.

Bionomics. Houston, 1984, 1987; Di Giulio *et al*. 2010*b*.

Larvae. Bologna and Pinto 2001; Di Giulio *et al*. 2010*a*, 2010*b*.

Anatomy. Kaszab 1959.

Notes

A considerably expanded definition of *Palaestra* is proposed in the taxonomic section. Numerous undescribed species exist in collections. In Appendices 1 and 3 we list, respectively, the Australasian and extraterritorial species referable to this genus based on the examination of types, descriptions or identified specimens.

The first instar larvae of three species have been described (two unidentified to species); they are phoretic and were collected on adults of *Ctenocolletes smaragdinus* (Smith), *Ctenocolletes nicholsoni* (Cockerell) and *Ctenocolletes tigris* Houston. They may be parasitoids of these Australian Stenotritidae bees (Houston 1984, 1987; Di Giulio *et al*. 2010*b*), although phoretic associations in Meloidae do not necessarily imply host associations (Pinto and Selander 1970). Adults of various species were collected on flowers of the following plant families and genera: Commelinaceae (*Commelina*), Fabaceae (*Acacia*,

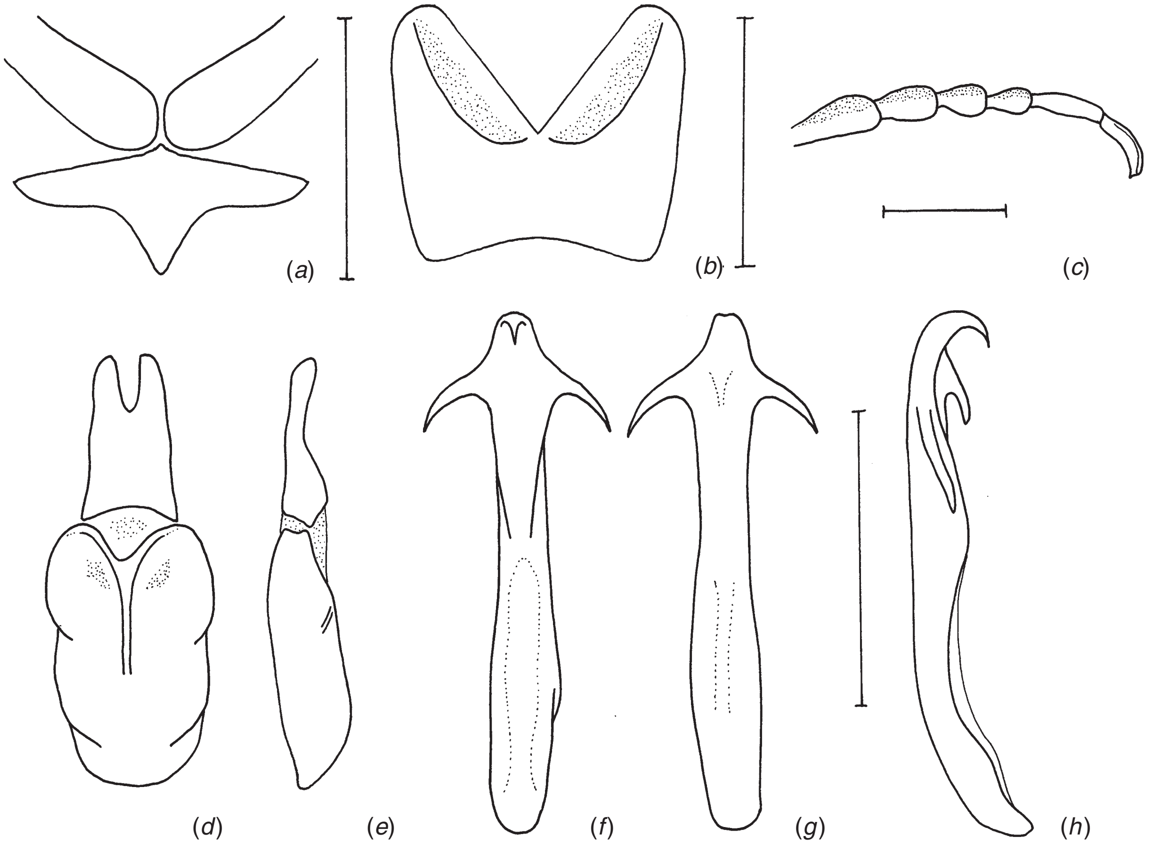

Fig. 17. *Palaestra* sp. (Group VIb) (WA, Bullfinch): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) male mesotarsomeres (lateral view); (*d*) tegmen, ventral; (*e*) tegmen, lateral; (*f*) aedeagus, dorsal; (*g*) aedeagus, ventral; (*h*) aedeagus, lateral. Scale bars: 1 mm.

Psoralea), Goupiaceae (*Goupia*), Myoporaceae (*Eremophila*), Myrtaceae (*Leptospermum*, *Micromyrtus*), Pittosporaceae (*Bursaria*), Poaceae (*Miscanthus*) and Thymelaeaceae (*Pimelia*). A few species, such as *P. helmsi*, are collected at light and probably are nocturnal. Adult seasonal distribution varies greatly. The following indicate the month (as Roman numerals) collections were made in the various geographic areas: Micronesia (v, xii), Melanesia (Fiji: ii, vi), New Guinea (xi), Australia (Queensland: i, ii, iv, xi, xii; Northern Territory: i, iii, xii; New South Wales: i, viii, x, xii; ACT: i; Victoria: x; Tasmania: xii; South Australia: viii, ix, xi; Western Australia: i, ii, vii, viii, ix, x, xii).

Tribe **HORIINI**

2. ***Horia*** Fabricius, 1787: 164. (Fig. 1*d*)

Hoplozonitis Blackburn, 1892: 228. *Type species*: *Hoplozonitis mira* Blackburn, 1892, by monotypy.

Type species: *Lymexylon testaceum* Fabricius, 1781 (= *Horia fabriciana* Betrem, 1929). Designated by Betrem, 1929. Eight spp. (two spp. in Australasia).

Geographic distribution

Afrotropical, southern Palaearctic, Oriental regions and Australasia (New Guinea and northern Australia) (Bologna and Pinto 2002 for details).

References

Taxonomy. Blackburn 1892; Gahan 1908, 1909; Cros 1924, 1927; Betrem 1929, 1932 (revision and key).

Bionomics. Bugnion 1910; Schroo 1920; Blair 1924; Cros 1938*a*; Mohamedsaid 1979; Bologna and Laurenzi 1994 (synthesis).

Larvae. Bugnion 1910; Cros 1924, 1929, 1938*a*, 1938*b*; Bologna and Laurenzi 1994; Bologna and Pinto 2001.

Notes

Two species of *Horia* occur in Australasia: *Horia mira* Blackburn, 1892 is known from Cape York and Chillagoe (QDPC) in northern Queensland; *H. blairi* Betrem, 1932 was described from New Guinea and also occurs in Queensland, Carmila (QMBA). Types of both species (at BMNH) were compared and their distinctness based on colour and shape of the male metafemur was confirmed. We also are aware of a small

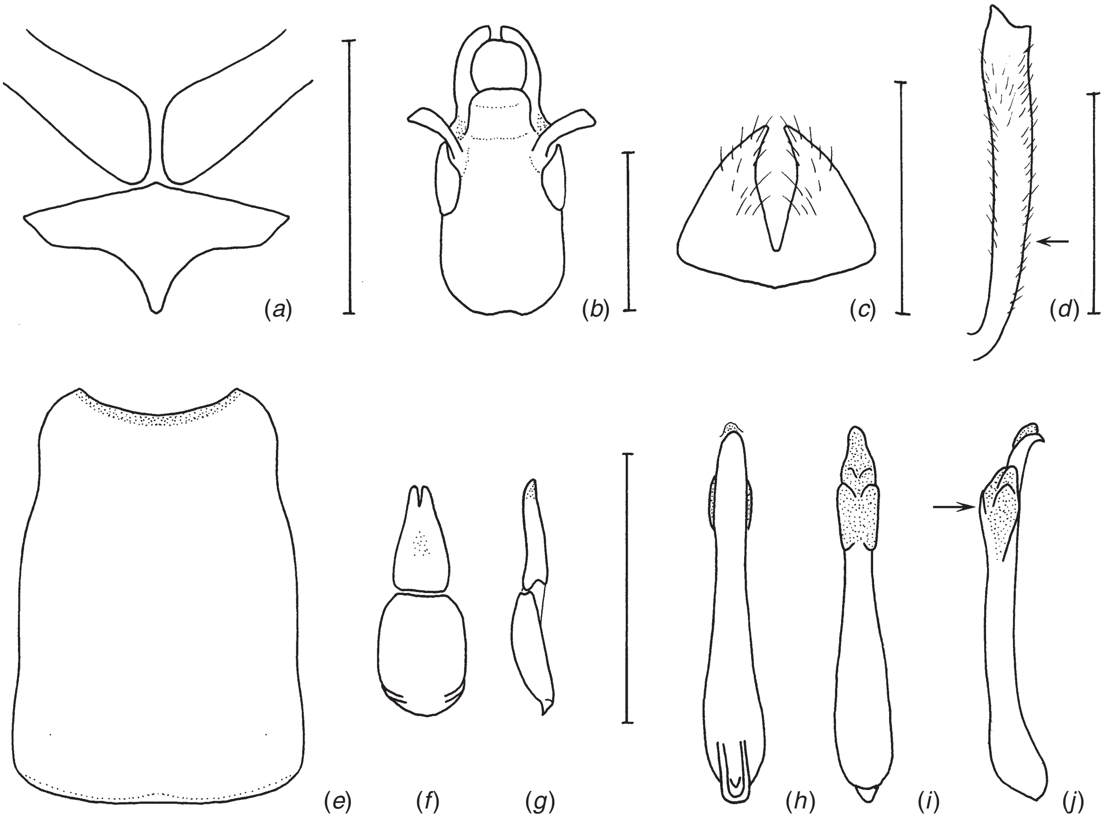

Fig. 18. *Palaestra* sp. (Group VIc) (WA, Mt Jackson): (*a*) mesepisterna and mesosternum; (*b*) head (dorsal view); (*c*) male last abdominal sternite; (*d*) male right protibia (posterior view; arrow pointing at dorsal spines); (*e*) pronotum (dorsal view); (*f*) tegmen, ventral; (*g*) tegmen, lateral; (*h*) aedeagus, dorsal; (*i*) aedeagus, ventral; (*j*) aedeagus, lateral (arrow pointing at ventral lobes). Scale bars: 1 mm.

number of *Horia* unidentified to species in ANIC and WAM. All are from coastal localities in northern and north-eastern Australia (Western Australia, Queensland).

Betrem's (1932) revision of *Horia* did not treat *H. mira* in detail and it is not included in the key to species. A comparison of *H. mira* with the Indonesian species *H. debyi* (Fairmaire, 1885) and *H. roepkei* Betrem, 1932 is needed.

We also studied 14 specimens collected in Papua New Guinea (Port Moresby) held at MSNG that may be assigned to a new species closely related to *H. blairi*.

The first instar larvae of three African and Oriental species are described; they are phoretic and parasitoids of anthophorine bees (Apidae).

3. ***Synhoria*** Kolbe, 1897: 256

Type species: *Horia cephalotes* Olivier, 1792, by subsequent designation (Cros 1924). Five spp. (one sp. in Australasia).

Geographic distribution

Afrotropical (including Madagascar and Comore Islands), Oriental (Indochina, China, Japan, Taiwan, Philippines and Indonesia), and Australasian regions (E Wallacea; New Guinea; Australia: northern Queensland; Northern Territory, Darwin).

References

Taxonomy. Gahan 1908; Cros 1924, 1938*a*, 1938*b*; Betrem 1929, 1932 (revision and key); Kôno 1936; Paulian 1956; Bologna 1978, 1994.

Bionomics. Cros 1924, 1938*a*, 1938*b*; Ishida 1982; Taketsuka 1984, 1986, 1989*a*, 1989*b*; Gess 1981; Bologna and Laurenzi 1994 (review).

Larvae. Cros 1924, 1938*a*, 1938*b*; Bologna and Laurenzi 1994 (review).

Anatomy. Beauregard 1890; Gupta 1971, 1978.

Notes

The validity of the four Afrotropical species needs confirmation due to extreme intraspecific variability.

One species of this genus, *S. maxillosa* (Fabricius, 1801), widely spread from China to Indonesia, also occurs on Halmahera and the Buru islands (Betrem 1932; Borchmann 1932), and in New Guinea (Mimika River: Blair 1915; Bara Bara: MSNG). We know of one specimen of *Synhoria maxillosa* from northern Queensland (Garradunga, NE Innisfail: QDPC). Another specimen collected in 'Darwin, NT, 5.xii.78' (ANIC) is labelled 'ex packing around timber from SE Asia'.

The first and other larval instars have been described. The genus is phoretic; larvae are parasitoids of anthophorine bees (Apidae).

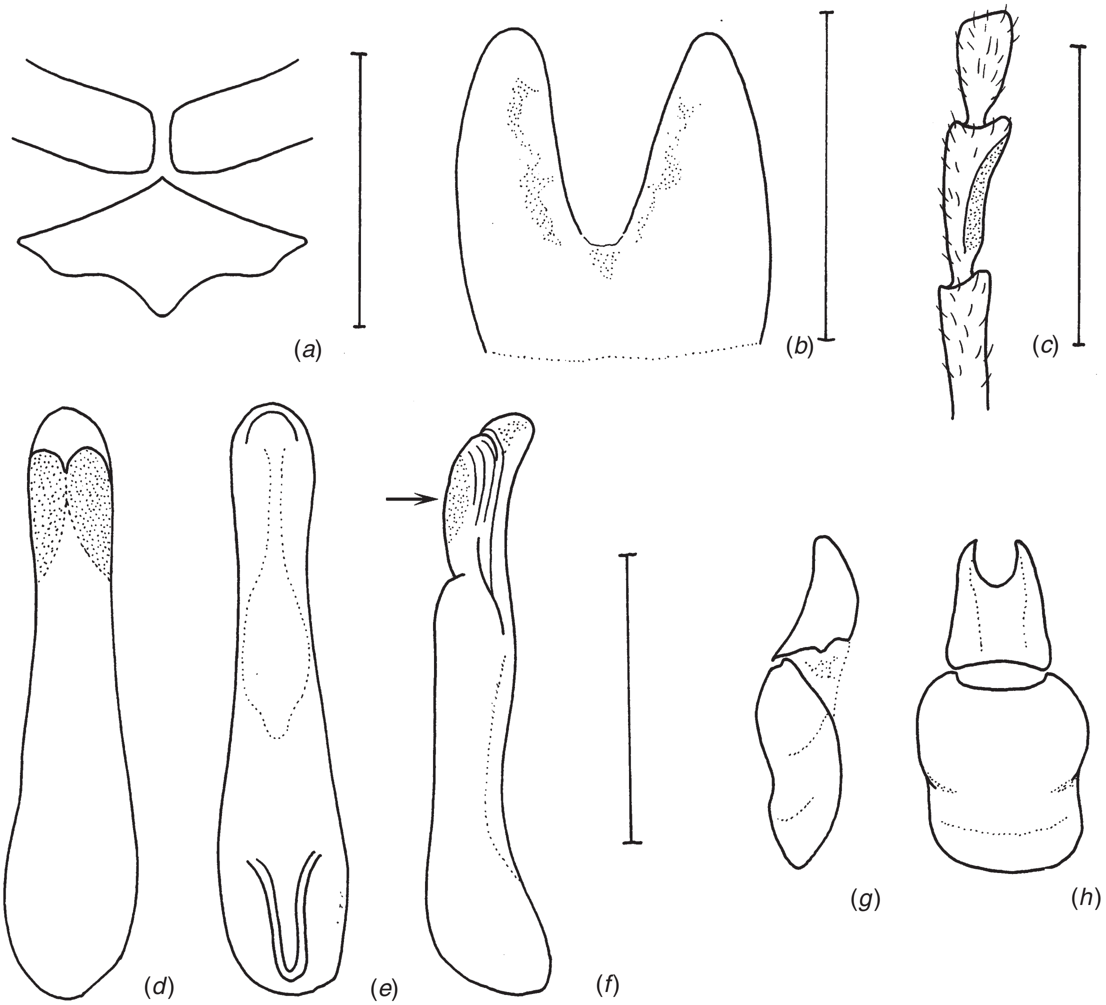

Fig. 19. *Palaestra* sp. (Group VId) (WA, Nyang): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) male mesotarsomeres I–III (dorsal view); (*d*) aedeagus, ventral; (*e*) aedeagus, dorsal; (*f*) aedeagus, lateral (arrow pointing at ventral lobes); (*g*) tegmen, lateral; (*h*) tegmen, ventral. Scale bars: 1 mm.

Tribe **NEMOGNATHINI**

4. ***Palaestrida*** White, 1846: 509. (Fig. 2*a*)

Type species: *Palaestrida bicolor* White, 1846, by monotypy, synonym of *Tmesidera assimilis* Hope, 1842. One species.

Geographic distribution

Endemic to Australia (Western Australia, South Australia, Victoria, New South Wales, Queensland, Tasmania).

References

Taxonomy. Blair 1920 (revision).

Notes

The monotypic *Palaestrida* is broadly distributed in Australia. Blair (1920) noted considerable intraspecific variation in *P. assimilis* and the existence of additional species cannot be precluded. No information exists on host plants. In Queensland adult activity seems restricted to January and December.

5. ***Australozonitis***, new genus (see 'Taxonomy' section) (Fig. 2*b*)

Type species: *Zonitis tricolor* Le Guillou, 1844, by present designation.

Eighteen nominal species. Several additional species are undescribed. There also may be others among the unexamined species tentatively retained in '*Zonitis*' as *incertae sedis* (Appendix 2).

Geographic distribution

Australasian region. Known to occur in New Guinea, Melanesia (Solomon Islands) and Australia, Tasmania included. We also know of one Afrotropical species from Malawi that belongs here (identified in BMNH as *Zonitis latipennis*).

References

Taxonomy. Fairmaire 1880; Blackburn 1889, 1899; Lea 1914, 1916, 1917. Several species were treated as *Zonitis* by these authors.

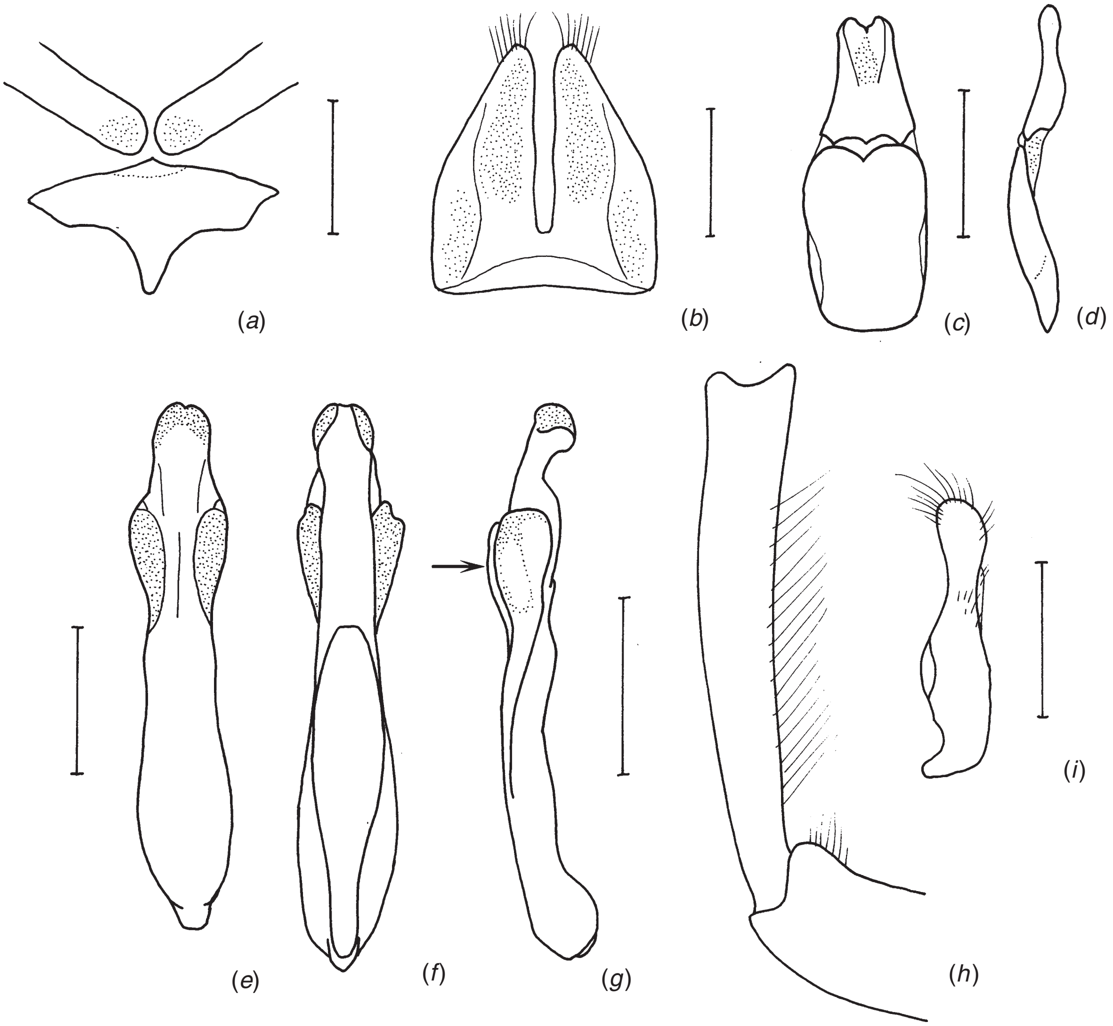

Fig. 20. *Palaestra* sp. (Group VIe) (WA, Margaret River): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) tegmen, ventral; (*d*) tegmen, lateral; (*e*) aedeagus, ventral; (*f*) aedeagus, dorsal; (*g*) aedeagus, lateral (arrow pointing at ventral lobes); (*h*) male left metatibia (anterior view); (*i*) male last hemisternite (lateral view). Scale bars: 1 mm.

Notes

The first instar larvae of seven unidentified species of Australian Nemognathini were described recently (Group 2 species in Di Giulio *et al.* 2010*b*). Although the three other Australian genera of the tribe cannot be discounted, it is likely that most, if not all, represent *Australozonitis*. None were associated with adults. Three of the species were taken from adult Stenotritidae bees of the genus *Ctenocolletes* (Houston 1984, 1987; Di Giulio *et al.* 2010*b*). The others were found attached to adult blister beetles, *Palaestra purpureipennis* and *Australozonitis handschini* (Borchmann), or taken in Malaise trap samples.

Adults of *Australozonitis* have been collected from the following plant families: Asteraceae (*Zinnia*), Myrtaceae (*Leptospermum*), Polygonaceae (*Fuchsia*, *Antigonum*). Some species, such as *A. lutea* and relatives were collected at light traps and appear to be nocturnal. Adult seasonal distribution is variable. The following indicate the months of collection (as Roman numerals) in the various geographic areas: Melanesia (Solomon Islands: ii, iv, vii, viii, ix, xii), New Guinea (iv, v), Australia (Queensland: i, iv, xi, xii; Northern Territory: iii, xii; New South Wales: i, ii, ix, x, xi, xii; ACT: i, xi, xii; South Australia: i; Western Australia: ix, xi).

6. ***Zonitoschema*** Péringuey, 1909: 274. (Fig. 2*c*)

Zonitoides Fairmaire, 1883: 31. (nec *Zonitoides* Lehman, 1862 (Gastropoda)); replaced by *Zonitopsis* Wellman.

Zonitopsis Wellman, 1910: 395. *Type species*: *Zonitoides megalops* Fairmaire, 1883, by monotypy as type species of *Zonitoides* Fairmaire; new name for *Zonitoides* Fairmaire.

Stenoderistella Reitter, 1911: 395. *Type species*: *Stenodera pallidissima* Reitter, 1908, by monotypy.

Type species: *Lytta coccinea* Fabricius, 1801, by subsequent designation (Aksentjev 1988). About 60 species (six nominal species in Australasia, plus some undescribed).

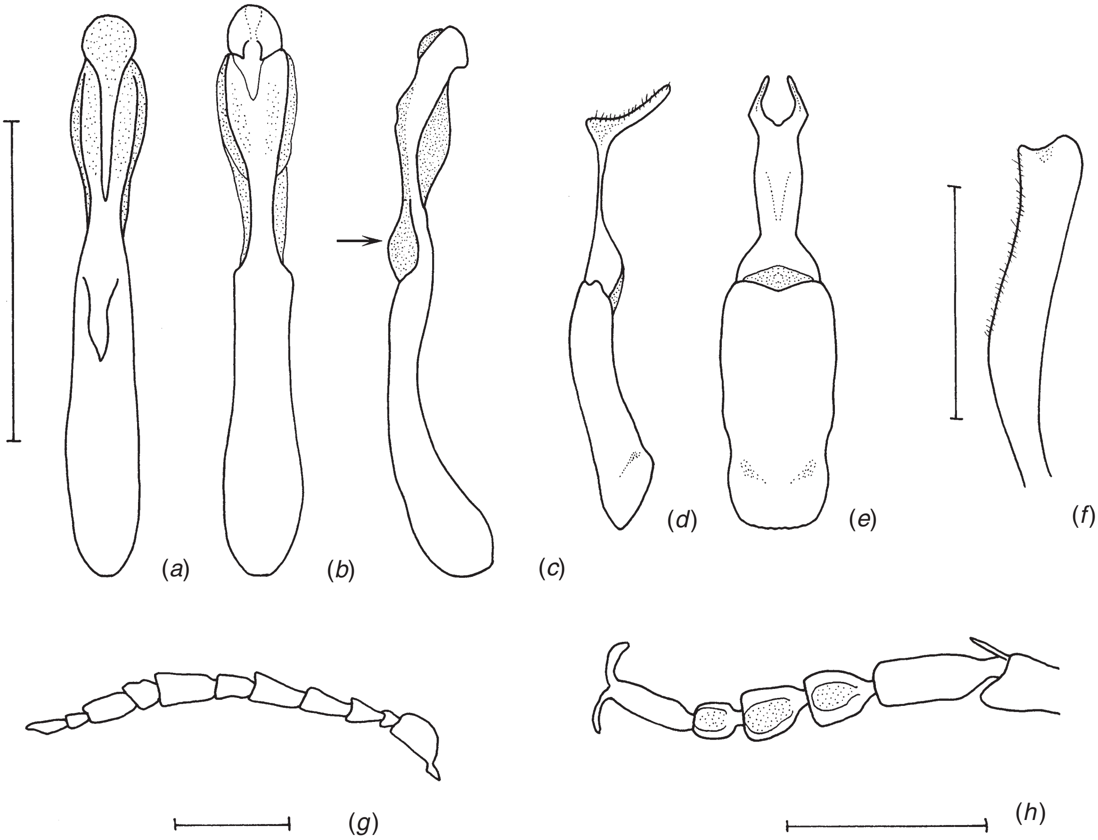

Fig. 21. *Palaestra* sp. (Group VIf) (QLD, Desailly, Mt Carbine): (*a*) aedeagus, ventral; (*b*) aedeagus, dorsal; (*c*) aedeagus, lateral (arrow pointing at ventral lobes); (*d*) tegmen, lateral; (*e*) tegmen, ventral; (*f*) male left protibia (anterior view); (*g*) male left antenna; (*h*) male mesotarsomeres (ventral view). Scale bars: 1 mm.

Geographic distribution

Afrotropical and Oriental regions, southern and eastern Palaearctic (Sahara, Levant, Arabian Peninsula, Iran, China, Japan, Taiwan and Korea) and Australasia (New Guinea, some Melanesian and Micronesian islands, northern Australia).

References

Taxonomy. Péringuey 1909 (partial key to South African spp.); Pic 1911; Kaszab 1960, 1962, 1983; Pardo Alcaide 1966; Mohamedsaid 1981; Bologna 1990.
Bionomics. Peyerimhoff 1931; Iwata 1933; Kifune 1961; Maeta 1978; Gess 1981.
Larvae. Iwata 1933; Kifune 1961.
Anatomy. Gupta 1971, 1978.

Notes

Aedeagus structure indicates that *Zonitoschema* is closest to *Australozonitis*. Earlier suggestions of close relationship and possible synonymy of *Zonitoschema* and the New World *Pseudozonitis* (Enns 1956; Pinto and Bologna 1999) is not supported by current studies. Species in both genera are primarily nocturnal and their resemblance is likely due to convergence. Similarly, a group of nocturnal Afrotropical species currently placed in *Zonitoschema* and listed in Appendix 3 as *incertae sedis* almost certainly represents another lineage based on its distinctive antennal and male genitalic structure (compare aedeagal structures, Figs 8*c* vs 8*h*).

Numerous undescribed species of this genus exist in collections. As noted by Bologna and Pinto (2002), some poorly known species described as *Zonitis* may belong to *Zonitoschema.*

The first-instar larva is phoretic. The larva is known for a single Japanese species. It develops as a parasitoid of Megachilidae (Kifune 1961), as does another species from southern Africa (Gess 1981).

Host plants are unknown. All probably are nocturnal. Two species from Queensland and the Solomon Islands, respectively, were collected at light in forested areas, an uncommon habitat for Meloidae. Certain Afrotropical species also were taken at light. Adult seasonal distribution as follows (months indicated in parentheses as Roman numerals): Melanesia (Solomon Islands: i, ii, iv, v, vi, ix, x, xii), New Guinea (ix, x), Australia (Queensland: vii, viii, x, xi).

Pulchrazonitis new genus (see 'Taxonomy' section) (Fig. 2*d*)

Type species: *Zonitis splendida* Fairmaire, 1879: 46, by present designation. One species.

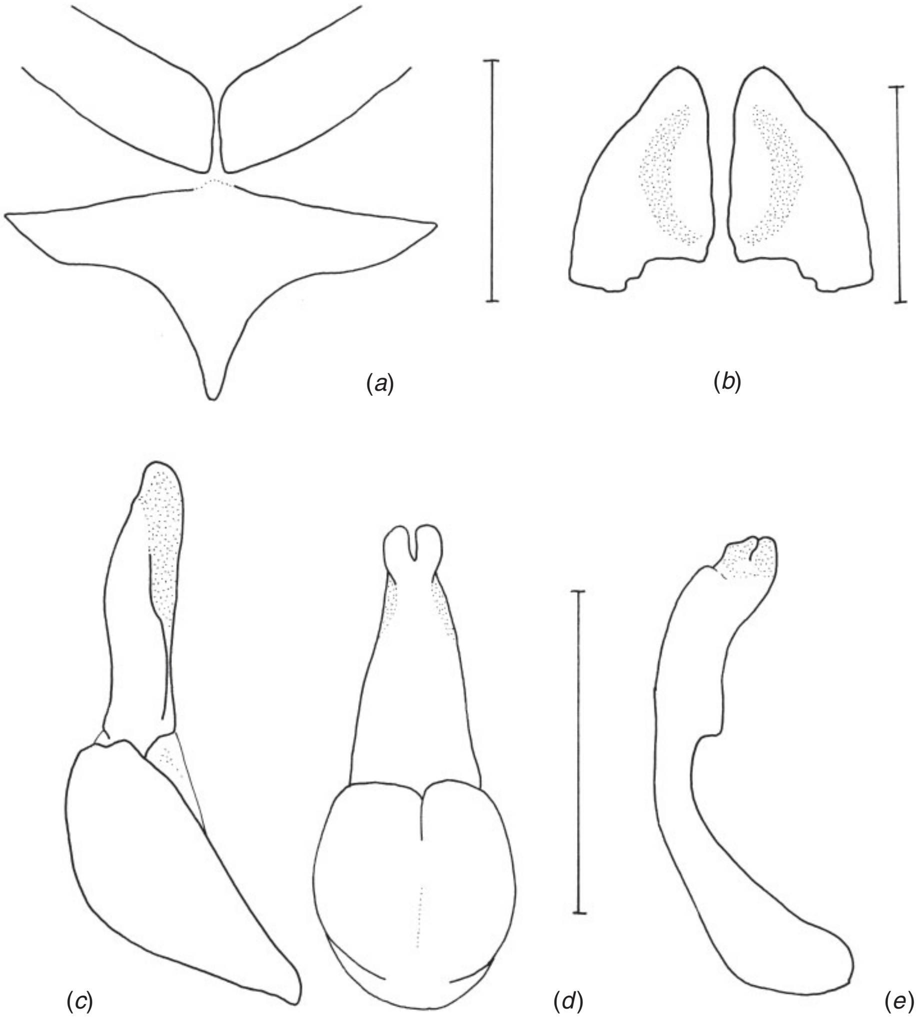

Fig. 22. *Australozonitis tricolor* (NSW, Bell): (*a*) mesepisterna and mesosternum; (*b*) male last abdominal sternite; (*c*) tegmen, lateral; (*d*) tegmen, ventral; (*e*) aedeagus, lateral. Scale bars: 1 mm.

Geographic distribution.

Endemic to Australia (Western Australia and South Australia).

References

Taxonomy. Fairmaire 1879, 1880; Blackburn 1899; Lea 1914.

Notes

The genus is monotypic. Lea (1914) considered *Zonitis gloriosa* Blackburn, 1899, from South Australia, as a synonym of *splendida*. This requires confirmation.

Host plants are unknown. Adults from Western Australia have been collected in January, February and November.

Discussion

The Meloidae of Australasia have been virtually ignored since the early decades of the 20th century. Perhaps this is due partly to an assumption by specialists that, with most species assigned to the cosmopolitan *Zonitis*, the fauna lacked distinction beyond a few novel lycid mimics. If Lea's (1914) observation that males of certain '*Zonitis*' possessed 'a curious notch on the front femora' had been followed up with an examination of genitalia in those species, it would have immediately alerted workers of a distinctive faunal element. In any event, it is now clear that the Australasian component of the family is more complex than previously thought. *Zonitis* does not occur in the region. A large group of species placed there are transferred to *Palaestra*, the genus previously restricted to lycid mimics. Several others are closest to *Zonitoschema* and treated in the new genus *Australozonitis*. Other Australian elements include the endemic monotypic genera, *Palaestrida* and *Pulchrazonitis*, the *brevicornis* group (*incertae sedis*), as well as the relatively widespread *Horia* and *Synhoria*.

The only tribe of the subfamily not occurring in Australasia is the non-phoretic Stenoderini. None of the three tribes that do occur is restricted to the region. The Australasian fauna is most similar to that of the Afrotropical and Oriental regions at the tribal and generic levels; there is no generic overlap with North or South America. Known distribution of the monotypic Palaestrini is from eastern Africa, north marginally to the southern

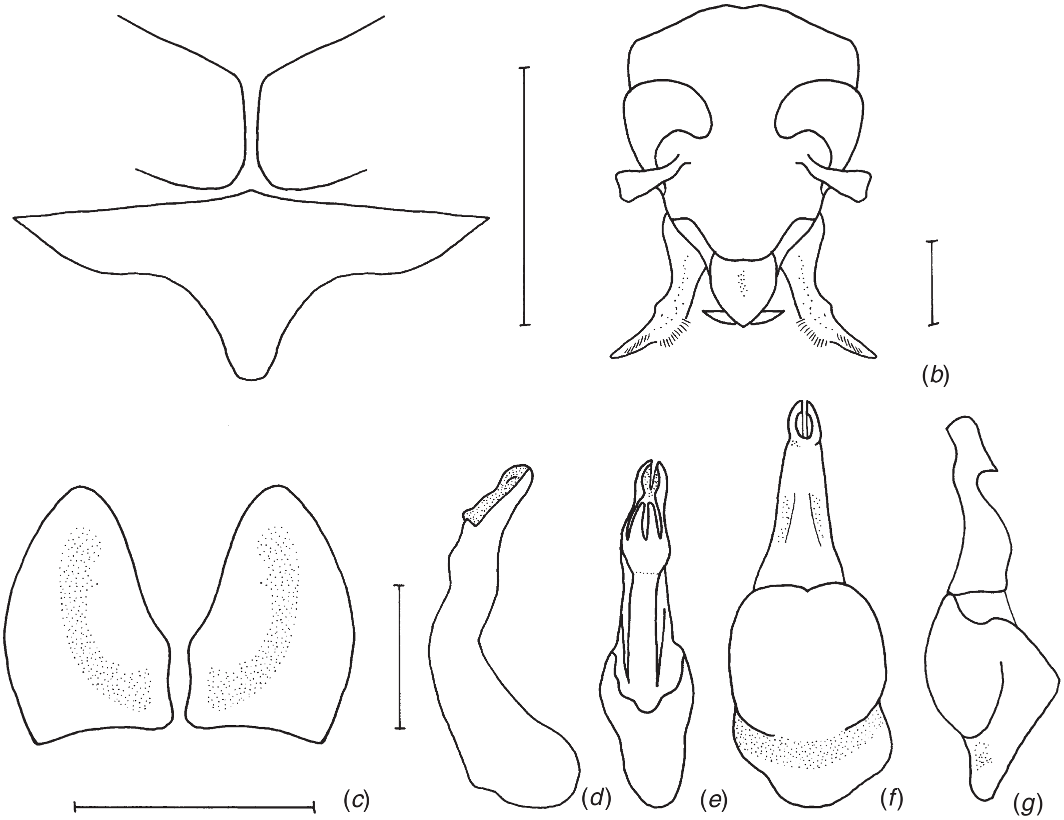

Fig. 23. *Pulchrazonitis splendida* (WA, Wilga): (*a*) mesepisterna and mesosternum; (*b*) head, dorsal; (*c*) male last abdominal sternite; (*d*) aedeagus, lateral; (*e*) aedeagus, ventral; (*f*) tegmen, dorsal; (*g*) tegmen, lateral. Scale bars: 1 mm.

Palaearctic (Negev), east to the Orient and into Australasia where *Palaestra* experienced major diversification. The Horiini are similarly distributed except one genus, *Cissites*, also occurs in the New World. The horiines reach but apparently have not penetrated deeply into Australia, being restricted to the more tropical north and north-eastern periphery of the country. The Nemognathini are virtually cosmopolitan (Bologna and Pinto 2001). Of the four Australasian genera assigned here, *Zonitoschema* has a roughly similar distribution as the Horiini and also lacks deep penetration into Australia. *Australozonitis* is closely related to *Zonitoschema* but is better represented throughout the region with considerable diversity in Australia itself. In this respect it is comparable to *Palaestra*. These two genera are the dominant Australasian groups of Meloidae. However, the distribution of *Australozonitis* beyond Australasia is questionable. We are aware of one African species and can only assume that others, perhaps placed currently in *Zonitis*, occur in Africa and south-eastern Asia. It may very well have the same regional distribution as *Zonitoschema* and *Palaestra*. The remaining two Nemognathini genera, *Pulchrazonitis* and the lycoid *Palaestrida*, are monotypic and restricted to Australia. Although not deviating greatly from other nemognathines they reveal no obvious relationship to one another or to other tribal members. Finally, the *brevicornis* group (*incertae sedis*) has genitalic features similar to *Nemognatha* but lacks the other apomorphies defining that genus (Enns 1956). Thus, to conclude, Australasian meloids do not show a major disjunction at the genus level from the Afrotropical and Oriental nemognathine faunas. Most of the endemicity that does occur is at the species level.

It is premature to summarise the degree to which Australasian species are distinctive other than stating that all appear to be endemic to the region (except *Synhoria maxillosa*, in common with the Oriental region). The species of *Horia*, *Synhoria* and *Zonitoschema* differ minimally morphologically from congeners in the Oriental and Afrotropical regions. The distribution of *Australozonitis* beyond Australasia, as indicated, remains questionable but in any case the genus does not differ greatly from *Zonitoschema* and does not represent a major disjunction. Although *Palaestra* is extremely heterogeneous as currently defined, we are unable to recognise obvious lineages within the genus. Revisionary studies are required. The genus is most diverse in Australia but this fauna is not obviously qualitatively distinct from extra-regional representatives. The obvious derived features found in several Australian species (modified antennae, profemoral notch, armed aedeagus) also characterise certain Afrotropical and Oriental species (groups IIa and III). Species that we would consider the most highly derived (Group II) and least derived (Group VIf) both occur in Australia. Thus, there is no indication that the Australasian component of *Palaestra* represents a disjunct monophyletic lineage.

All Nemognathinae known, except the Palaearctic Stenoderini, have first instar larvae which are phoretic on bees. The other two subfamilies, the Eleticinae and most Meloinae,

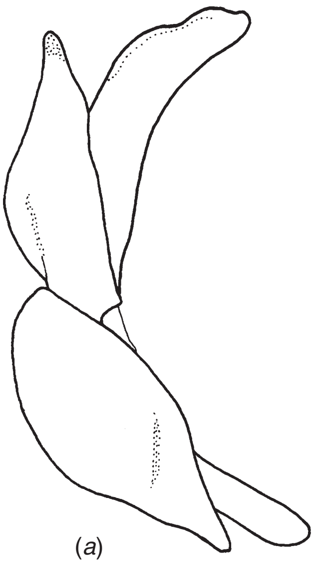

Fig. 24. *Zonitoschema testaceonotata* (Solomon Is, Kolombamara): (*a*) tegmen and aedeagus, lateral; (*b*) tegmen, dorsal. Scale bars: 1 mm.

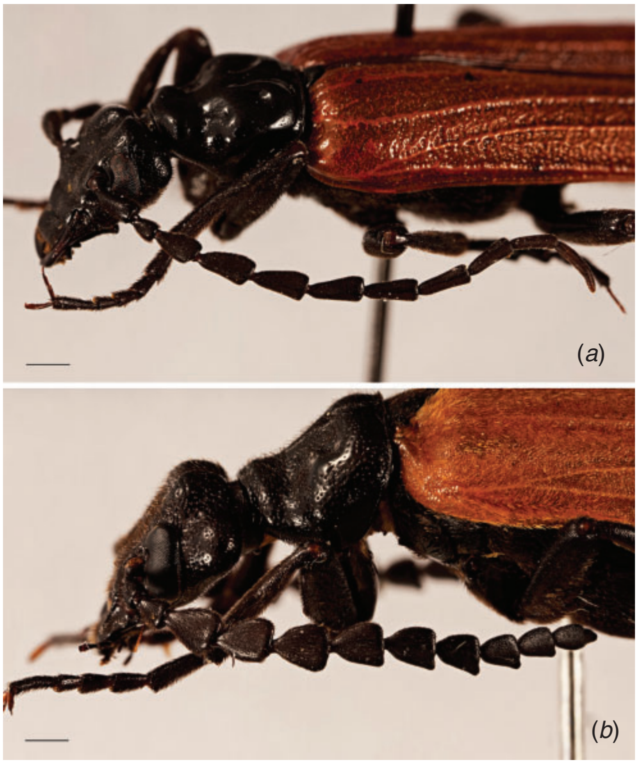

Fig. 25. Antennae, anterior: (*a*) *Palaestra rufipennis*, Palaestrini (QLD, Kroombit Tops); (*b*) *Palaestrida assimilis*, Nemognathini (QLD, Mt Moffatt NP). Scale bars: 1 mm.

Fig. 26. Horiini. Head, dorsal: (*a*) *Horia blairi* (QLD, Carmila); (*b*) *Synhoria maxillosa* (QLD, Innisfail; photo Stefano De Faveri, QDPC).

have non-phoretic larvae (Bologna and Pinto 2001). As stated by Bologna *et al.* (2008), the absence of non-phoretic groups in Australasia suggests that meloid distribution to the region depended on over-water bee dispersal. Furthermore, the absence of the basal subfamily Eleticinae, which has a typical Gondwanan distribution, and the minimal disjunction of Australasian taxa from the Oriental and Afrotropical nemognathine faunas suggests that this dispersal was from the north and relatively recent, probably sometime after the northward migration of the Australian plate and its mid-Miocene collision with the south-eastern Asian plates. This route and timing of faunal and floral interchange between Australia and the Oriental and Afrotropical regions, referred to as Indian Ocean Rim dispersal (e.g. Schwarz *et al.* 2006), is considered typical of numerous minimally differentiated Australasian taxa (Raven and Axelrod 1972) including bees (Michener 1979; Danforth and Ji 2001; Fuller *et al.* 2005) and other Coleoptera (Matthews 2000). The Meloidae, including a segment of the Australian fauna, are most diverse in arid and semi-arid habitats. Significantly it is not until mid-Miocene (~15 Mya) that the development of aridity in Australia begins (Martin 2006). The question of why Meloidae have failed to establish in cool and moist New Zealand perhaps is more a function of inappropriate habitat than remoteness, as successful over-water dispersal of medium-sized to large ground-nesting bees from Australia apparently has occurred (Michener 1979).

Thus far the only Australian bees associated with Meloidae are several species of the genus *Ctenocolletes* (Stenotritidae) (Di Giulio *et al.* 2010*b*). The Stenotritidae, sister to the Colletidae, are believed to be an endemic Australian element of Gondwanan origin (Almeida *et al.* 2012). This should not appear to conflict with the assumed recent arrival of meloids to Australia. For one thing, the bee associations represent records of first instar larvae on the bodies of adult bees. They do not necessarily represent host relationships as phoretic meloid larvae are often found on hairy insects which do not serve as hosts (Pinto and Selander 1970). In any case, nemognathines are known to utilise more than one host group. Several species are known to parasitise different genera as well as different families of bees (Selander and Bohart 1954; Erickson *et al*. 1976).

The geographic distribution of meloids within Australia has never been examined. To summarise the limited locality data of material studied we categorised species of the seven genera by occurrence in the three broad Australian biotic regions (e.g. Chenoweth and Schwarz 2011): Torresian (north and north-eastern tropical–subtropical, summer rainfall), Bassian (moist south-eastern and south-western temperate, winter rainfall) and Eyrean (arid–semiarid, inland and NE coast). Table 1 shows there are no obvious geographic restrictions for the family as a whole. *Palaestra* and *Palaestrida* appear to be broadly distributed, as does *Australozonitis*, although the diversity of the latter may be less in arid areas. All three genera are represented in the SW and SE Bassian zones. The relatively few collection records of *Zonitoschema* and the two horiine genera, *Synhoria* and *Horia*, are restricted to the Torresian zone.

As indicated, two of the seven Australian genera are endemic. Revisionary studies are required to determine the level of species endemicity in other groups, but at present we are aware of only four extracontinental species. All are Torresian within Australia. *Synhoria maxillosa* is distributed also in Wallacea and most of the Oriental region. *Horia blairi* also occurs in New Guinea. *Australozonitis bizonata* is known also from the Bismarck and Solomon Islands as is *A. lutea*, although conspecificity of the latter is questionable.

Australia itself contains 70 described and ~25 known undescribed species of Meloidae. Combined, this amounts to ~4% of family diversity (~2700 species). This is considerably less than the meloid fauna recorded for continental United States, which is roughly equivalent to Australia in size (~7.5 million km^2). The USA contains 310 species in two subfamilies, or ~12% of family diversity. Although the number of nemognathine genera is similar in both areas, nemognathine species diversity is somewhat greater in Australia (eight genera, 77 species in USA; seven genera, 95 species in Australia). We assume the number of Australian species will climb even further once the continent, especially the arid interior, is better sampled.

Levels of intrageneric variation are not easy to compare across meloid taxa but, clearly, the anatomical diversity among species of *Palaestra* is not only unique in the Nemognathinae, but exceptional within the family as well. This diversity is in male structure. Much of it consists of antennal and various leg modifications almost certainly associated with courtship. Although atypical of nemognathines, there is ample precedence for similar levels of interspecific variation of these structures in numerous genera of Meloinae (e.g. Selander 1964; Pinto and Selander 1970; Turco and Bologna 2011). It is the variation of male genitalia, both of the gonoforceps and aedeagus, but particularly the aedeagus that is without precedence in the family. Male genitalia in meloids often differ enough as to be useful for species separation but these differences are relatively minor usually involving, for example, variation in aedeagal hook size and position, or at most, the presence of one or two dorsal hooks (e.g. Selander 1960; Bologna and Di Giulio 2008). In *Palaestra*, the aedeagus may bear one, two or three pairs of lateral hooks of considerably variable size, or none at all. Although usually paired, three hooks, only two of them paired, occur in some species (Group VIb). Variation in overall shape and size as well as in structure of the ventroapical surface also occurs. A confusing aspect to this variation is that it is poorly correlated with other sexually dimorphic characters. For example, males of several species with modified antennae and notched profemora have an aedeagus with one or two pairs of hooks (Group IIa). Yet other species with the antennal and profemoral modifications completely lack aedeagal hooks (Group IIb). Other species without hooks also lack antennal and femoral modifications. The implications of this genitalic variation for sexual behaviour are likely to be significant.

Part of the distinction among the subfamilies of Meloidae has rested on differences in sexual behaviour and structures associated with this behaviour (Selander 1964; Bologna 1991; Turco *et al*. 2003). Our studies of Palaestrini indicate that the differences may not be that clear cut. To briefly review: the Meloinae include several sexually dimorphic groups whose males possess distinct structural modifications that are clear adaptations for stereotypic and overtly tactual courtship display (reviewed in Bologna *et al*. 2010). Additionally, the meloine aedeagus is armed with 1–2 dorsal hooks and a sclerotised and hooked ejaculatory rod which projects ventroapically through the median orifice or ostium. These dorsal and ventral hooks grasp the vaginal walls of the female, providing a secure coupling mechanism. Selander (1964) considered this a likely adaptation for the prolonged (one hour or more) bouts of linear copulation characterising Meloinae. This is in contrast to behaviour in Nemognathinae where relatively simple courtship is correlated with minimal levels of sexual dimorphism, and an unarmed aedeagus that does not provide secure genital coupling is associated with brief (a few minutes at most) bouts of dorsoventral copulation (Selander 1964). Relatively simple courtship and dorsoventral copulation also

Table 1. Number of species of Meloidae occurring in the three biotic regions of Australia
Assignment of species to region based primarily on map in Fig. 1 in Chenoweth and Schwarz (2011)

Region	Genera of Meloidae						
	Australozonitis	*Horia*	*Palaestra*	*Palaestrida*	*Pulchrazonitis*	*Synhoria*	*Zonitoschema*
Bassian	11	–	18	1	1	–	–
Eyrean	2	–	16	1	–	–	–
Torresian	8	2	6	1	–	1	2

appear typical of the primitive subfamily Eleticinae (Pinto *et al*. 1996; Bologna *et al*. 2001).

Sexual behaviour has not been observed in *Palaestra*. Yet, on the basis of morphology, it is clear that certain species at least must deviate from the nemognathine pattern. The relatively strong sexual dimorphism in antennae, femora and tarsi in several species suggests complex courtship. The extensive differences in aedeagal structure, strongly armed in certain species but unarmed in others, pose intriguing questions regarding the duration, position and intrageneric uniformity of copulatory behaviour. An understanding of this behaviour in *Palaestra* would be helpful in determining the polarity of copulatory position within the nemognathine–meloine lineage, a question originally posed by Selander (1964). Although sexual behaviour also has not been examined in the other genera of Australasian Meloidae, the absence of epigamic dimorphism and relatively simple male genitalic structure in these groups imply typical nemognathine behaviour.

As noted, *Palaestra* previously was restricted to a small number of lycid mimics. Lycoid features also characterise the monotypic *Palaestrida* and certain species of *Australozonitis* (e.g. *A. opacorufa*). Within the Australian insect fauna many examples of species mimicking lycids of the genera *Metriorrhynchus* and *Porrostoma* can be found. Lycid beetles lead mimicry rings all over the world but they are particularly common in Australia, involving not only many beetle families (e.g. *Eroschema*, Cerambycidae; *Rhinotia*, Belidae; *Pseudolycus*, Oedemeridae; *Anilicus* and *Rousia*, Elateridae; *Morpholycus*, Pythidae) but also other insect orders (e.g. *Snellenia*, Lepidoptera, Oecophoridae; *Cyana*, Lepidoptera, Arctiidae) (Nicholson 1927–1929; Monteith 2008). Oedemeridae (*Pseudolycus*) and Meloidae (*Palaestra*) not only are excellent morphological mimics but also share similar defence chemicals (cantharidin) which, in both families, strongly resemble those present in the haemolymph of Lycidae (Moore and Brown 1989). This chemical protection may have been the driving force for the convergence towards the lycid phenotype found in *Palaestrida* and certain species of *Palaestra* and *Australozonitis*.

A satisfactory understanding of the origin and relationships of Australasian meloids will require a far better knowledge of Nemognathinae than is now available. This is a large subfamily with 35 recognised genera assigned worldwide (Pinto and Bologna 1999; Bologna and Pinto 2002) and other undescribed new genera under study (J. D. Pinto and M. A. Bologna, unpubl. data). However, generic limits and phylogenetic relationships are poorly understood. The most recent attempts to bring structure to the subfamily are based on select character sources and relatively few genera (MacSwain 1956; Kaszab 1959; Bologna and Pinto 2001). Similarly, revisionary studies of Australasian groups do not exist, and concepts of species diversity and distributions are rudimentary. Clearly the meloids in this part of the world represent an intriguing fauna with unexpected character variation which, when better understood, portends to add significantly to the systematics of the family. Future studies must also take into consideration the Afrotropical and Oriental elements to which the Australasian blister beetles are closely tied.

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Appendix 1. Checklist of Australasian Meloidae

All new combinations represent transfers from *Zonitis*; species followed by museum acronym indicates types examined; asterisk [*] indicates male genitalia studied

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PALAESTRINI

Australia, mainland

Palaestra aspericeps (Blackburn, 1899), comb. nov. BMNH
Palaestra bipartita (Fairmaire, 1879)*, comb. nov. MNHN
Palaestra carpentariae (Blackburn, 1899)*, comb. nov. BMNH
Palaestra cyanipennis (Pascoe, 1862)*, comb. nov. ANIC, MNHN
Palaestra distortipes (Lea, 1916), comb. nov. SAM
Palaestra flavicrus (Fairmaire, 1879), comb. nov. MNHN
Palaestra foveicollis Blair, 1920 BMNH
Palaestra hakeae (Lea, 1914), comb. nov. SAM
Palaestra helmsi (Blackburn, 1892)*, comb. nov. SAM
Palaestra indigacea (Fairmaire, 1880), comb. nov.
Palaestra janthinipennis (Fairmaire, 1880), comb. nov.
Palaestra nigroaenea (Fairmaire, 1879), comb. nov. MNHN
Palaestra purpureipennis (Waterhouse, 1875)*, comb. nov. BMNH
Palaestra quadrifoveata Fairmaire, 1880*
Palaestra queenslandica (Blackburn, 1899)*, comb. nov. BMNH
Palaestra rostrata (Blessig, 1845), comb. nov.
Palaestra rubricollis (Hope, 1842)*, comb. nov. OUMNH
Palaestra rubripennis Laporte de Castelnau, 1840* MNHN
Palaestra rufipennis (Westwood, 1841)* OUMNH
Palaestra rufocincta Fairmaire, 1880 MNHN
Palaestra rugata (Fairmaire, 1880), comb. nov. MNHN
Palaestra rugosipennis (Fairmaire, 1879)* ANIC, BMNH, MNHN
Palaestra sedilloti (Fairmaire, 1880)*, comb. nov. MNHN
Palaestra semirufa (Fairmaire, 1880)*, comb. nov. MNHN
Palaestra violacea (Hope, 1842), comb. nov. OUMNH
Palaestra violaceipennis (Waterhouse, 1875)*, comb. nov. BMNH
Palaestra yorkensis (Blackburn, 1899)*, comb. nov. SAM

Australia, Tasmania

Palaestra rubripennis Laporte, 1840*

Micronesia (Caroline Islands and Guam)

Palaestra blairi Bologna, Turco & Pinto n. name for *Zonitis oceanica* Blair, 1940, preoccupied by *Zonitis oceanicus* Pic, 1915* BMNH

New Caledonia

Palaestra guerini (Moutrosier, 1861), comb. nov.

HORIINI

Australia, mainland

Horia blairi Betrem, 1932 BMNH
Horia mira (Blackburn, 1892) BMNH
Synhoria maxillosa (Fabricius, 1801)

Halmahera and Buru Islands and New Guinea

Horia blairi Betrem, 1932
Horia sp. near *blairi* MSNG
Synhoria maxillosa (Fabricius, 1801)

NEMOGNATHINI

Australia, mainland

Australozonitis andersoni (Blackburn, 1889), comb. nov. BMNH
Australozonitis apicalis (MacLeay, 1872)*, comb. nov.
Australozonitis bizonata (MacLeay, 1872)*, comb. nov. BMNH, MNHN
Australozonitis cylindracea (Fairmaire, 1880)*, comb. nov.
Australozonitis dichroa (Germar, 1848)*, comb. nov. MNHN
Australozonitis flaviceps (Waterhouse, 1875), comb. nov. BMNH
Australozonitis fuscicornis (MacLeay, 1872)*, comb. nov.
Australozonitis handschini (Borchmann, 1937)*, comb. nov. NMB
Australozonitis longiceps (Lea, 1917), comb. nov. SAM
Australozonitis lutea (MacLeay, 1872)*, comb. nov. BMNH

(*continued next page*)

Appendix 1. (*continued*)

Australozonitis nigroplagiata (Fairmaire, 1880)*, comb. nov. BMNH
Australozonitis opacorufa (Fairmaire, 1880)*, comb. nov. MNHN
Australozonitis pallicolor (Fairmaire, 1880), comb. nov. MNHN
Australozonitis pallidula (Wellman, 1910)*, comb. nov. ANIC
Australozonitis rostrata (Blessig, 1861), comb. nov.
Australozonitis seminigra (Fairmaire, 1879), comb. nov. MNHN
Australozonitis tenuicornis (Fairmaire, 1880), comb. nov. BMNH
Australozonitis tricolor (Le Guillou, 1844)*, comb. nov. BMNH, MNHN
Palaestrida assimilis Hope, 1842* OUMNH, BMNH
Pulchrazonitis splendida (Fairmaire, 1879)*, comb. nov. MNHN
Zonitoschema cowleyi (Blackburn, 1899)*, comb. nov.
Zonitoschema nigroapicata (Fairmaire, 1880)*, comb. nov.

Australia, Tasmania
Australozonitis tricolor (Le Guillou, 1844), comb. nov. BMNH, MNHN

Bismarck and Solomon Islands
Australozonitis bizonata (McLeay, 1872)*, comb. nov. BMNH, MNHN
Australozonitis lutea (McLeay, 1872), comb. nov. (uncertain identification)
Zonitoschema bradleyi Mohamedsaid, 1981
Zonitoschema megalops (Fairmaire, 1883)
Zonitoschema testaceopunctata Kaszab, 1958* (syn., *testaceonotata* Pic, 1935)

New Guinea
Zonitoschema nitidissima Pic, 1911

New Hebrides
Zonitoschema vonhayekae Mohamedsaid, 1981
Zonitoschema hebridisensis Mohamedsaid, 1981

INCERTAE SEDIS
Australia, mainland
'*Zonitis*' *annulata* MacLeay, 1872
'*Zonitis*' *brevicornis* Blackburn, 1889
'*Zonitis*' *bimaculicollis* Lea, 1916
'*Zonitis*' *breviceps* Lea, 1916
'*Zonitis*' *dolichocera* Wellman, 1910 (syn., *longicornis* Motschulsky, 1872 nom. preocc.)
'*Zonitis*' *leai* Kaszab, 1958
'*Zonitis*' *limbipennis* Fairmaire, 1880
'*Zonitis*' *longipalpis* Blackburn, 1899
'*Zonitis*' *metasternalis* Lea, 1914
'*Zonitis*' *murrayi* Blackburn, 1889
'*Zonitis*' *nigroapicata* Fairmaire, 1880
'*Zonitis*' *obscuripes* Fairmaire, 1879
'*Zonitis*' *picticornis* Lea, 1914
'*Zonitis*' *posticalis* (Fairmaire, 1879) (described as *Cantharis*)
'*Zonitis*' *pubipennis* Lea, 1916
'*Zonitis*' *rustica* Blackburn, 1889
'*Zonitis*' *subrugata* Blackburn, 1899
'*Zonitis*' *xanthosoma* Lea, 1916

Halmahera and Buru Islands
'*Zonitis*' *batjanensis* Pic, 1911
'*Zonitis*' *marginiventris* Fairmaire, 1887 (possibly belonging to *Zonitoschema*)
'*Zonitis*' *tenuemarginata* Fairmaire, 1887

Seram Islands
'*Zonitis*'*amboinensis* Pic, 1916
'*Zonitis*' *tenuemarginata* Fairmaire, 1887

New Guinea
'*Zonitis*' *mitshkei* Pic, 1911
'*Zonitis*' *neoguineensis* Pic, 1911
'*Zonitis*' *semicaerulea* Pic, 1911

(*continued next page*)

Appendix 1. (*continued*)

New Caledonia

'*Zonitis*' *atriceps* Fauvel, 1905

'*Zonitis*' *melanoptera* Wellman, 1910 (syn., *nigripennis* Fauvel 1905, nom. preocc.). Note that also *melanoptera* Wellman is preoccupied by *Zonitomorpha melanoptera* (Fairmaire, 1894) from India, described as *Zonitis;* see also *Zonitis leai* Kaszab from Australia.

Tonga

'*Zonitis*' *angulata* Fabricius, 1787 (syn., *angulifera* Blanchard, 1853). Described from New Amsterdam Island in the southern Indian Ocean, but this record is very uncertain. Afterwards re-cited from Tonga.

Appendix 2. Undescribed Australasian species studied

Male genitalia examined in all, except *

PALAESTRINI

Australia, mainland

Palaestra sp. (Australia)
Palaestra sp. (NSW, Sydney National Park; Waterfall)
Palaestra sp. (NSW, Armidale; Ebor)
Palaestra sp. (SA, Old Gerabullan Well)
Palaestra sp. (SA, Mudla Miracka (Waterhole))
Palaestra sp. (WA, Cervantes)
Palaestra sp. (WA, Margaret River)
Palaestra sp. (WA, Douglas)
Palaestra sp. (WA, Mt Jackson)
Palaestra sp. (WA, Tangadee)
Palaestra sp. (WA, Lake Cohen)*
Palaestra sp. (WA, Newman)
Palaestra sp. (WA, Nyang)
Palaestra sp. (NT, Alice Springs)
Palaestra sp. (NT, Barrow Creek, ~41 km N)
Palaestra sp. (NT, Timber Creek)
Palaestra sp. (QLD, Auburn River NP)
Palaestra sp. (QLD, Desailly)
Palaestra sp. (QLD, Cooper Creek)
Palaestra sp. (QLD, Windorah)
Palaestra sp. (QLD, Mt White)
Palaestra sp. (QLD, Tamborine)

Fiji

Palaestra sp.

New Guinea

Palaestra sp. (Madang District, Finistere Mts)
Palaestra sp. (Maroba District)

NEMOGNATHINI

Australia, mainland

Australozonitis sp. (NT, near Alice Springs)
Australozonitis sp. (QLD, Millstream Falls)
Australozonitis sp. (QLD)
Australozonitis sp. (WA, Hines)

New Guinea

Zonitoschema sp. (Lakekamu Basin)
Zonitoschema sp. (Lakekamu Basin)

Solomon Islands

Australozonitis sp. (Solomon Islands)

Appendix 3. Extraterritorial species studied of genera occurring in Australasia

Male genitalia examined in all

PALAESTRINI

Palaestra bytinskii (Kaszab, 1957), comb. nov., Palaearctic
Palaestra kittenbergeri (Kaszab, 1954), comb. nov., Afrotropical
Palaestra sternalis (Kaszab, 1954), comb. nov., Afrotropical
Palaestra subviridipes (Pic,1926), comb. nov., Oriental
Palaestra woodi (Pic, 1932), comb. nov., Afrotropical
Palaestra zavattarii (Kaszab, 1949), comb. nov., Afrotropical
Palaestra sp., Afrotropical (Ethiopia)
Palaestra sp., Oriental (Sri Lanka)

HORIINI

Horia debyi (Fairmaire, 1885), Oriental
Horia fabriciana Betrem, 1932, Afrotropical, Oriental
Horia nitida Gahan, 1908, Afrotropical
Synhoria cephalotes (Olivier, 1795), Afrotropical
Synhoria senegalensis (Laporte de Castelnau, 1840), Afrotropical
Synhoria testacea (Fabricius, 1781), Afrotropical

NEMOGNATHINI

'*Zonitis*' *latipennis* (Pic, 1909) or near, Afrotropical
Zonitoschema bivittipennis Kaszab, 1981, Afrotropical
Zonitoschema capensis Kaszab, 1961, Afrotropical
Zonitoschema coccinea (Fabricius, 1801), Afrotropical
Zonitoschema gigantea (Fairmaire, 1894), Afrotropical
Zonitoschema griseohirta Pic, 1914), Afrotropical
Zonitoschema japonica (Pic, 1910), Palaearctic
Zonitoschema paolii (Pic, 1928)
Zonitoschema sp. Afrotropical (Kenya, Meru)

INCERTAE SEDIS

'*Zonitoschema*' *alluaudi* Pic, 1913, Afrotropical
'*Zonitoschema*' *elongaticeps* (Pic, 1935), Afrotropical
'*Zonitoschema*' *jansei* (Kaszab, 1951), Afrotropical
'*Zonitoschema*' *posticalis* (Péringuey, 1892), Afrotropical