



# The first known larva of the Australian genus *Mystropomus* Chaudoir (Coleoptera: Carabidae: Paussinae)

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**Abstract** The monogeneric subtribe *Mystropomina* Chaudoir (Carabidae: Paussinae: Ozaenini) contains two species endemic to Australia: *Mystropomus subcostatus* Chaudoir and *Mystropomus regularis* Bänninger. In this paper, we describe and illustrate the larva of *M. subcostatus* providing the first larval description in this subtribe, thereby filling an important gap in our knowledge of paussine larval morphology. We compare the structural features of this larva with the other known larvae in the subfamily and provide an identification key to larvae of Australian paussine genera. We find no external structural features that indicate that this larva lives with ants, as do many other members of the carabid beetle subfamily Paussinae.

**Key words** Australia, flanged bombardier beetle, *Mystropomus*, Ozaenini.

## INTRODUCTION

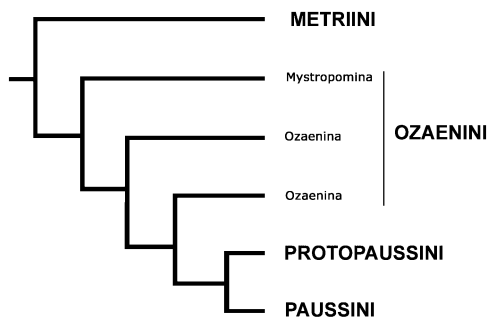
The carabid beetle subfamily Paussinae is a pantropical group that includes many myrmecophiles (obligate associates of ants). To date, approximately 800 species are described and classified within four tribes: *Metriini*, *Ozaenini* (paraphyletic), *Protopaussini* and *Paussini* (Deuve 2004, 2005, 2007; Lorenz 2005) (Fig. 1). Larvae are known from 22 species representing nine genera and three tribes (see Di Giulio and Moore 2004; Moore and Di Giulio 2006). All paussine larvae have a unique, complex terminal disk, consisting of highly modified urogomphi and the eighth and ninth abdominal segments. This structure is an undisputed synapomorphy of the Paussinae.

The natural history of most paussine larvae is not known. MacSwain and Garner (1956) erroneously reported that larvae of *Metrius contractus* Eschscholtz specialise on millipedes, but their observations were based upon pterostichine carabid larvae that they misidentified as *Metrius* (Moore and Di Giulio 2008). In fact, most of the described paussine species are myrmecophilous during at least one phase of their life history (see Geiselhardt *et al.* 2007 for a recent review), and both adults and larvae that live with ants have adaptations for this lifestyle (Di Giulio and Moore 2004; Di Giulio 2008). While very few paussine larvae have been observed alive in the field, their external morphology often provides clues about their behaviour (Di Giulio and Moore 2004; Moore and Di Giulio 2006). All known free-living, non-myrmecophilous paussine larvae live in burrows that they excavate in sand or soft wood, and they use their terminal disk as an operculum to their galleries. These larvae have multibranching urogomphi which

loosely attach to the other components of the terminal disk, and they use the mobility of the disk to capture living insect prey (Costa *et al.* 1988; Di Giulio and Vigna Taglianti 2001; Moore and Di Giulio 2006). In myrmecophilous larvae, however, the branches of the urogomphi are fused into a plate-like structure that is, in turn, fused to the other components of the disk rendering it less mobile. The fused disk of the *Arthropterus* W.S. MacLeay larva, described by Di Giulio and Moore (2004), provided evidence that these larvae are myrmecophilous even though they have not yet been collected from ant nests.

*Mystropomus* Chaudoir is classified within the monogeneric subtribe *Mystropomina* of the Ozaenini. Based on studies of adult external morphology, the *Mystropomina* attaches near the base of the evolutionary tree of Paussinae and is possibly the sister group of all other members of the subfamily other than the *Metriini* (Fig. 1) (Di Giulio *et al.* 2003). *Mystropomus* contains two species, both with two recognized subspecies, all of which are endemic to Australia. *Mystropomus regularis* Bänninger is found in the rainforests of coastal Queensland and reaches its northernmost limit of distribution in north-eastern Queensland (Williams 2002), whereas *Mystropomus subcostatus* Chaudoir is found in montane rainforests and wet sclerophyll forests of coastal New South Wales (Figs 2,3). Little is known about the natural history of these common, large-bodied carabid beetles (Darlington 1961), other than that adults are flightless, and like most carabids they are thought to be night-active predators of arthropods. Whereas most of the described Paussinae species are myrmecophilous, members of *Mystropomus* are not suspected to be associated with ants. In this paper, we provide the first description of the larva of the subtribe *Mystropomina*, thereby filling an important gap in our knowledge of paussine larval morphology. Although the total

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**Fig. 1.** Phylogenetic tree of Paussinae tribes and subtribes of Ozaenini based on previous morphological study.



**Fig. 2.** *M. subcostatus* Chaudoir, adult male.

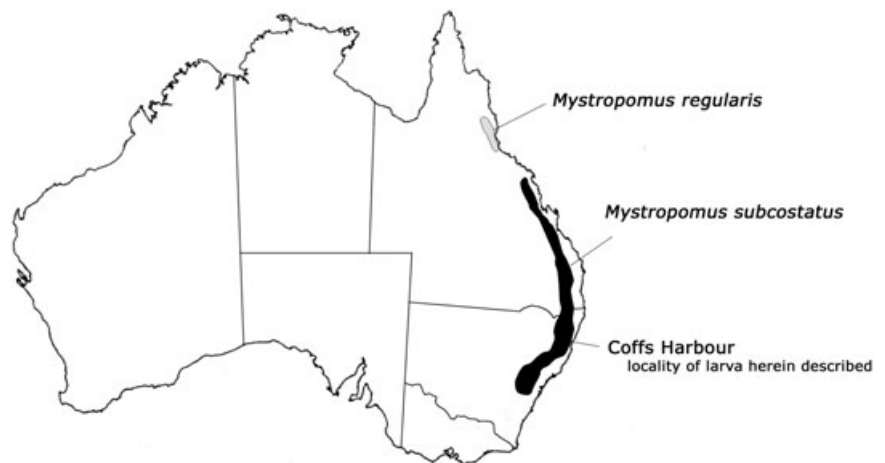
number of described Paussinae larvae is relatively small, those that are known provide useful characters for inferring phylogenetic relationships within the subfamily (Di Giulio *et al.* 2003; Di Giulio and Moore 2004). Comparisons of the structural features of this larva with the other known larvae in the subfamily revealed characters of potential phylogenetic significance, which will be included a revision of Paussinae larvae (A. Di Giulio and W. Moore in prep. 2011). This larva was collected in a Berlese funnel, so there is no direct evidence of its behaviour or life history. However, we examined external structural features to determine if there was any indication that this larva might be associated with ants, as are many other larvae in the subfamily.

**MATERIALS AND METHODS**

**Material examined**

One third-instar larva preserved in 75% ethyl alcohol. ‘Bruxner Park, N.S.W. Coffs Harbour 25/6/1967, ANIC Berl. 29, R.W. Taylor, coll’. Berlese funnel of ‘leafmould’ from New South Wales in 1967. Identified by Barry P. Moore in 1980 ‘ex syst., loco’. Deposited in the Australian National Collection (CSIRO Canberra, Australia). Given the known distribution of the two species of *Mystropomus*, we surmise that the larva belongs to the type species of the genus: *M. subcostatus* (Fig. 3).

For general terminology of larval structures, we refer to Lawrence (1991). Notation of primary setae and pores follows the system of Bousquet and Goulet (1984), modified for *M. contractus* Eschscholtz (Bousquet 1986); according to this system, we consider as ‘secondary’ the setae on the third-instar larva not recognised as homologous to the ancestral primary carabid pattern. When all the primary setae were recognised on the sclerites and parts of the body, only the secondary setae are mentioned. As some of the sensilla of *Mystropomus* larva present on the abdomen and terminal disk are homologous to those recognised by Bousquet (1986) in *M. contractus* (sensilla S–I to S–V), by Di Giulio *et al.* (2000) in *Pachyteles* Perty (sensilla S–I to S–VII) and by Di Giulio and Moore



**Fig. 3.** Map of distribution of *M. subcostatus* and *M. regularis* (modified from Lawrence *et al.* 2001).

(2004) in *Arthropterus* sp. (sensilla S–I to S–VIII), we adopted the same nomenclature used by these authors. Notations for microsculpture and urogomphal lobes follow those proposed by Bousquet (1986) for *M. contractus* and later modified by Vigna Taglianti *et al.* (1998) for the Ozaenini. An asterisk (\*) following a coded seta indicates that the homology between the structure on the *Mystropomus* larva and the corresponding code is questionable. External structure was studied and drawn by using Olympus SZX12 stereomicroscope equipped with drawing tube.

## RESULTS

### Description of third-instar larva of *M. subcostatus*

#### Diagnosis

Ligula with apical lateral protuberances; urogomphi with five elongate lobes: lobe E undivided, lobe D emerging subbasally from lobe E; sensilla S–II at distal margin of dorsal plates of two different sizes with very-long and partially fused bases; apex of lobe B distinctly up-curved.

#### Description

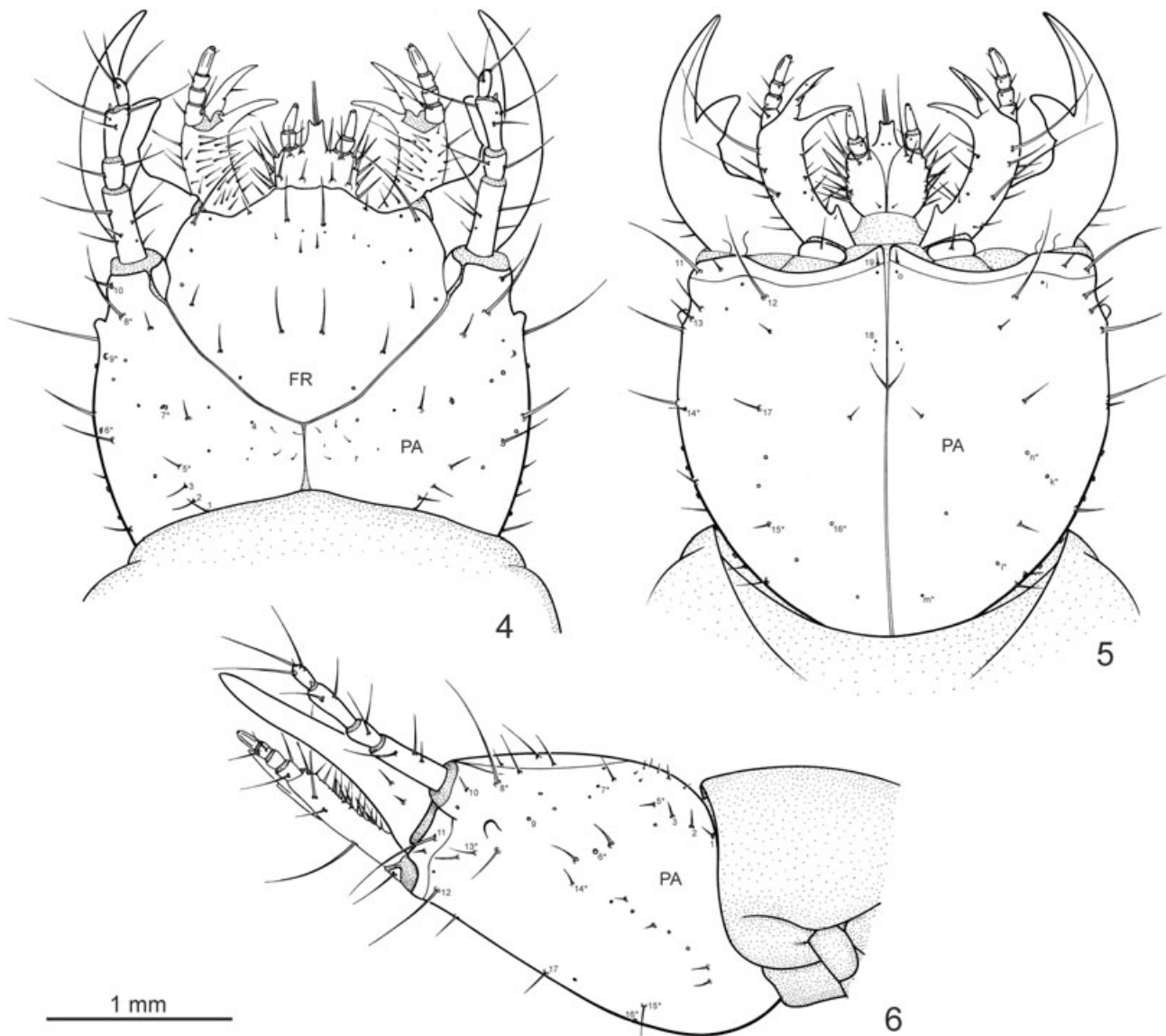
**Measurements.** Body length approximately 10.8 mm (from tip of mandibles to apex of terminal disk); cephalic capsule maximum width 2.3 mm, medial dorsal length (from occipital foramen to anterior margin of frontoclypeolabrum) 1.7 mm; cephalic capsule ventral length (along gular suture) 2.1 mm; prothorax maximum width 2.5 mm, medial length 0.9 mm; terminal disk maximum width (at level of lateral plates) 3.4 mm; dorsal plates length (from base, near articulation, to medial apex) 1.6 mm.

**Habitus and colouration.** Body soft, weakly sclerotized, not physogastric. Pronotum more sclerotised than mesonotum and metanotum. Abdomen bellows-like (Figs 14–15), light yellow, with terminal disk well-sclerotized, pale to light brown from base to apex; cephalic capsule, anterior margin of cephalic capsule and mandibles strongly sclerotized, dark brown; antennae, maxillae and labium thickly sclerotized and light brown. Coxae weakly sclerotized and yellowish; trochanter, femur, tibia and tarsus well-sclerotized and yellowish brown; tarsal claws heavily sclerotized and dark brown.

**Microsculpture.** Cephalic capsule, mouthparts, thoracic tergites and legs smooth. Lateral and anteriomedial part of epipharynx with thin, elongate sculpticells medially directed. Membranous areas of body and sclerites of the abdomen rugose. Surface of plates and urogomphi of terminal disk as well as pygidium, with pointed or multipointed microsculpture.

**Chaetotaxy.** Frontoclypeolabrum (Fig. 7) without secondary setae; setae FR<sub>1</sub> and FR<sub>3</sub> subequal in length; FR<sub>2</sub> slightly shorter than FR<sub>1</sub>, posterior to the level of FR<sub>3</sub>; FR<sub>4</sub>\* shorter than FR<sub>3</sub>; seta FR<sub>5</sub>\* very small, lateral and slightly anterior to FR<sub>4</sub>\*; FR<sub>6</sub> small, slightly medial and posterior to FR<sub>7</sub>; seta FR<sub>7</sub> longer than other frontal setae, anteromedially directed; setae

FR<sub>8</sub> and FR<sub>9</sub> moderately long, anteromedially directed, with bases not visible in dorsal view; setae FR<sub>10</sub>\* and FR<sub>11</sub>\* just behind anteromedial prominence of frontoclypeolabrum; seta FR<sub>11</sub>\* slightly posterior to and longer than FR<sub>10</sub>\*; pore FR<sub>d</sub>\* slightly posterior to FR<sub>11</sub>\*. Parietale (Figs 4–6) with several small secondary setae between PA<sub>7</sub>\* and basal stem of epicranial suture; 7–8 ventrolateral spine-like secondary setae posterior to PA<sub>14</sub>\*; PA<sub>8</sub>\* elongate, distinctly anterior to PA<sub>9</sub>\*. Antennomere I (Fig. 8) with seven secondary setae; II with two secondary setae, one medial and one lateral; IV with AN<sub>6</sub> short (Fig. 8). Mandible (Fig. 9) with one subbasal small secondary seta; seta MN<sub>1</sub> short; seta MN<sub>2</sub> and pore MN<sub>a</sub> not visible. Setal group gMX (Fig. 10) on stipes composed of approximately 35 spine-like setae; seta MX<sub>5</sub>\* dorsal; seta MX<sub>6</sub> small, subapical, in a medial groove of lacinia; seta MX<sub>7</sub> very strong and elongate (Fig. 11); seta MX<sub>8</sub>\* very small, subapical; MX<sub>9</sub> not visible; maxillary palpomere I with two strong, elongate, secondary setae, one dorsal and one ventral; palpomere IV with small meso-dorsal secondary seta, one secondary ventral pore, three longitudinal subapical digitiform sensilla and apical sensorial area composed of several small papillae. Prementum (Figs 12,13) with approximately 30 secondary spine-like setae on lateral and dorsal surfaces, inserted in sclerotized protuberances; seta LA<sub>1</sub> close to midline; labial palpomere II with one subapical secondary seta, medially directed, three longitudinal subapical digitiform sensilla and apical sensorial area composed of several small papillae; LA<sub>6</sub> elongate, inserted at tip of the ligula. Pronotum, mesonotum and metanotum (Fig. 18) with approximately 22 setae on each side of ecdysial line (identification not possible). Coxae, trochanters and femurs with several spine-like secondary setae present mostly on ventral side. Abdominal tergites I–VII (Fig. 14) with few (less than 10) short setae on each side (identification not possible). Tergal side of dorsal and lateral plates of terminal disk with stiff pointed setae (sensilla S–VII) of various lengths, with cylindrical bases protruding from plates: approximately 20–23 on each dorsal plate (epipleurite IX + tergite VIII) and approximately 15 on each lateral plate (epipleurite VIII); margins of dorsal and lateral plates (Figs 16,17) with sensilla S–II (and a few sensilla S–I); each dorsal plate with 16–18 S–II of two sizes, large and small S–II evenly distributed in alternate positions along distal margin; small S–II often inserted at base of large S–II; inner margin of each dorsal plate (Figs 16,17) with five small S–II obliquely directed, increasing in size from base to apex; margin of each lateral plate with 12 sensilla S–II: short S–II at base and long S–II at apex of each lateral plate; ventral side of terminal disk with many sensilla S–I (Fig. 16) sparsely distributed: approximately 130 S–I on each dorsal plate, mostly medial and approximately 30 on each lateral plate (mostly along inner margin). Epipleurites (Figs 14,15) of abdominal segments I–III with few (less than 10) short and thin setae, those of segments IV–VII with setae and sensilla S–II. Hypopleurites of segments I–IV with setae, V–VII with setae and sensilla S–II. Sternal area of segments I–III with setae, that of IV with setae and sensilla S–II, that of segment V and VI with S–I with somewhat inflated apex and S–II apically enlarged and with a



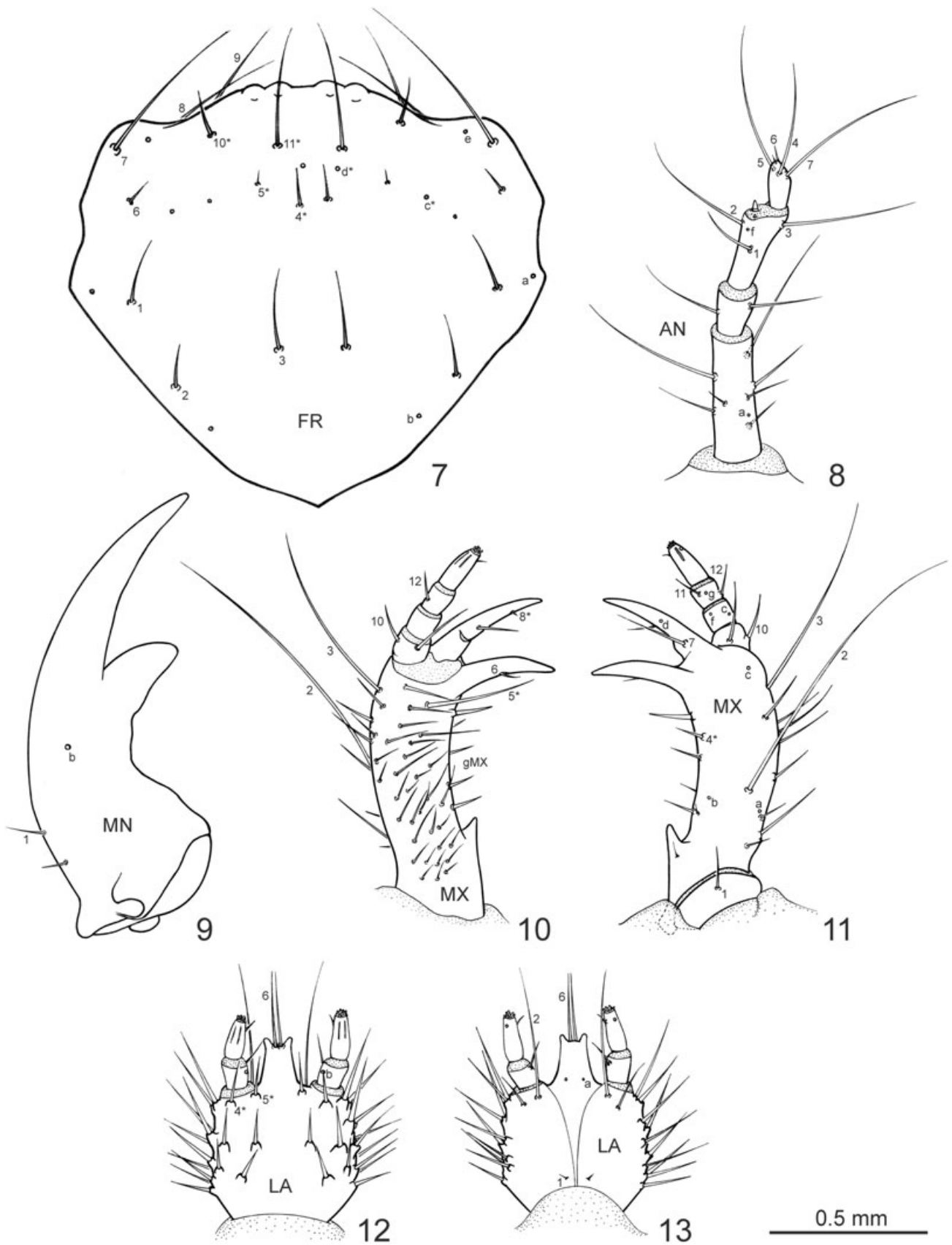
**Figs 4–6.** *Mystropomus subcostatus* third-instar larva: (4) head, dorsal view; (5) head, ventral view; (6) head, lateral view. FR, frontoclypeolabrum; PA, parietale.

protruding base and that of segments VII–VIII with S–I. Urogomphi (Fig. 17) with many S–I, mainly on dorsal and apical areas of branches; branch C with one subapical, ventral S–IV, branch E with one S–V subapically on ventral side. Pygidium with few sensilla S–I (Fig. 17).

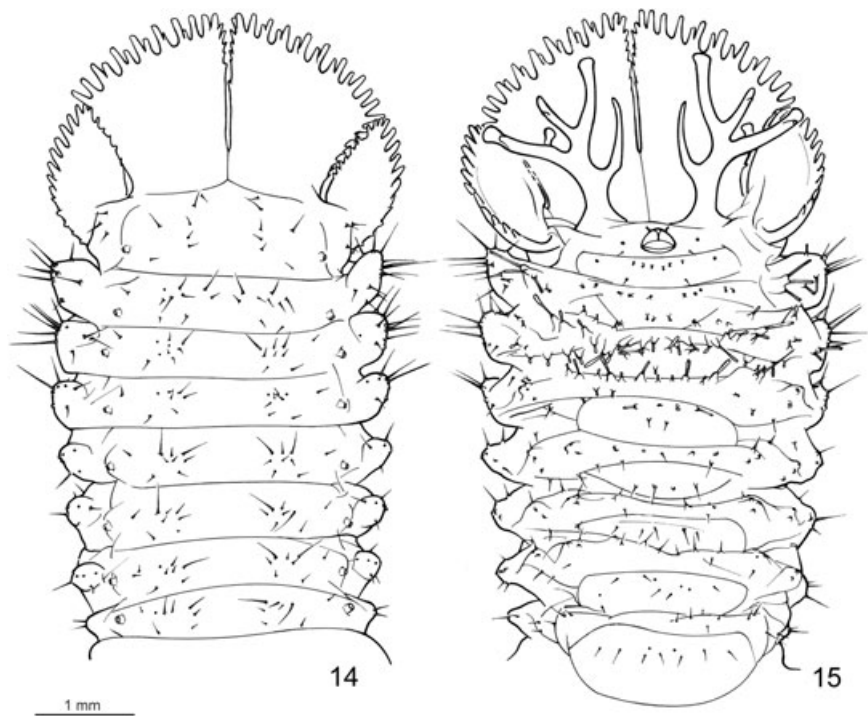
**Head.** Cephalic capsule (Figs 4–6) transverse (maximum width/dorsal length ratio = 1.35), hyperprognathous, slightly rounded laterally, regularly tapered at basal half into a distinct neck; maximum width at level of posterior corner of frontoclypeolabrum; occipital foramen dorsally displaced. Frontoclypeolabrum (Figs 4,7) shield-like, slightly transverse, with surface medially convex and laterally concave, anteriorly sloped (Fig. 6); basal stem of epicranial suture approximately one-third of frontoclypeolabrum length, anterior frontal arms only slightly sinuate. Frontoclypeolabrum anteriorly produced into wide-toothed prominence (Fig. 7) slightly posterior to

anterior margin, laterally extended to adnasalia; labral tooth (labral spine sensu; Beutel 1992) not visible; adnasalia slightly rounded and slightly protruding. Parietale (Figs 4–6) with one stemma on each side; ocular and cervical grooves absent; ventral walls of parietale medially fused, forming a complete gular suture (Fig. 5). Antennae (Figs 4,6,8) four-jointed, distinctly shorter than mandibles, forwardly directed; antennomere I approximately 2.5 times longer than II; III approximately two times longer than II; IV slightly shorter than II; III with small, conical sensorial appendage. Mandibles (Fig. 9) long and slender, falcate, approximately three times as long as their basal width, evenly curved along lateral margin; penicillus absent; terebra double-edged: both dorsal and ventral cutting edge regularly concave; retinaculum subtriangular, slightly curved inward, with smoothed apex. Maxillae (Figs 10,11) with long and slender stipes distinctly curved





**Figs 7–13.** *Mystropomus subcostatus* third-instar larva: (7) frontoclypeolabrum; (8) left antenna, dorsal view; (9) left mandible, dorsal view; (10) left maxilla, dorsal view; (11) left maxilla, ventral view; (12) labium, dorsal view; (13) labium, ventral view. AN, antenna; FR, frontoclypeolabrum; LA, labium; MN, mandible; MX, maxilla.



**Figs 14–15.** *Mystropomus subcostatus* third-instar larva: (14) abdomen, dorsal view; (15) abdomen, ventral view. Sensilla on terminal disk and urogomphi are not drawn.

inward, approximately three times as long as their basal width; ental surface with conspicuous basal tooth, triangular, forwardly directed, with acute apex; setal protuberances absent along inner side; maxillary palpomeres gradually decreasing in length from I to III; IV digitiform, distinctly longer than others, subequal to II and III combined; lacinia (Figs 10,11) as long as galea, inwardly curved at apical third and apically pointed; galea slender, pointed, slightly curved inward, not clearly divided into two joints; galeomeres ventrally fused. Labium (Figs 12,13) with subquadrate prementum with setal protuberances present on dorsal surface and sides; ligula very long and stout, longer than labial palpomere I, slightly tapering from base to apex, apically with two lateral digitiform protuberances external to setae LA<sub>6</sub>; labial palpomere I short and wider than II; II digitiform, approximately two times as long as I.

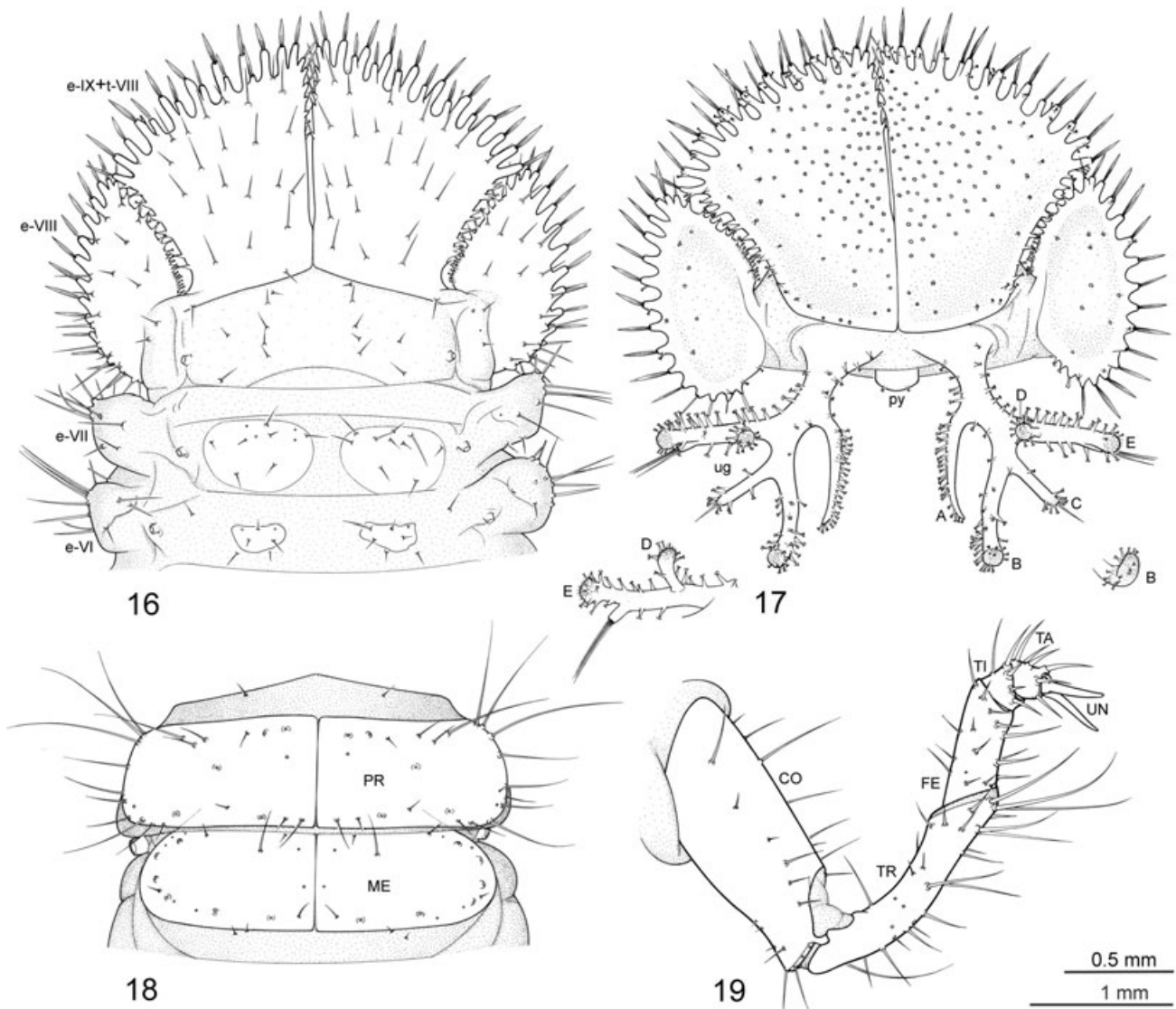
**Thorax.** Tergites (Fig. 18) slightly decreasing in length from pronotum to metanotum. Pronotum wider than mesonotum and metanotum, transverse, 2.5 times wider than long. Mesonotum and metanotum rounded laterally, widely transverse, approximately three times wider than long; longitudinal ecdysial line well-marked on pronotum and mesonotum, less evident, but present, on metanotum.

**Spiracles.** Thoracic and abdominal spiracles (Fig. 14) annular with conical, protruding peritremes. Mesothoracic spiracles anterolaterally on mesopleura, diameter almost two times wider than diameter of abdominal spiracle I. Abdominal spiracle I diameter slightly wider than diameter of abdominal spiracles II–VIII; II–VIII subequal.

**Legs.** Five-jointed (Fig. 19), progressively shorter from foreleg to hindleg. Coxae cylindrical, elongate, approximately as long as corresponding trochanters and femurs combined; trochanters obliquely truncate and ventrally expanded at apex; femurs

approximately half as long as trochanters and approximately three times as long as tibiae; tibiae cylindrical, approximately as long as tarsi; tarsi more slender than tibiae, conical, tapered from base to apex, with two strong and straight claws; anterior claw longer than posterior.

**Abdomen.** Abdominal sclerite boundaries barely discernable, recognised by reduction of pointed microsculpture, reduction of protrusion and presence of setae or sensilla S–II; segments progressively wider from I to VII (Figs 14,15). Tergum of segments I–VII flattened with two small oval setiferous sclerites rather widely separated; segments with swollen, setiferous pleural and sternal areas. Epipleurites distinctly protruding, gradually more developed from I to VIII; epipleurites VIII (Figs 14–17) flattened and enlarged into two sclerotized lateral plates, concave, suboval, almost two times longer than wide; epipleurites IX greatly enlarged and fused with tergum of segment VIII into two completely divided subrectangular, sclerotized plates (dorsal plates = anal plate sensu; Bousquet 1986), enlarged from base to apex; dorsal plates wider than lateral plates; apex of the abdomen, including segments VIII–X forming a sclerotized terminal disk; lateral plates, dorsal plates and urogomphi articulated at base by membranes, dorsal and lateral plates moving against urogomphi. Hypopleurites bulged. Median, inner and outer sternites gradually narrowed from segments I to V; median sternite absent in segments VI–VIII; sternum VI–VIII without sclerites. Urogomphi and pygidium oriented in a vertical plane (Fig. 17); urogomphi (Figs 15,17) branched, each composed of five slender, cylindrical lobes: A, B, C, D, E (respectively from inner to outer) mostly developed on a single plane and with rounded apices; lobe A inserted more basally than others, slender, slightly curved basally and apically and tapered to tip,



**Figs 16–19.** *Mystropomus subcostatus* third-instar larva: (16) terminal disk and abdominal segments VI–VII, dorsal view; (17) terminal disk and urogomphi, apical view, with different views of branches B, D and E at the bottom; (18) pronotum and mesonotum; (19) right anterior leg, posterolateral view. A–D, lobes of urogomphi; CO, coxa; e, epipleurite; FE, femur; ME, mesonotum; PR, pronotum; py, pygidium; t, tergum; TA, tarsus; TI, tibia; TR, trochanter; ug, urogomphus; UN, claw. Roman numerals identify abdominal segments.

not reaching apex of lobe B; lobe B elongate with single, markedly up-curved apex (Fig. 17); lobe C short, subbasally emerging from side of lobe B; lobe D club-shaped, dorsally emerging subbasally from lobe E; lobe E approximately as long as lobe B; pygidium (Figs 15,17) ring-like, suboval, medioventral between urogomphal insertions.

**Key to larvae of the Australian Paussinae genera**

The purpose of the following key is to aid in the identification of Paussinae larvae of the Australian genera *Mystropomus* and *Arthropterus* and to distinguish them from all other carabid larvae. The larva of the genus *Megalopaussus* Lea (see Nagel 1994) is not included in this key as it is still unknown.

- 1 Abdomen linear, with segments VIII–IX not modified; segment IX with pair of tubular urogomphi (rarely reduced or absent)..... most Carabidae
- Abdomen up-curved, with segments VIII–IX (mostly epipleurites and tergites) highly modified, transformed into a transverse sclerotized terminal disk composed of flat plates; segment IX with pair of branched or plate-like urogomphi (Paussinae)..... 2
- 2 Head hyperprognathous (bent upwards); neck constricted (Figs 4–6); coronal suture present (Fig. 4); sensorial appendage on antennomere III small and conical (Fig. 8); mandibles long and slender, sickle-shaped (Fig. 9); urogomphi multilobed (Fig. 17); tarsi with two claws (Fig. 19); pygidium between uro-



- mphi (Fig. 17) near the middle of the terminal disk (Metriini, Ozaenini)..... 3
- Head prognathous; neck not constricted; coronal suture absent; sensorial appendage on antennomere III large, bulbous or conical; mandibles short and broad, subtriangular; urogomphi flattened, plate-like, not lobate; tarsi with one claw; pygidium ventral to urogomphi and terminal disk (Paussini)..... 5
- 3 Anterior margin of frontoclypeolabrum with medial teeth (Fig. 6); urogomphi with five lobes (A, B, C, D, E), lobe E undivided (Fig. 17) (Metriini, Mystropomina)..... 4
- Anterior margin of frontoclypeolabrum without teeth; urogomphi with six or more lobes, lobe E subapically divided into E1 and E2 lobes..... Ozaenina
- 4 Stipes of maxillae without a basal tooth; lobe A short, lobe D at the common base of lobes B–C.... Metriini
- Stipes of maxillae with an acute basal tooth (Figs 10,11) in inner margin; lobe A elongate; lobe D at the base of lobe E (Fig. 17).....
- ..... *Mystropomus* Chaudoir (Mystropomina)
- 5 Long clavate setae (sensilla S–VIII, see Di Giulio & Moore, 2004) present on dorsal surface of head, thorax and terminal disk; lacinia present, with strong hook-like spines along occlusal margin; mandible without prostheca; leg segments not fused.....
- ..... *Arthropterus* W.S. MacLeay (Paussini)
- Setae on dorsal surface of head, thorax and terminal disk not clavate; lacinia absent; mandible with digitiform prostheca; leg segments fused.....
- ..... all other genera of Paussini

## DISCUSSION

There is no indication based on external structure that the larva of *Mystropomus* is myrmecophilous. It is not physogastric, and the components of the terminal disk are free to articulate with one another which would allow it to use an ambush feeding strategy and to trap prey as has been described for other paussine larvae that live in galleries (Costa *et al.* 1988; Di Giulio and Vigna Taglianti 2001; Moore and Di Giulio 2006).

*Mystropomus* has two unique larval characteristics that might be revealed to be diagnostic of the species, genus or subtribe as additional larvae are described. These are: (1) lateral protuberances at the apex of the ligula (Fig. 12); and (2) urogomphi with lobe D arising from lobe E (Fig. 17). In addition, the larva has some characters that are consistent with the prevailing hypothesis that *Mystropomina* attaches near the base of the evolutionary tree of Paussinae. For example, larvae of *Mystropomus* and *Metrius* Eschscholtz are the only Paussinae that have denticulations of the anterior margin of frontoclypeolabrum. Denticulate anterior margins are also present in the larvae of some other carabid beetles such as Gehingiini, Opisthiini, Carabini and Nebrini, and it is considered to be a plesiomorphic character state within Carabidae (Beutel 1992).

There are also several structural features that are shared only in the larvae of *Metrius* and *Mystropomus*, including: (1) the presence of sensilla S–I on the abdominal sterna; (2) sensilla S–II flattened; (3) terminal disk with five urogomphal lobes (Fig. 17) (short in *Metrius* and elongate in *Mystropomus*); and (4) urogomphal lobes B and E simple rather than partially or totally divided into two sublobes. These are either plesiomorphic characteristics which were also present in the common ancestor of the Paussinae, or they might be apomorphic characters signifying a sister group relationship between *Metrius* and *Mystropomus*. Future phylogenetic analyses of the entire subfamily Paussinae based on larval morphology (A. Di Giulio and W. Moore in prep. 2011) and molecular sequence data (W. Moore in prep. 2010) will help distinguish these two possibilities.

## ACKNOWLEDGEMENTS

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## REFERENCES

- Beutel RG. 1992. Study on the systematic position of Metriini based on characters of the larval head (Coleoptera: Carabidae). *Systematic Entomology* **17**, 207–218.
- Bousquet Y. 1986. Description of first-instar larva of *Metrius contractus* (Coleoptera: Carabidae) with remarks about phylogenetic relationships and ranking of the genus *Metrius*. *The Canadian Entomologist* **118**, 373–388.
- Bousquet Y & Goulet A. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Canadian Journal of Zoology* **62**, 573–588.
- Costa C, Vanin SA & Casari-Chen SA. 1988. *Larvas de Coleoptera do Brasil*. Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo, Brazil.
- Darlington PJ. 1961. Australian carabid beetles V. Transitions of wet forest faunas from New Guinea – Tasmania. *Psyche* **68**, 1–24.
- Deuve T. 2004. Nouveaux Ozaenini Néotropicaux (Coleoptera: Paussidae). *Revue Française d'Entomologie (N.S.)* **26**, 117–130.
- Deuve T. 2005. Nouveaux Ozaeninae (Eustrini et Ozaenini) de la region neotropicale et du Nepal (Coleoptera, Caraboidea, Paussidae). *Revue Française d'Entomologie (N.S.)* **27**, 103–116.
- Deuve T. 2007. Nouveaux Paussidae, Carabidae, et Trechidae de la Chine et du Sud-Est Asiatique. *Coléoptères* **13**, 51–62.
- Di Giulio A. 2008. Fine morphology of the myrmecophilous larva of *Paussus kannegieteri* (Coleoptera: Carabidae: Paussinae: Paussini). *Zootaxa* **1741**, 37–50.
- Di Giulio A & Moore W. 2004. The first-instar larva of the genus *Arthropterus* (Coleoptera: Carabidae: Paussinae): implications for evolution of myrmecophily and phylogenetic relationships within the subfamily. *Invertebrate Systematics* **18**, 101–115.
- Di Giulio A & Vigna Taglianti A. 2001. Biological observations on *Pachyteles* larvae (Coleoptera: Carabidae: Paussinae). *Tropical Zoology* **14**, 157–173.
- Di Giulio A, Fausto AM, Taddei AR & Vigna Taglianti A. 2000. The terminal disk of *Pachyteles* larvae (Coleoptera, Carabidae, Paussini).



- nae): a morphological study. In: *Natural History and Applied Ecology of Carabid Beetles Proceedings of the IX European Carabidologists' Meeting (26–31 July, 1998, Camigliatello, Cosenza, Italy)* (eds P Brandmayr, G Lövei, T Zetto Brandmayr, A Casale & A Vigna Taglianti), pp. 89–93. Pensoft, Sofia.
- Di Giulio A, Fattorini S, Kaupp A, Vigna Taglianti A & Nagel P. 2003. Review of competing hypotheses of phylogenetic relationships of Paussinae (Coleoptera: Carabidae) based on larval characters. *Systematic Entomology* **28**, 509–537.
- Geiselhardt SF, Peschke K & Nagel P. 2007. A review of the myrmecophily in ant nest beetles (Coleoptera: Carabidae: Paussinae) linking early observations with recent findings. *Naturwissenschaften* **94**, 871–894.
- Lawrence JF. 1991. Order Coleoptera. In: *Immature Insects*, Vol. 2. (ed. FW Stehr), pp. 144–298. Kendall/Hunt Publishing Company, Dubuque, IA, USA.
- Lawrence JF, Moore BP, Pyke JE & Weir TA. 2001. Updated by A. A. Calder (2002). Adephaga. *Australian Faunal Directory*. Australian Biological Resources Study, Canberra. [Accessed 31 Aug 2007.] Available from URL: <http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna/afd/index.html>
- Lorenz W. 2005. *Systematic List of Extant Ground Beetles of the World (Coleoptera 'Geadephaga': Trachypachidae and Carabidae Incl. Paussinae, Cicindelinae, Rhysodinae)*, 2nd edn. Published by the author, Tutzing, Germany.
- MacSwain JW & Garner WV. 1956. Notes of two millipede-feeding carabids. *Pan-Pacific Entomologist* **32**, 54.
- Moore W & Di Giulio A. 2006. Description and behaviour of *Goniotropis kuntzeni* larvae (Coleoptera: Carabidae: Paussinae: Ozaenini) and a key to genera of Paussinae larvae. *Zootaxa* **111**, 1–19.
- Moore W & Di Giulio A. 2008. *Metrius* Eschscholtz (Carabidae: Paussinae) is not a millipede specialist. *Pan-Pacific Entomologist* **84**, 33–34.
- Nagel P. 1994. Die taxonomische Stellung van *Megalopaussus amplipennis* Lea (Carabidae: Paussinae). *Entomologische Blätter für Biologie und Systematik der Käfer* **90**, 80–98.
- Vigna Taglianti A, Santarelli FM, Di Giulio A & Oliverio M. 1998. Phylogenetic implications of larval morphology in the tribe 'Ozaenini' (Coleoptera: Carabidae). In: *Phylogeny and Classification of Caraboidea (Coleoptera: Adephaga). Proceedings of a Symposium. XX International Congress of Entomology* (eds GE Ball, A Casale & A Vigna Taglianti), pp. 273–296. Museo Regionale Di Scienze Naturali, Torino, Italy.
- Williams G. 2002. A taxonomic and biogeographic review of the invertebrates of the Central Eastern Rainforest Reserves of Australia (CERRA) World Heritage Area, and Adjacent Regions. *Technical Reports of the Australian Museum* **16**, 1–208.

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