The systematics of Dysmorphocerinae (Cantharidae) based on larvae

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Running title. The systematics of Dysmorphocerinae based on larvae

Abstract. Dysmorphocerinae is a subfamily of Cantharidae erected for a group of genera with a mainly gondwanan distribution whose adult forms could not be reliably assigned to any other subfamily. The systematic position and monophyly of Dysmorphocerinae remains questionable, as recent molecular and morphological studies have produced conflicting

results. Despite the importance of immature morphology for characterising lineages of Cantharidae, so far, the larvae of only two dysmorphocerine species had been briefly described: *Neoontelus* sp., from New Zealand, and *Afronycha picta* (Wiedemann), from South Africa. Their morphologies considerably differ from one another, and the larvae cannot be readily attributed to any subfamily, as usually occurs with cantharid larvae. Here, we fully describe for the first time the larvae of *Asilis* Broun (New Zealand) and *Plectonotum laterale* Pic (Brazil) and redescribe *Neoontelus* Wittmer (New Zealand). We also diagnose larvae of *Heteromastix* Boheman (Australia) and *A. picta*. Dysmorphocerinae cannot be clearly diagnosed because each genus has a unique combination of features, though *Neoontelus* is the most divergent. We conclude that the Dysmorphocerinae may not be monophyletic with *Plectonotum laterale*, *Asilis*, *Neoontelus*, *Heteromastix* showing a closer relationship to Malthininae and *Afronycha* more aligned with Silinae or Cantharinae. The double gland openings present on the body of *Neoontelus* reported by Crowson (1972) are reinterpreted as a complex character involving a single posterior pore linked to a gland and an anterior sensillum that may serve as a trigger for the release of defensive chemicals. These are also reported in *Asilis* and *Heteromastix* and may be a potential synapomorphy for part of the Dysmorphocerinae. *Neoontelus* has a series of unique features, including a cotyliform glandular pore on abdominal segment IX.

Keywords. Classification, Immatures, Morphology, Soldier beetle, Systematics

Introduction

Cantharidae larvae are usually easily recognised by their soft body densely covered with short pubescence, giving them a velvety appearance; other characters, like the prognathous and slightly flattened head, and body with lateral and transversal ampullae with pairs of glandular pores are also diagnostic (Crowson 1972; Ramsdale 2010). They have a rich diversity of structures useful for characterising lineages of Cantharidae and have enabled the production of identification keys, the recognition of genera and groups of species, and the definition of subfamilies (cf., Bøving & Craighead 1931; Striganova 1962; Fitton 1976; Klausnitzer 1997; Biffi & Casari 2017; Biffi & Rosa 2019; Biffi et al. 2022). As highlighted by Crowson (1972), the known Cantharidae larvae seem to fall readily into groups corresponding to the four commonly accepted subfamilies of the adults at that time (Cantharinae Imhoff, Malthininae Kiesenwetter, Chauliognathinae LeConte, and Silinae Mulsant) apart from one, an 'aberrant' cantharid larva. This larva was briefly described and referred to by Crowson (1972) as *Oontelus*-like, based on adults that he collected in the same vicinity which, according to W. Wittmer, resembled *Oontelus* Solier, 1849, a genus known from South America with serially punctate elytra. This genus was named in the same year as Crowson's publication as *Neoontelus* Wittmer, 1972.

The *Neoontelus* larva considerably differs from known Cantharidae larvae, such as the body devoid of velvety pubescence, absence of stemmata, and abdominal terga with lateral outgrowths and double glandular pores (Figure 1). Given the unusual features of that larva, Crowson suggested that an independent subfamily should be erected for it.

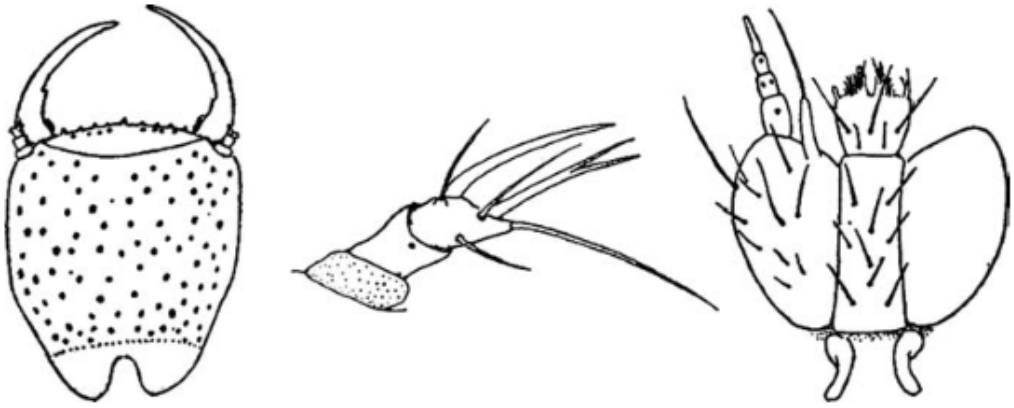

Figure 1. Original illustrations from Crowson (1972) of head capsule, antenna and maxillo-labial complex of an '*Oontelus*-like' larva from New Zealand, currently assigned to *Neoontelus* Wittmer, 1972.

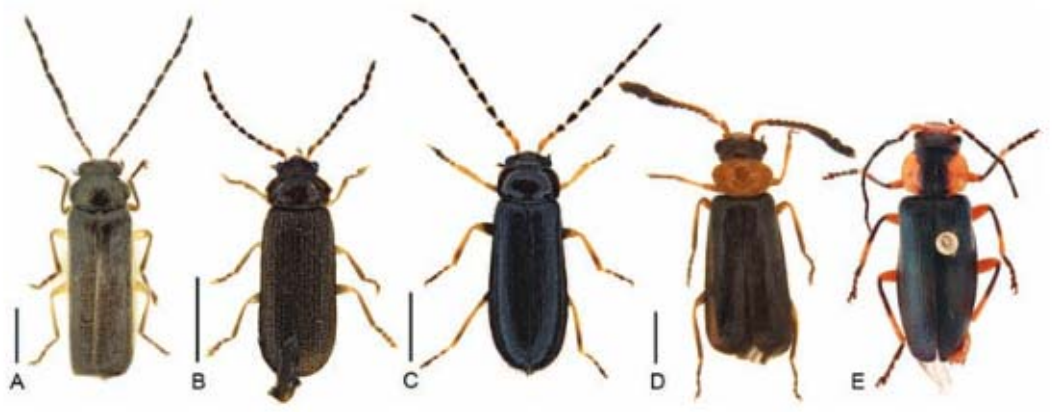

Figure 2. Representatives of adults of Dysmorphocerinae, dorsal habitus. **A**. *Plectonotum laterale* Pic, 1906, Brazil; **B**. *Neoontelus* sp. New Zealand; **C**. *Asilis* sp., New Zealand; **D**. *Heteromastix crassicornis* Lea, 1895, Australia; **E**. *Afronycha* sp., South Africa.

In a thorough study of adult Cantharidae, Brancucci (1980) erected Dysmorphocerinae (Figure 2) for a group of genera that included *Neoontelus* which exhibited structures that resembled the morphology of members of the subfamilies Cantharinae, Silinae or Malthininae. Though Brancucci (1980) identified a single synapomorphy for Dysmorphocerinae in a hand-worked phylogeny (the ovipositor with a strongly developed paraproct), he suggested that future studies would enable a subdivision of this subfamily. At

present, Dysmorphocerinae is distributed mostly in the southern hemisphere, with 14 genera and ca. 350 species (Table 1) (Delkeskamp 1977; Wittmer 1979; Calder 1998; Ramsdale 2002; Constantin 2008, 2010, 2020; Fanti & Menufandu 2022; Biffi 2022).

Table 1. Diversity of Dysmorphocerinae genera.

Genus	Number of species	Distribution
Heteromastix Boheman, 1858	92	Australia and New Guinea
Geigyella Wittmer, 1972	51	New Guinea
Asilis Broun, 1893	39	New Zealand
Neoontelus Wittmer, 1972	4	New Zealand
Afronycha Wittmer, 1949	42	South Africa
Compsonycha Wittmer, 1949	12	South Africa
Flabelloontelus Pic, 1911	1	Mexico
Plectonotum Gorham, 1885	53	Central and South America
Plectocephalon Pic, 1928	1	Chile and Argentina
Hyponotum Wittmer, 1949	16	Chile and Argentina
Oontelus Solier, 1849	30	Brazil, Chile and Argentina
Dysmorphocerus Solier, 1849	4	Chile
Micronotum Wittmer, 1949	5	Chile and Argentina
Hansasilis Pic, 1936	4	Brazil and Argentina

Most studies of Dysmorphocerinae are limited to descriptions of new species and revisions of a few genera (e.g., Wittmer 1967, 1979; Constantin 2008, 2010, 2020), otherwise, little is known about their natural history. South American species occurring from low to high altitudes, collected from lower vegetation during the day and occasionally attracted to light traps (Constantin 2018, 2020), New Zealand members with adults found on flowers and larvae collected from leaf litter (Kuschel 1990; Klimaszewski & Watt 1997), and the larva of South African *Afronycha picta* feeding on fly larvae in fresh cow pats (Prins 1984). Apart from Crowson (1972), the only other known larva described of Dysmorphocerinae is that of *A. picta* (Wiedemann, 1821), from South Africa, by Prins (1984). It has the usual Cantharidae features and differs significantly from *Neoontelus* which exhibits characteristics typically found in Malthininae (Crowson 1972), whilst the former has characters in common with Cantharinae and Silinae, challenging Crowson's assertion that larval features group them according to the subfamilial classification based on adult

characters. The conflict between larval and adult morphologies prompted us to address two hypotheses: that Dysmorphocerinae, unlike the other cantharid subfamilies, is a monophyletic group that contains species with highly variable larval morphologies, or the subfamily is not monophyletic.

The phylogenetic relationships among the cantharid subfamilies remain questionable and their monophyly requires further testing (Brancucci 1980; Lawrence et al. 2011; Kundrata et al. 2014; Zhang et al. 2018; Hsiao et al. 2021; Cai et al. 2022). While the number of terminal taxa has not been sufficient to test their monophyly, few of these phylogenetic studies have included members of Dysmorphocerinae. Detailed examination of Dysmorphocerinae may provide key evidence for their systematic position within Cantharidae or reinforce Brancucci's (1980) suspicion that the subfamily may be an artificial assemblage of genera.

Here, we provide a comparative morphological study of larvae of Dysmorphocerinae along with the first descriptions of *Plectonotum laterale* Pic, 1906, based on a specimen from Brazil, and generic descriptions of *Asilis* Broun, 1893 from New Zealand, based on eight species. The specimen of *Neoontelus* studied by Crowson (1972) is revisited and re-described fully. We diagnose the larvae of *Heteromastix* Boheman, 1858 from Australia, based on six species and re-describe *Afronycha picta* after a re-interpretation of Prins' (1984) description based on fresh larval material. We discuss salient larval characters and compare these to the other cantharid subfamilies and species lineages and propose that the Dysmorphocerinae may not be monophyletic with *Plectonotum laterale*, *Asilis*, *Neoontelus*, *Heteromastix* more aligned to Malthininae and *A. picta* more similar to Silinae or Cantharinae.

Material and methods

Morphological descriptions are based on different sets of specimens. The slide-mounted dissected larva previously studied by Crowson (1972) is deposited in the Natural History Museum (London, United Kingdom – BMNH). Six larvae of Australian *Heteromastix* spp. are deposited at the Australian National Insect Collection (Canberra, Australia – ANIC). Twenty-two larvae of *Asilis* spp. from nine localities in New Zealand are deposited in the National Museum (Prague, Czech Republic – NMPC) and the New Zealand Arthropod Collection (Auckland, New Zealand – NZAC) and one larva of *Afronycha* sp. is deposited in The National Museum (Bloemfontein, South Africa – BMSA). After dissection and examination, we mounted the sclerites of each specimen in individual slides or onto cards. For *Plectonotum laterale*, the description is based on the last-instar larval exuvia of a single specimen reared to adulthood in the laboratory. Larvae and parts of the exuvia are fixed in 70% ethanol and preserved in the Immature Coleoptera Collection in Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil – MZUSP), while gold-coated pieces are card-mounted together with the adult and are preserved in the general Coleoptera collection (MZUSP). Full data of the examined material are given in Table 2.

Morphological terminology used in the descriptions follows Ramsdale (2010), Lawrence et al. (2010) and Biffi & Casari (2017).

Dissected mouthparts and other parts were mounted in temporary slides for observation and illustration under camara lucida attached to the microscope. Photographs were taken with a Canon EOS Rebel T3i camera equipped with Canon MP-E 65 mm macro-lens and additional extension tubes attached to a StackShot macro-rail, and Leica DFC500 camera mounted on a Leica M205C stereomicroscope. Multi-focal images were processed with the Zerene Stacker software (version 1.04) and Leica Application Suite (LAS) V4.9.

SEM images from gold-coated specimens were made with a Carl Zeiss LEO 440 scanning electron microscope at MZUSP. µCT-scanning was performed using a General Electric Phoenix v|tome|x m microfocus microscope at the MZUSP. One *Asilis* specimen fixed in 100% ethanol was immersed in iodine solution for four days. 1,200 images were taken for a full 360° rotation. 3D reconstructions of the resulting scan projection data were done with the Phoenix datos|x 2, GE Sensing and Inspection Technologies GmbH, and saved in TIFF file format.

Table 2. Species, locality and dates of the examined material.

Species	Locality	Material examined
Plectonotum laterale Pic, 1906	BRAZIL: São Paulo, Parque Estadual da Cantareira, 3.iii.1993, Exp. MZUSP lgt. (MZUSP 6127)	1 larval exuvia, 1 adult,
Neoontelus sp	NEW ZEALAND, Northland (ND), Whangarei, Mount Manaia, 17.10.1956, R.A. Crowson leg. prep. Leaf litter, "Cantharidae nr. [near] *Oontelus*" (NHMUK010132743)	1 slide-mounted larva,
Asilis sp. 1	NEW ZEALAND: Marlborough (MB), Hanmer Forest Park, beginning of Chatterton Track; 530 m 42.4927–4939°S, 172.819–820°E; 380 m; 7–9.xii.2016; M. Fikáček & M. Seidel lgt., "patches of low sparse bushes (mixed broadleaf and *Libocedrus*), in places with dense fern understory at the bank of Chaterton River", MM63.	8 larvae, NMPC
Asilis sp. 2	NEW ZEALAND: Wellington (WL); Rimutaka Forest Park, Wainuiomata; Nikau Track; 140–180 m; 41.2795-28223S, 174.997978°E; 380 m; 29.xi.–1.xii.2016; M. Fikáček & M. Seidel lgt., "stream collecting in Nikau Stream: in submerged mosses", MM40.	1 larva, NMPC
Asilis sp. 3	NEW ZEALAND: Taranaki (TK), Mt. Egmont Nat. Park, unnamed stream at Pukeiti Rhod. Garden; 39.20242°S, 173.98140°E; 393 m; 20.xi.–13.xii.2016; M. Fikáček & M. Seidel lgt., "stony stream in lowland broadleaf forest: stream collecting in submerged/emerged moss in the stream", MM09.	1 larva, NMPC.
Asilis sp. 4	NEW ZEALAND: Westland (WD), Lake Wombat Track 2.5 km S of Franz Josef; 43°24.80'S, 170°10.43'E; 200 m; 21.–23.ii.2016; Seidel, Sykora, Leschen & Maier lgt., "sifting of leaf litter in native forest", 2016-NZMS50.	4 larvae, NMPC
Asilis sp. 5	NEW ZEALAND: Fiordland (FD), Gertrude Valley at Homer Tunnel; 44°45.86'S, 168°0.35'E; 800 m; 29.i.–1.ii.2016; Seidel, Sykora & Fikáček lgt., "sifting of leaf litter in low *Nothofagus* forest with many lichens close to border to subalpine tussock", 2016-NZ040.	1 larva, NMPC

Asilis sp. 6	NEW ZEALAND: Waikato (WO), Rirongia Forest Park, Mangakara Nature Walk + lower part of Ruapane Link Track; 37.966°S, 175.144-149°E; 177–235 m; 18.xi.2016; Fikáček & Seidel lgt., "lowland broadleaf forest with podocarps, nikau palms and *Ripogonum* lianas; sparse understory: floating emerged mosses in small stream", MM01.	3 larvae, NMPC
Asilis sp. 7	NEW ZEALAND: Westland (WD), Kelly Creek at Otira Hwy.; 42°48.06'S, 171°34.26'E; 380 m; 24.–26.ii.2016; Seidel, Sykora, Leschen, Maier & Lambert lgt., "sifting of leaf litter in native forest", 2016-NZ-MS73.	1 larva, NMPC
Asilis sp. 8	NEW ZEALAND: Buller (BR), Tiropahi River at Tiropahi Track 6 km SW of Charleston; 41°57.65'S, 171°25.97'E; 120 m; 25.ii.2016; Seidel, Sykora, Leschen, Maier & Lambert lgt., "sifting of leaf litter in native forest", 2016-NZ-MS82 / 2016-NZ-MS50.	3 larvae, NMPC
Heteromastix sp. 1	AUSTRALIA, Queensland, Lamington Nat.Pk., Binna Burra, 25 Mar.-4 Apr.1985, pyrethrin fogging bark of trees, J. & N. Lawrence	1 larva, ANIC
Heteromastix sp. 2	AUSTRALIA, Tasmania, Mt. Wellington, 9 Apr.1982, Fern Tree, G. Bornemissza, Berlesate ANIC 918	1 larva, ANIC
Heteromastix sp. 3	AUSTRALIA, Western Australia, Quininup 29km SSE Manjimup, 13-16 Jul. 1980, S. & J. Peck SBP112, berlesate karri forest litter	1 larva, ANIC
Heteromastix sp. 4	AUSTRALIA, Far North Queensland, 13.44S 143.20E, 11km WbyN of Bald Hill, Mcllwraith Range, 27 June-12 July 1989, T.A. Weir 520m, search party campsite, Berlesate, ANIC, 1107, leaf & log litter closed forest	1 larva, ANIC
Heteromastix sp. 5	AUSTRALIA, New South Wales, 28.24S 152.40E NSW, Unumgar S.F. 430m nr Woodenbong, Pole Bridge Road 788 2-11 Jan.1987, A. Newton & M. Thayer, dry rainf. Arauc.-Euc. FMHD #87-174 Berlesate leaf & log litter.	1 larva, ANIC
Heteromastix sp. 6	AUSTRALIA, Victoria, Cape Conran, 18km E Marlo, 22 May 1984, berl. rotten *Banksia* bark, J.F. Lawrence.	1 larva, ANIC
Afronycha sp.	RSA [Republic of South Africa], Eastern Cape Province, Silaka Nature Reserve, Forest, pig dung + chicken livers pitfall, 21-25. ii.2022. E. Khawli	1 larva, BMSA

Illustrations and photographs were edited in Adobe Photoshop CS6 and Adobe Illustrator CS6.

Results

Adult and larval associations

The larva from Parque Estadual da Cantareira, Brazil, was reared to a female in the laboratory. The species was identified as *Plectonotum laterale* following Wittmer (1967)

after the examination of males and females from the same locality. *Plectonotum laterale* is widespread through the Atlantic Forest, in north-eastern Argentina (Misiones province), Paraguay and Brazil, from Rio Grande do Sul to Minas Gerais and Rio de Janeiro states. The species is recorded herein for the first time in São Paulo state.

The larvae from New Zealand and Australia have been assigned to genus level. Adult specimens of *Neoontelus* are rare and the three species are recorded from the North Island and from Marlborough, in the northern South Island, whilst *Asilis* is common and widely distributed throughout New Zealand (Wittmer 1972). The restricted distribution and diversity of larval forms have confirmed that Crowson's larva is *Neoontelus* and the others must be *Asilis*.

Australian larvae have been identified as *Heteromastix*. Cantharidae are represented in Australia by only three genera in three subfamilies: *Chauliognathus* Hentz, 1830 (Chauliognathinae), *Sphaerarthrum* Waterhouse, 1884 (Silinae) and *Heteromastix* (Dysmorphocerinae) (Calder 1998). The latter genus is widespread in Australia and contains the highest cantharid diversity in the country with 77 described species (Calder 1998). Although none of the larvae available have been directly associated with adult specimens, they can be reliably regarded as *Heteromastix* because they lack the diagnostic characters attributed to the other subfamilies (cf. Fitton 1976) and are morphologically similar to *Asilis*. Furthermore, larval specimens occur where no other genera exist apart from *Heteromastix* species (Table 2).

One larva from the province of Eastern Cape, South Africa, has been identified as *Afronycha* sp. Five cantharid genera have been recorded in South Africa, with the vast majority of the species belonging to Dysmorphocerinae (35 species in *Afronycha* and 12 in *Compsonycha* Wittmer, 1949) (Delkeskamp 1977). Apart from members of *Afronycha*, which have adults of some species reaching up to 10 mm, species of all the other genera are small,

rarely exceeding 5 mm of length. The aforementioned larva is 11 mm long, which corresponds well to a species having large adults, such as those of *Afronycha*. Furthermore, it matches the description of *A. picta* given by Prins (1984).

Descriptions

***Plectonotum laterale* Pic**

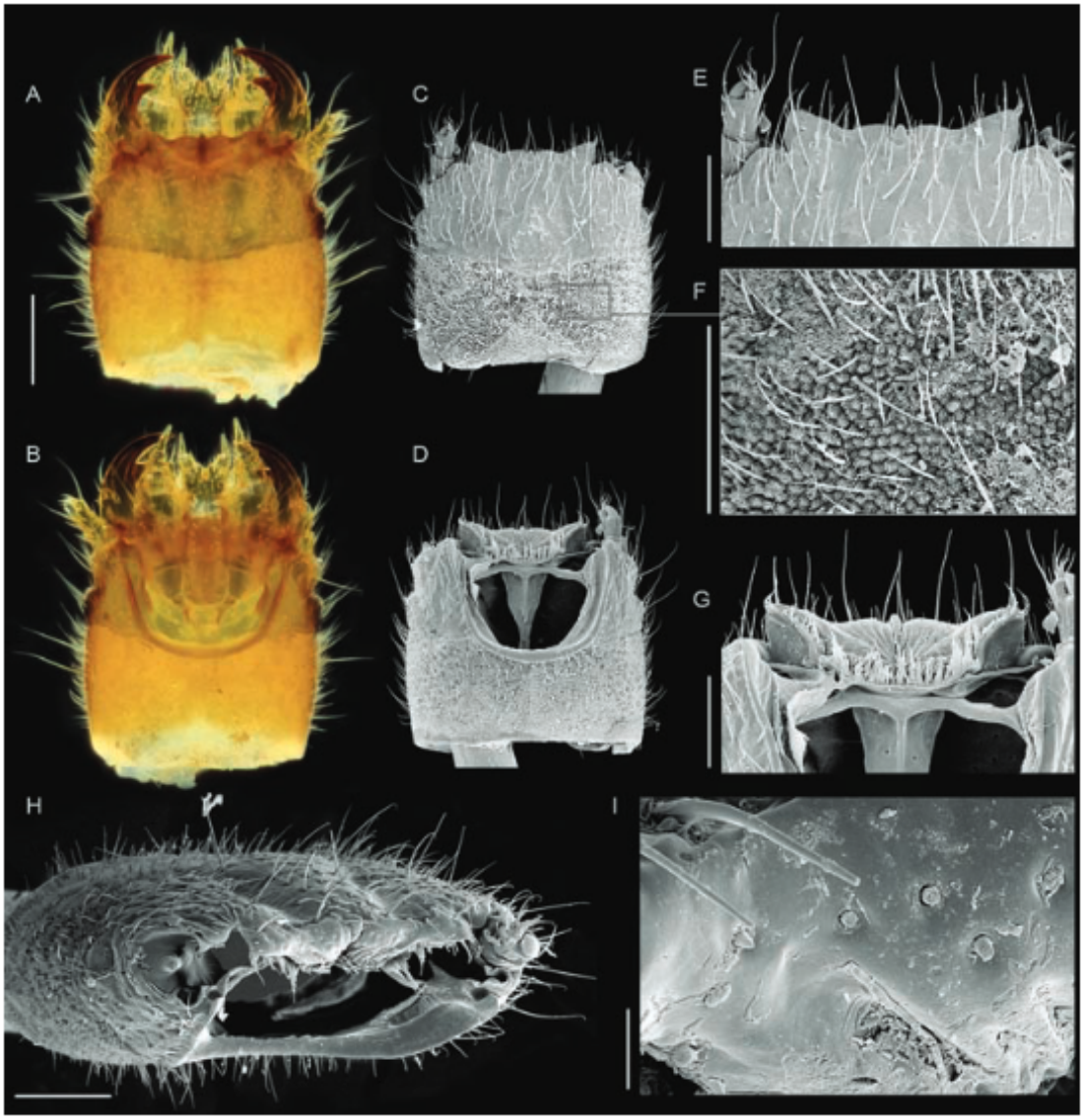

Figure 3. *Plectonotum laterale* Pic, 1906, head capsule of last instar larval exuvia. **A–B.** Multifocal photograph of the head with antennae and mouthparts in dorsal and ventral views; **C–I.** SEM images of the head capsule;

right antenna and mouthparts removed. **C.** Dorsal; **D.** Ventral; **E.** Nasale in dorsal view; **F.** Detail of the pubescence in the posterior part of the head; **G.** Tentorium and nasale in ventral view; H. Head capsule, fronto-lateral view; I. Nasale with wart-like sensilla in anterior view. Scale bars: A–D = 0.2 mm, E–H = 0.1 mm, I = 0.01 mm.

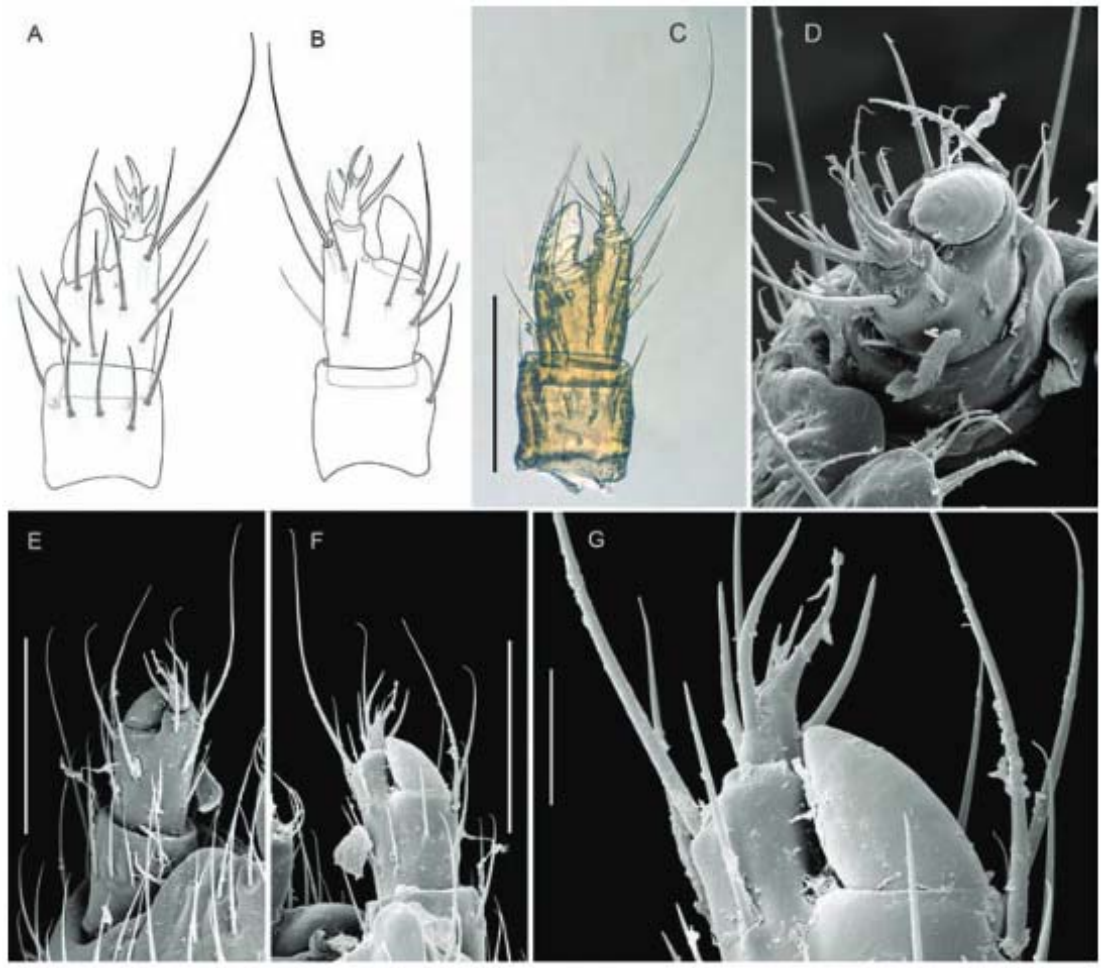

Figure 4. *Plectonotum laterale* Pic, 1906, illustration, optic micrograph and SEM images of left antenna. **A–B.** Dorsal and ventral views; **C.** Dorsal view. **D.** Apex of antenna in fronto-ventral view; **E–F.** Dorsal and ventral views; **G.** Apex of antenna, showing third antennomere and subterminal sensorium. Scale bars: 0.1 mm.

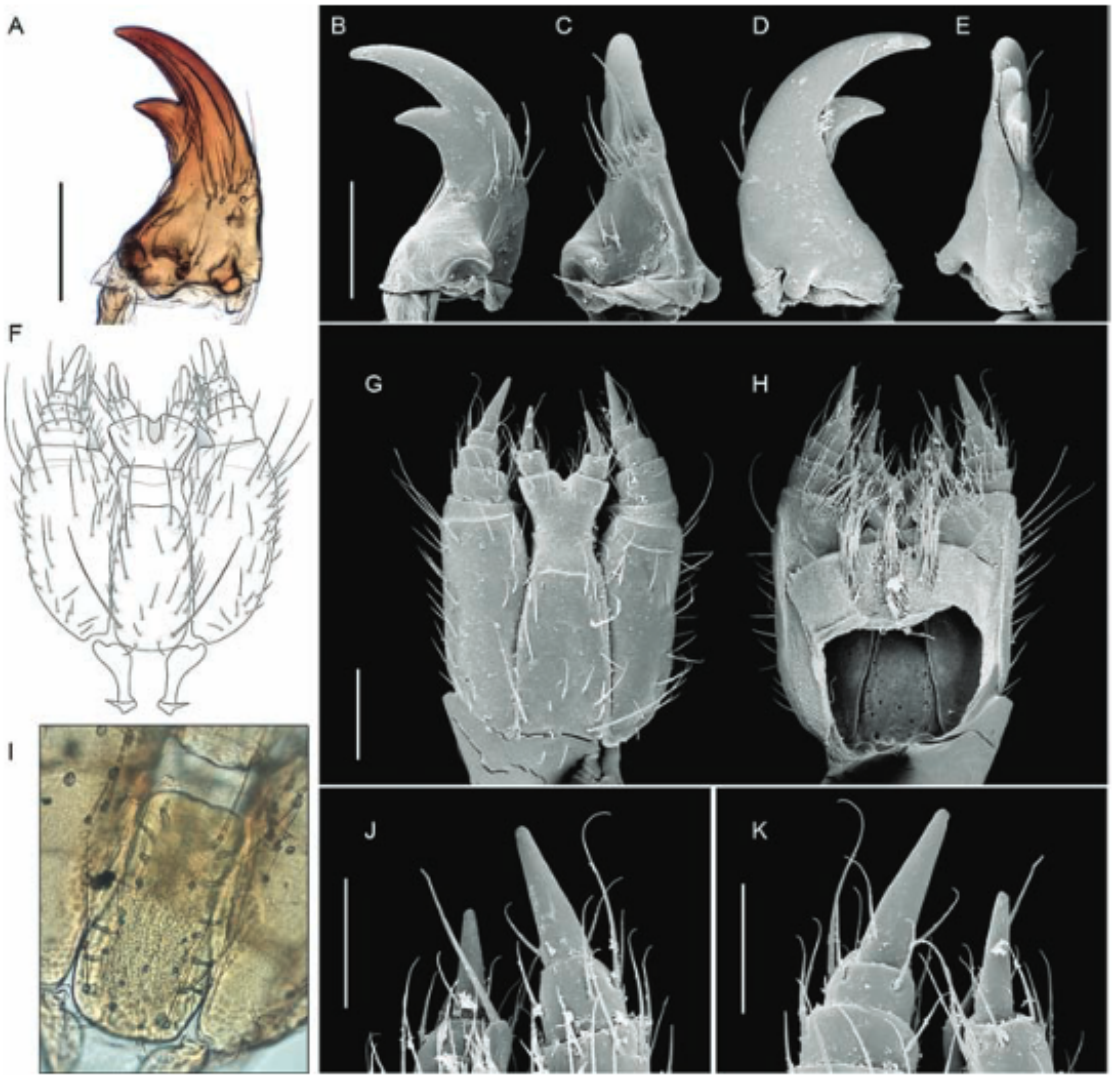

Figure 5. *Plectonotum laterale* Pic, 1906, mouthparts of last instar larval exuvia. **A.** Optic micrograph of the right mandible; **B–E.** SEM images of the right mandibula in dorsal, lateral, ventral and mesal views; **F–I.** Maxillo-labial complex in illustration (**F**), SEM images (**G–H**), and optic micrograph (**I**); **J–K.** Last labial and maxillary palpomeres in dorsal and ventral views. Scale bars: A–E, G–F = 0.1 mm, J–K = 0.05 mm.

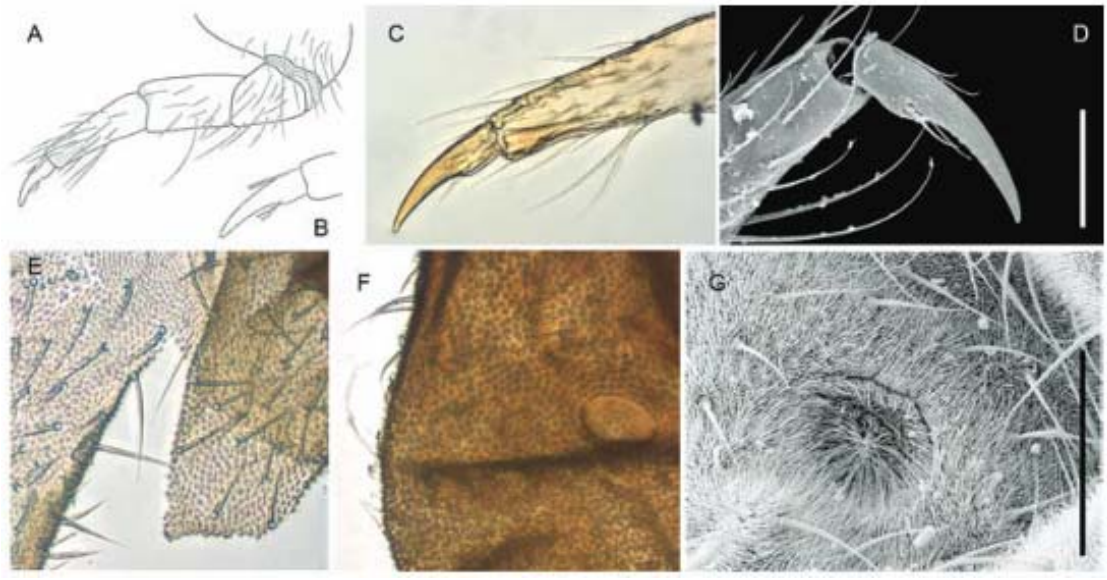

Figure 6. *Plectonotum laterale* Pic, 1906, illustration, optic micrograph and SEM images of prothoracic leg, integument and glandular pore. **A–D.** Right prothoracic leg and pretarsus; **E.** Thoracic integument, showing groups of short setae and sparser long setae; **F–G.** Integument and thoracic glandular pore. Scale bars: 0.05 mm.

Description of last instar larva: Head capsule length: approximately 0.55 mm. Coloration. Head capsule (Figure 3A–B) yellowish brown, lustrous on anterior half and opaque on posterior half; median tooth of nasal and paranasal lobes brown; brown area surrounding stemmata, ventrally a slightly darker band surrounding maxillo-labial complex. Mandibles brown at distal half and yellowish brown at basal half. Thorax and abdomen light brown, darker dorsally. Vestiture. Head capsule (Figure 3C–H) covered with long and thick setae of varied lengths; integument divided into two clearly-defined regions; anterior half with integument smooth, lustrous; posterior half densely covered with tufts of very short setae, giving a grainy aspect; sparse long and thick setae throughout; thorax and abdomen (Figure 6E–G) covered with velvety pubescence, with long sparse setae; under high magnification (1,000 times) integument covered with dense tufts of very short setae, giving a grainy aspect (Figures 3F, 6E–F). Head (Figure 3). Head partially retracted into prothorax; prognathous and flattened dorso-ventrally. Head capsule as long as wide, lateral margins almost straight,

slightly narrowed anterior and posteriorly; occipital foramen broad, as wide as head capsule; epicranial and gular sutures absent; one large and prominent stemma on each side, behind antenna. Nasale (Figure 3E, G–H) projecting, sinuous, shorter than paranasal lobes; anterior margin with a median rounded tooth delimited by paramedian grooves, sides individually

slightly rounded, without lateral teeth; paranasal lobes projecting, triangular with apex rounded; each paranasal lobe with one long and thick seta at middle of angular area and short setae near apex; median tooth without setae, flanked by a pair of long setae; one long and three short setae on either side; nasal ventrally transverse, oblique, smooth sclerotised plate ventrally, with deep median longitudinal groove and shallow lateral oblique convergent grooves (Figure 3G); wart-like sensilla on oblique plate anteriorly (Figure 3I); basally (Figure 3G), with a transverse fringe of short thick setae directed frontwards. Antennae (Figure 4) with three antennomeres; long and thin setae with deep channels at base, more concentrated ventrally (Figure 4A–C); antennomere I short, subquadrate, nearly as long as wide; four setae ventrally and one seta on inner margin; two campaniform sensilla ventrally, near distal margin; antennomere II longer, almost twice longer than wide, partially retracted into antennomere I; apex with a cylindrical lateral projection bearing antennomere III; large oblong sensorium beside lateral projection, with sclerotised band at inner and outer margins; numerous thick ventral and dorsal setae, thicker and longer laterally, near distal margin; one large dorsal campaniform sensillum near distal margin and a tiny wart-like sensillum between sensorium and apical projection; antennomere III minute, with four long and thick spine-like lateral projections, two shorter apical and four dorsal projections. Mandibles (Figure 5A–E) symmetrical, arcuate; incisors acute; retinaculum dorsal, curved downwards, apex acute; mesal channel well-developed, sinuous, extended from apex to beyond middle, tapering towards base; an oblong, slightly grooved concavity below retinaculum extending

posteriorly; a fringe of short, fine clear setae at mesal margin of mandible, beside channel; penicillus not observed; groups of setae dorsally near middle and near acetabulum. Maxillae (Figure 5F–H). Cardo elongate and curved, broader anteriorly, tapering and abruptly broader posteriorly. Stipes elongate, narrower basally, nearly parallel, translucent, slightly sclerotised. Numerous setae ventrally, more concentrated near lateral margins, longer toward the apex, insertions with deep channels; dorsal area with fringe of fine long setae near base of palpi and at the inner margin; galea elongate, nearly as long as two basal palpomeres, broader basally, tapering from apical half, with three long apical setae; lacinia formed by a fringe of long and fine setae, densely distributed near inner margin. Maxillary palpi (Figure 5J–K) with four palpomeres progressively decreasing in length from I to III; longitudinal sclerites at inner and outer margins; palpomere I wider than long, with numerous thin setae on dorsal face and a row of four ventral setae with a deep channel at base; palpomere II wider than long, with one ventral campaniform sensillum and two setae near lateral margins, few fine setae dorsally; palpomere III wider than long, with one ventral campaniform sensillum and two setae near lateral margins, and one long fine dorsal seta; palpomere IV conical, elongate, tree times longer than wide at base, one seta dorsally, one seta ventrally, near the base. Labium (Figure 5F–G, I). Postmentum elongate, subparallel, translucent; short and long ventral setae with basal channels, two anterior and two posterior longer setae; dorsal surface with three dense longitudinal bands of fine setae anteriorly; prementum trapezoidal, wider apically; strong sclerite at lateral margins and at apex, between palpi; few ventral setae with deep channel at base; two campaniform sensilla and long setae dorsally; palpi (Figure 5J–K) with two palpomeres; palpomere I barrel like, nearly as long as wide, bearing one campaniform sensillum and two long ventral setae and four dorsal setae with basal channels; palpomere II conical, elongate, almost three times longer than wide at base, one dorsal setae and one ventral campaniform sensillum near base. Legs (Figure 6A–D). Robust, slightly increasing in

size from anterior to posterior; with numerous long setae; coxae short, conical, inserted distant one from another; femora short, cylindrical, nearly twice longer than wide; tibiae elongate, slightly tapering apicad, a pair of apical internal sclerites; pretarsi narrow, curved, slightly grooved; nearly half of tibiae length, distal two thirds tapering apicad, with two dorsal setae near base and one seta on either side near basal ventral third. Thorax and abdomen. Pro-, meso- and metathorax and abdominal segments I–IX with one pair of large round latero-dorsal glandular pores (Figure 6F–G), sensilla indistinct; meso- and metathoracic and abdominal glandular pores I–VIII on weak latero-dorsal ampullae; abdominal terga without lateral outgrowths; abdominal segment X membranous, without hooks or outgrowths. Spiracles observed.

Remarks: A single larva of *Plectonotum laterale* was reared to adult in the laboratory.

Neoontelus Wittmer

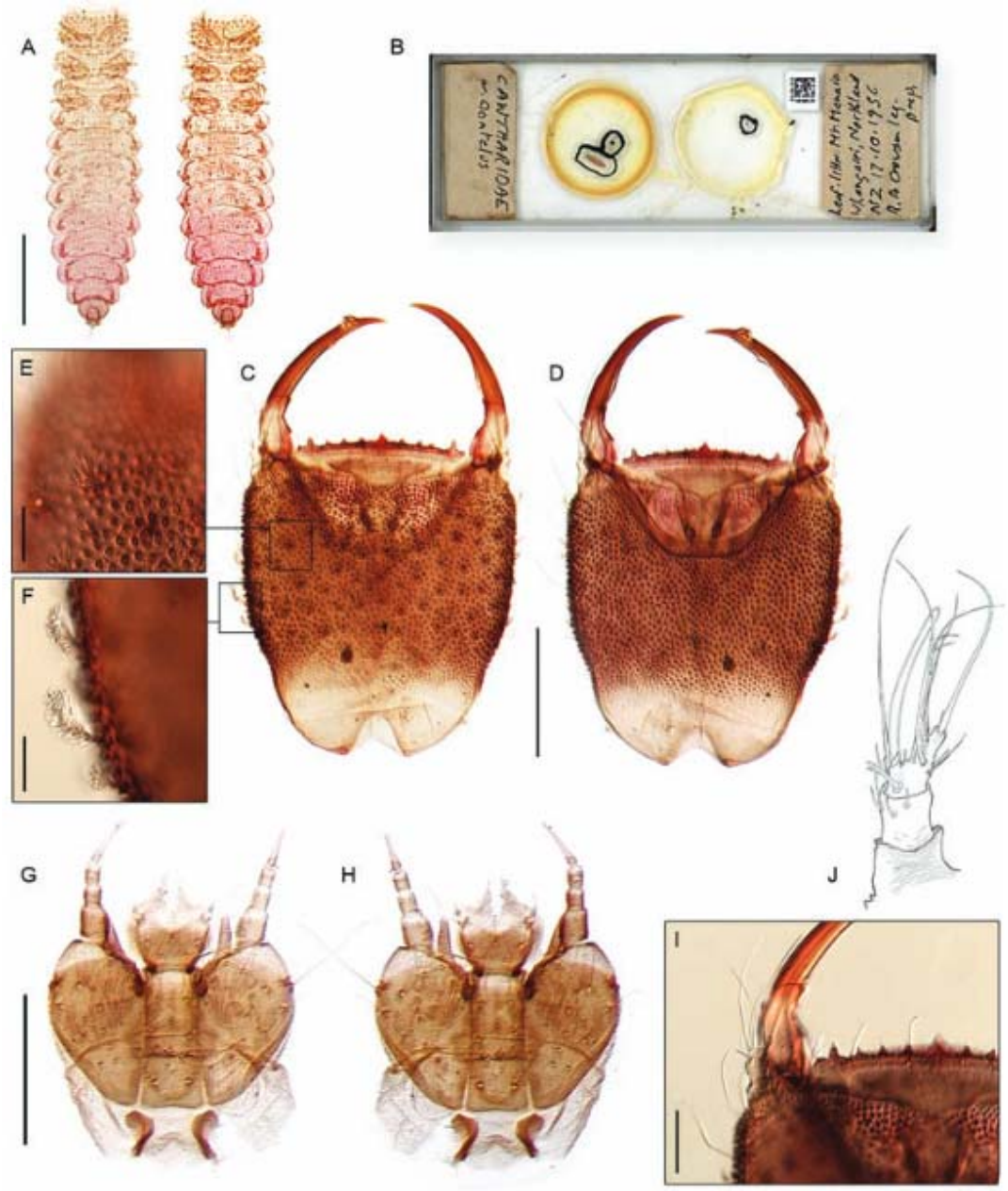

Figure 7. *Neoontelus* larva on slide described by Crowson (1972). **A.** Dorsal and ventral habitus of larva, head removed. **B.** Crowson's slide labelled as "Cantharidae nr [near] *Oontelus* / Leaf litter, Mount Manaia, Whangarei, Northland, NZ, 17.10.1956, R.A. Crowson leg. prep." (NHMUK010132743). **C–D.** Head capsule in dorsal and ventral views. **E–F.** Details of the microscupture and vestiture of head capsule, showing granules and plumose setae. **G.** Nasale, left antenna and base of mandible, dorsal view. **H.** Maxillo-labial complex. **I.** Hypopharynx. **J.** Left antenna, dorsal view. Scale bars: A–B = 1 mm, C–D, H–I = 0.25 mm, E–F = 0.05 mm, G = 0.1 mm.

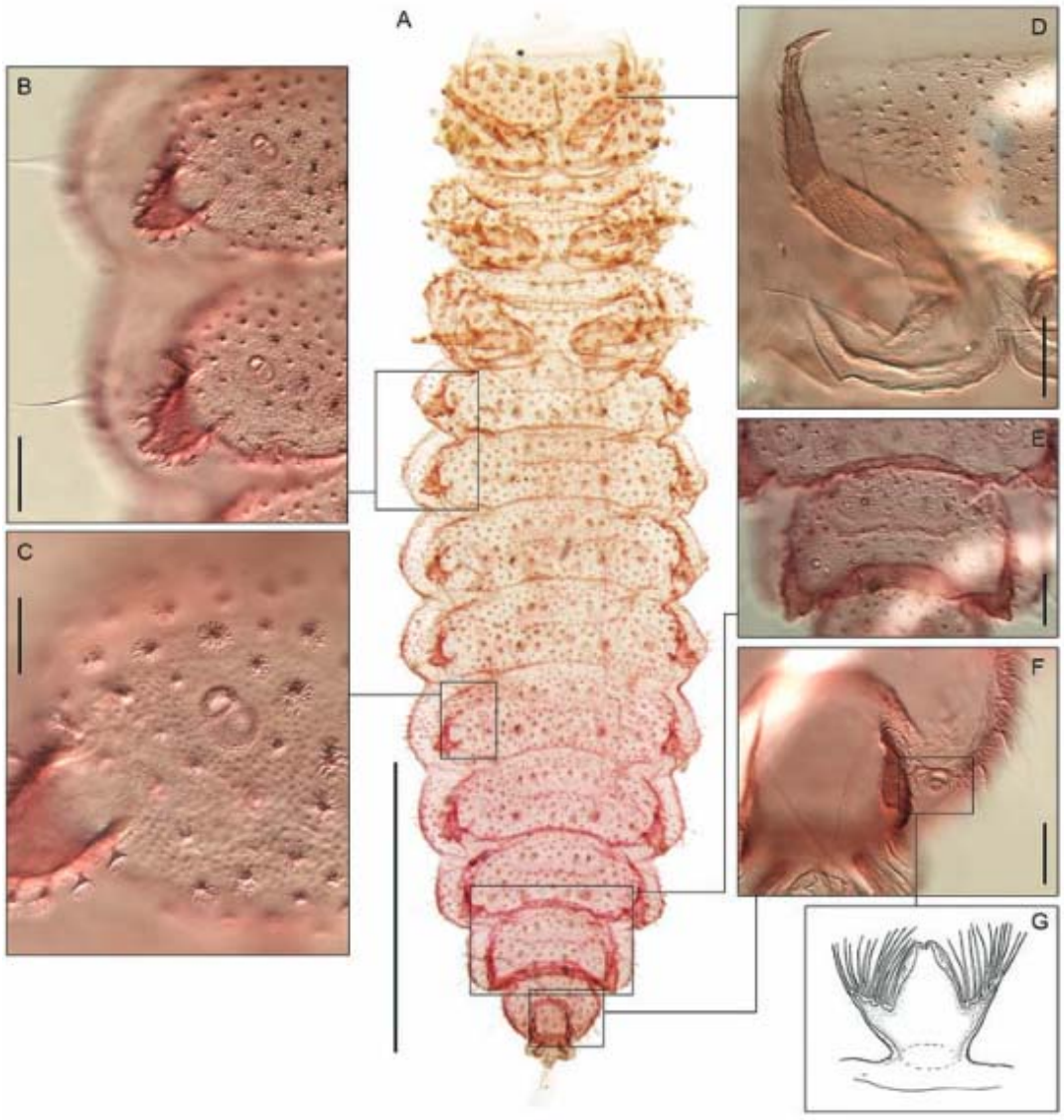

Figure 8. *Neoontelus* larva on slide described by Crowson (1972). **A.** Thorax and abdomen, head capsule removed. **B.** Detail of abdominal ampullae showing scoli, glandular pores and plumose setae. **C.** Detail of abdominal ampullae showing scolus, glandular pore flanked by sensillum, and plumose setae. **D.** Prothoracic leg. **E.** Eighth abdominal segment. **F.** Detail of ninth and tenth abdominal segment. **G.** Cross section of cotyliform glandular pore on abdominal segment IX. Scale bars: A = 1.0 mm, B, D–E = 0.1 mm, C, F = 0.05 mm.

Description: Body length: approximately 4.0 mm. Coloration. Head capsule and mandibles darker in colour; posterior fourth of head, base of mandibles and maxillo-labial complex light

brown; thorax and abdomen testaceous brown. Vestiture. Head capsule (Figure 7C–F) densely covered with granules, denser ventrally, except at nasal and basal fourth of head, which are smooth; dorsally with evenly scattered elongate plumose setae (Figure 7E–F); a row of 14 long curved setae behind nasale directed anteriorly; thorax and abdomen (Figure 8A–F) without velvety aspect, sparsely covered with granules, long and short fine setae dispersed amongst granules; plumose setae on prothorax dorsally and ventrally, and meso- and metathorax laterally. Head (Figure 7C–D) partially retracted into prothorax; prognathous, flattened dorso-ventrally. Head capsule longer than wide, lateral margins slightly arched anteriorly, abruptly narrowed posteriorly; occipital foramen narrow, forming a deep dorsal notch; epicranial stem and gular sutures absent; stemmata absent. Nasale (Figure 7G) slightly arched; paranasal lobes composed of a pair of narrow protruding digitiform lobes; a median sharp triangular tooth not delimited by paramedian grooves, three smaller triangular teeth at each side, and a series of tiny sharp teeth in between; median tooth without setae; ventrally with a transverse fringe of short thick setae directed anteriorly. Antennae (Figure 7J) with membranous antennifer and three antennomeres; antennomere I short, subquadrate, nearly as long as wide; antennomere II short with an apical prolongation at inner margin, bearing one long terminal seta; outer apical margin bearing a very elongate, flagelliform, membranous subapical sensorium flanked by a long thick seta and two short thick setae; antennomere III inserted subapically at inner margin of prolongation of antennomere II; antennomere III very slender, flagelliform, ramified distally. Mandibles (Figure 7C–D) symmetrical (abrasions and distortions at the outer apex of the left mandible and inner mesal margin of right mandible are considered as artefacts), falciform, slender, very elongate, half the length of head capsule; incisors acute, sharp; retinaculum at basal third, dorsal, small, barely projecting mesally; mesal channel present, mesal fringe of setae apparently absent and penicillus formed by a fringe of fine setae; outer margins with very long setae near acetabulum. Maxillae (Figure

7H–I). Cardo robust, curved, broad and rounded anteriorly, tapering posteriorly. Stipes short and broad; outer margins broadly rounded, wider medially, strongly narrowed basally; translucent, slightly sclerotised, anterior apex membranous; few long ventral setae inserted in stout punctures, one longer seta at each lateral margin; dorsal surface with a diagonal irregular band of fine long setae near inner margin medially, and field of widely scattered asperities laterally; galea palpiform, one-segmented, elongate, stout, nearly as long as basal palpomere, broader basally, tapering from apical half, with one very long apical seta and one campaniform sensillum latero-externally; lacinia indistinct or absent. Maxillary palpi very long, almost as long as maxillae, with four palpomeres; palpomeres I to III barrel-like, progressively decreasing in length and width, bearing setae; palpomere IV slender, as long as two preceding palpomeres, with a short basal ventral seta; two campaniform sensilla near apex of palpomere III and 1 campaniform sensillum at base of palpomere IV. Labium (Figure 7H). Postmentum elongate, parallel-sided, translucent, membranous anteriorly; few short setae along ventral surface and a pair of very long basal setae; prementum trapezoidal, wider and membranous apically, with two short setae posteriorly and three long setae anteriorly; strong sclerite at lateral margins; labial palpi very short, with two palpomeres; palpomere I barrel-like, nearly as long as wide; palpomere II conical, elongate, longer than palpomere I, bearing a long apical seta. Hypopharynx (Figure 7I) densely pilose, with short fine setae. Legs (Figure 8D) slender; coxae broad, conical, inserted distant one from the other; distance between coxae slightly increasing from posteriorly, with intercoxal process shorter on proventer; femora long, cylindrical, nearly three times longer than wide; tibiae elongate, slightly tapering apicad; pretarsi narrow and smooth, nearly straight, one third of tibiae length, with few basal setae. Thorax and abdomen (Figure 8A–F). Pro-, meso- and metathorax and abdominal segments I–VIII with one pair of dorsolateral glandular pores juxtaposed with a sensillum, those on the pronotum on the anterolateral edge, those of the

meso- and metanotum are more distal from the anterior edge, those on abdominal terga I-VII are midlateral, and the one on the tergite VIII is posterolateral; each glandular pore (Figure 8B–C) posterior, small, rounded, with granulate callus and a small opening; sensilla elliptical to conical, with granulate rim and one adpressed seta; meso- and metathoracic and abdominal glandular pores I–VIII not on weak latero-dorsal ampullae; dorsal ampullae with well-developed postero-lateral scoli with plumose setae (Figure 8B–C); segment IX (Figure 8F, G) with large cotyliform structure consisting of a papilliform glandular pore contained within a trichome; abdominal segment X (Figure 8A, F) membranous, tubular and ventral, without hooks or outgrowths; spiracles not observed, large ventral pore present associated with dense trichome.

Remarks: The larva of *Neoontelus* was originally diagnosed by Crowson (1972) as having "the whole dorsal body surface set with asperities and scales instead of setae, there are lateral outgrowths on the terga of abdominal segments I–VIII, ocelli are wanting, the glandular openings on the terga of the meso- and abdominal segments I–VIII are double on each side, those of abdominal segment IX are ventral rather than dorsal, the mandibles are more slender than those of any other cantharid larvae known (most similar to *Malthodes*), the form of the antennae is equally unusual". It can be attributed to Cantharidae by a combination of characters e.g, head prognathous, flattened and devoid of epicranial and fronto-clypeal sutures, each thoracic and abdominal terga with a pair of glandular pores, abdomen with transversal and latero-dorsal ampullae, and a membranous pygopod-like segment X.

The 'aberrant' larva was collected by Crowson (1972) in 1956 from Mount Manaia (Whangarei, New Zealand) and was provisionally attributed to South American genus *Oontelus* based on adults collected in the vicinity having the elytra with regular rows of very large deep punctures. Wittmer (1972) transferred New Zealand species of *Asilis* having these elytral punctures to his new genus *Neoontelus* and Delkeskamp (1977) assigned that larva to

either *Neoontelus* or *Asilis*. *Neoontelus striatus* (Broun 1880) is the only species recorded from Whangarei (Wittmer 1979).

The larva of *Neoontelus* is remarkably different from other Cantharidae. Its head is covered with granules, the body devoid of velvety pubescence, though the thorax has plumose setae; the occipital foramen is narrow, and stemmata absent; nasale flat, not forming frontal plate; paranasal lobes as tiny digitiform projections; antenna very small, with an elongate, ramified antennomere III; mandibles extremely elongate, falciform, with very reduced basal retinaculum; labial palpi very short; and abdominal ampullae with postero-lateral scoli; ventral glandular pore on segment IX with associated trichome (Figure 8F, G). The 'double glandular openings', as described by Crowson (1972), are a single glandular pore juxtaposed to a sensillum (see discussion below).

Asilis Broun

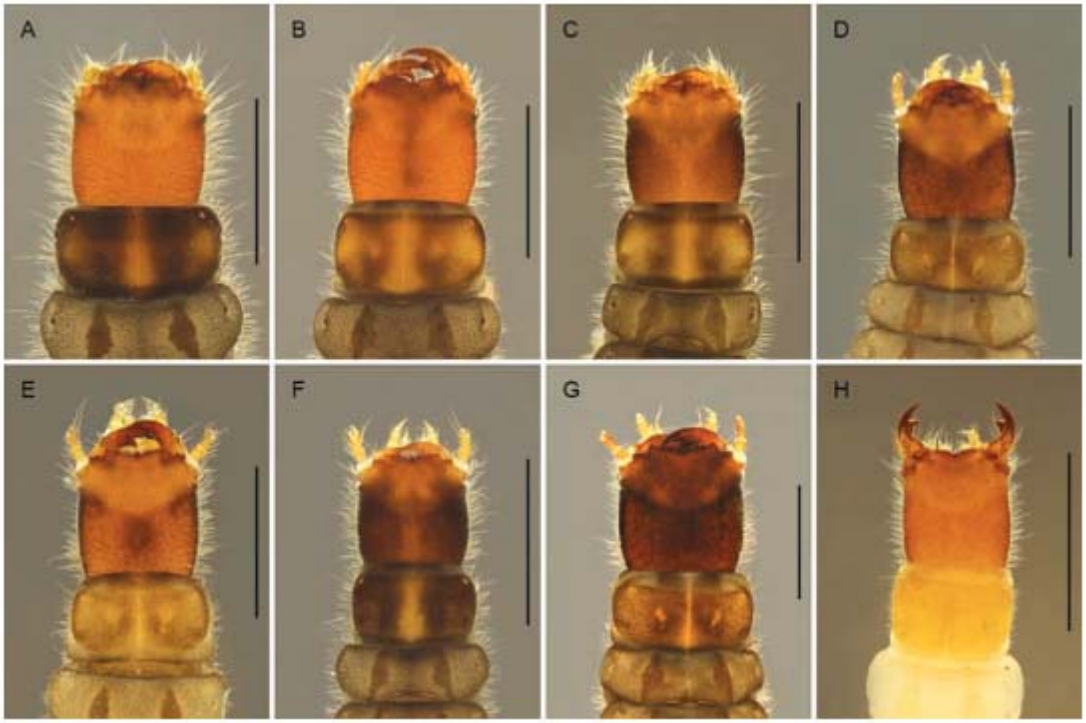

Figure 9. Morphological and chromatic diversity of head and prothorax of *Asilis* species., dorsal view. **A.** *Asilis* sp. 1, from Hanmer Forest Park, Marlborough. **B.** *Asilis* sp. 2, Rimutaka Forest Park, Wellington. **C.** *Asilis* sp. 3, Mt. Egmont Nat. Park, Taranaki. **D.** *Asilis* sp. 4, Franz Josef, Westland. **E.** *Asilis* sp. 5, Gertrude Valley, Fiordland. **F.** *Asilis* sp. 6, Pirongia Forest Park, Waikato. **G.** *Asilis* sp. 7, Kelly Creek, Westland. **H.** *Asilis* sp. 8, Tiropahi River, Buller. Scale bars: 1.0 mm.

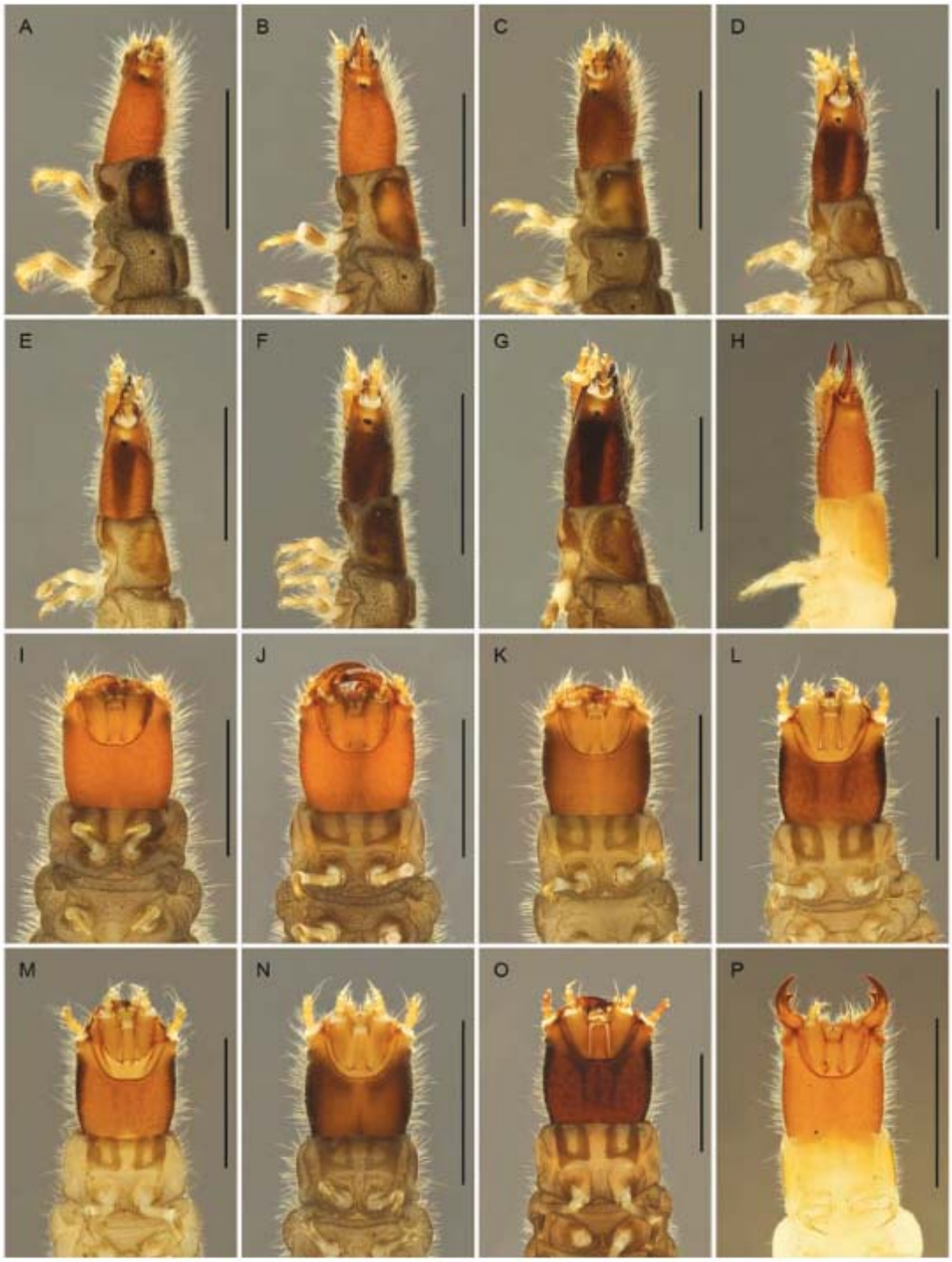

Figure 10. Morphological and chromatic diversity of head and prothorax of *Asilis* species., lateral and ventral views. **A, I.** *Asilis* sp. 1, from Hanmer Forest Park, Marlborough. **B, J.** *Asilis* sp. 2, Rimutaka Forest Park, Wellington. **C, K.** *Asilis* sp. 3, Mt. Egmont Nat. Park, Taranaki. **D, L.** *Asilis* sp. 4, Franz Josef, Westland. **E, M.** *Asilis* sp. 5, Gertrude Valley, Fiordland. **F, N.** *Asilis* sp. 6, Rirongia Forest Park, Waikato. **G.** *Asilis* sp. 7, Kelly Creek, Westland. **H, O.** *Asilis* sp. 8, Tiropahi River, Buller. Scale bars: 1.0 mm. Scale bars: 1.0 mm.

Description of late instar larva: Total length. Approximately 7.0 mm. Coloration (Figures 9A, 10A, I). Head orangish-brown, slightly lighter at anterior half and dark brown at the margin of nasale; a slightly darker area behind stemmata, without distinct darker spots or bands; antennae and mouthparts slightly translucent, orangish to light brown, apex of mandibles darker. Pronotum dark brown with one orangish median longitudinal band and two barely defined lighter lateral spots; ventrally, prothorax grey with a pair of broad rectangular frames-like darker markings extending from the anterior margin to the insertion of coxae. Meso- and metathorax and abdomen grey, each with one pair of irregular longitudinal dark brown bands. Vestiture. Body densely covered with long and yellowish setae. Dorsal surface of head capsule divided into two distinct regions delimited by a broadly arched line: posteriorly, head slightly darker, with velvety appearance, densely covered with short setae and longer thicker setae; anteriorly, integument smooth with sparse longer setae. Thorax and abdomen with integument velvety, with dense very short pubescence and long and thick sparser setae. Abdominal sternites I–VIII with two pairs of juxtaposed long and stiff setae inserted in large and dark punctures; sternite IX with numerous long setae latero-posteriorly. Head (Figures 8A, 9A, I) elongate, sub-rectangular, flattened dorsoventrally, lateral margins rounded; posterior region partly retracted into prothorax; lateral margins nearly parallel anteriorly, arched posteriorly. Sutures indistinct; gular suture barely marked anteriorly. Stemmata large, translucent, located behind the antennae. Nasale (Figure 11A) emarginate with a median triangular tooth; median tooth elevated and delimited by paramedian grooves; anteriorly, six to seven very large and broad sensilla each side, seen from above; paranasal lobes prominent and triangular. Frons with a row with four pairs of long setae parallel to nasale; another row with four pairs of long setae behind the previous row. Nasale densely pubescent ventrally (Figure 11B); setae distributed especially in transverse rows: anterior row with long ramified, moderately stout setae not reaching lateral margins, interrupted at middle

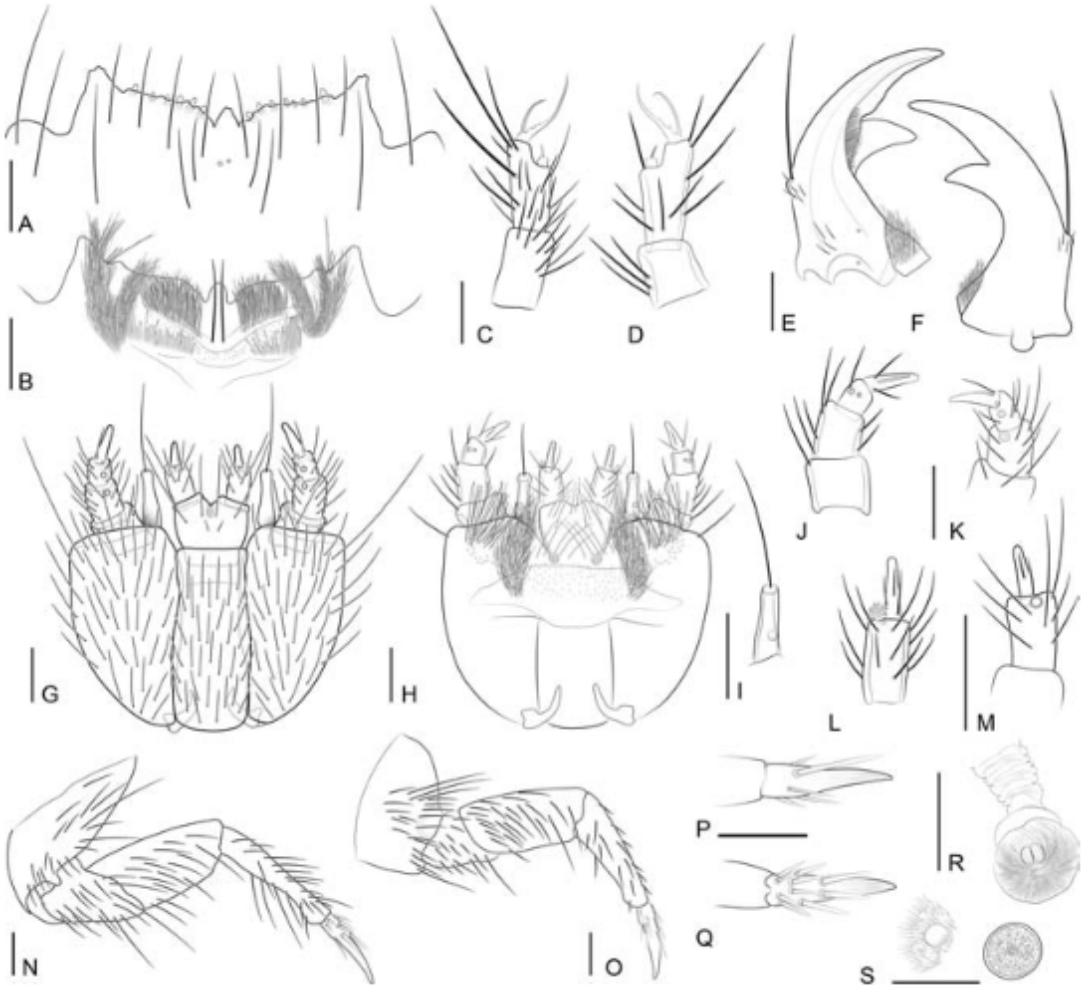

Figure 11. Morphology of *Asilis* sp. 1, from Hanmer Forest Park, Marlborough. **A.** Nasale, dorsal view. **B.** Nasale, ventral view. **C–D.** Right antenna, dorsal and ventral views. **E–F.** Left mandible, dorsal and ventral views. **G–H.** Maxillo-labial complex and hypopharynx, ventral and dorsal views. **I.** Galea, dorsal view. **J–K.** Left maxillary palpus, dorsal and ventral views. **L–M.** Right labial palpus, ventral and dorsal views. **N–O.** Prothoracic leg, anterior and posterior views. **P–Q.** Prothoracic pretarsus, dorsal and ventral views. **R.** Mesothoracic spiracle. **S.** Glandular openings. Scale bars: A–O = 0.1 mm, P–S = 0.05 mm.

by two very long and thick simple setae; posterior row with stout ramified setae, interrupted at middle; laterally, two bands of ramified thin setae extending anteriorly. A group of three ramified setae at the base of each paranasal lobe; groups of tiny teeth between the two rows of ramified setae. Antennae (Figure 11C–D) with three antennomeres: antennomere I

elongate, with nine setae more concentrated dorsally; antennomere II longer than I, densely pubescent, setae longer near the apex; apex abruptly constricted latero-externally, forming a lateral projection bearing antennomere III; one broad sensorium beside the lateral projection, with one apical seta; thick setae densely concentrated especially on dorsal face; antennomere III elongate, flagelliform, acute, with one long and thick spine-like basal process and two minute setae on short protuberances; Mandibles (Figure 11E–F) symmetrical, robust, arcuate; incisor narrow, apex sharp; retinaculum dorsal, apex acute. External margin with a small, rounded setose lobe at basal third and one very long seta, almost reaching mandible apex. About four setae dorsally near acetabulum. Mesal channel well-developed, extended from the incisor to the base of the mandible; a dense fringe of long, fine setae at ventral margin of distal third of longitudinal channel, below retinaculum. Penicillus membranous, triangular and covered with ramified fine setae. Maxillo-labial complex (Figure 11G–H) covered with long simple setae in ventral view. Maxillae: cardo elongate and curved; stipes elongate with lateral margin arched; dorsally with long, wide and ramified setae near the apex and a dense band of thinner and ramified setae directed frontwards near the internal margin; microspiny area among the setae. Galea (Figure 11I) elongate, digitiform, broader basally, slightly tapering apicad, with one very developed dorsal sensillum and one long apical seta, longer than the galea. Lacinia formed by a fringe of long, fine and ramified setae, densely distributed near inner margin. Maxillary palpi (Figure 11J–K) with four palpomeres: palpomere I wider than long with about four ventral setae and one dorsal seta; palpomere II elongate, with one well-developed ventral sensillum, about seven ventral setae and four latero-external and two latero-internal dorsal setae; palpomere III elongate, narrower than II, with one well-developed ventral sensillum, about three long ventral setae, and dorsally, one large and one small sensillum and one latero-external seta; palpomere IV narrow, elongate, slightly narrowed apicad, with one ventral sensillum at the base and one thick seta at the

external margin; dorsally with one seta near the base and one wide seta at the middle, and one long seta latero-externally, almost reaching the apex. Labium elongate and narrow; postmentum with narrow distal translucent band; prementum slightly wider than long, slightly narrowed basally, with two long ventral setae at the base of each palpus and two short setae near the middle; dorsally, with one sclerite each side and several long and ramified setae each side directed midwards and microspines at the base. Labial palpi (Figure 11L–M) inserted at the apex of prementum, with two palpomeres; basal palpomere elongate, with one very developed ventral sensillum, about six long ventral setae, and about four dorsal setae; latero-external margin with a group of wide and short setae at the apex; distal palpomere much narrower, elongate, with one wide ventral seta at the middle of distal third and two wide dorsal setae at the base and one latero-externally. Hypopharynx (Figure 11H) densely covered with long ramified setae at sides, and simple setae and tiny teeth in the middle. Legs (Figure 11N–Q) slender and long, slightly increasing in size from anterior to posterior; inserted close to each other; covered with long setae; coxae very wide, about 2.5 times wider than long, densely covered with long setae; setae denser on external side; trochanters triangular; femora long and wide; tibiae about 0.3 times femora width, slightly narrowed at the apex; pretarsi (Figure 11P–Q) elongate, about 0.6 times the tibia length, with 12 stout setae, 10 of which distributed at the dorsal and lateral faces and two at the ventral face. Thorax and abdomen (Figure 12). Prothorax rectangular, wider than long, smooth, without lobes, furrows or bumps; a distinct median longitudinal ecdysial line. Spiracles (Figure 11R) circular, bicameral, surrounded by short and thin setae. Pro-, meso- and metathorax and abdominal segments I–IX with one pair of large round latero-dorsal glandular pores (Figures 11S, 12), each flanked posteriorly by one large sensillum surrounded by spiniform setae; meso- and metathoracic, and abdominal glandular pores I–VIII on well-defined latero-dorsal ampullae, and sensilla located on the margin of shallow pits; abdominal

terga with well-defined lateral and transversal ampullae, lateral ampullae without outgrows or scoli; abdominal segment X membranous, without hooks or outgrowths; urogomphi absent.

Figure 12. Morphology of *Asilis* sp. 1, from Hanmer Forest Park, Marlborough, µCT scan images. **A–B.** Dorsal and lateral habitus showing the position of the glandular openings (gp), sensilla (sl) and pits on abdominal lateral ampullae. **C.** Cross-section image of abdominal lateral ampulla showing the glandular opening connected to a glandule (g). **D.** Cross-section image of abdominal lateral ampulla at the level of the glandular opening,

showing internal glandule. **E.** Cross-section image of abdominal lateral ampulla at the level of the sensillum, showing the pit connected to an oblique dorso-ventral muscle bundle (m). Scale bar: A–B = 2.0 mm.

Remarks: By contrast to the more restricted distribution of *Neoontelus*, the genus *Asilis* is widespread in New Zealand (Wittmer 1979). The eight larval morphotypes are similar in terms of morphology and coloration and are considered as members of *Asilis*. One species from Marlborough, Hanmer Forest Park (*Asilis* sp. 1, Table 2) is detailed for a thorough morphological description.

The larval morphotypes we examined represent eight different *Asilis* species based on the slightly different densities and lengths of the body pubescence and coloration of the integument (Figures 9–10). Closer examination reveals that the relative size of the head, and the proportions and chaetotaxy of the mouthparts and antennae are useful features to distinguish species; however, the most reliable diagnostic feature is the outline of the nasale, which is distinct for each species and constant amongst individuals within the same population (Figure 13A–H).

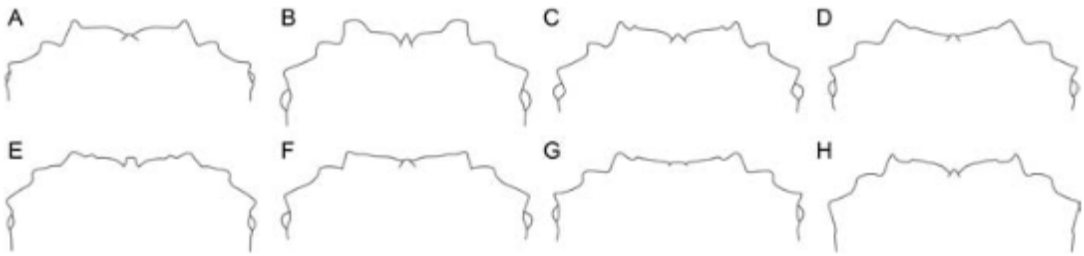

Figure 13. Morphological diversity of nasales in *Asilis* species. **A.** *Asilis* sp. 1, from Hanmer Forest Park, Marlborough. **B.** *Asilis* sp. 2, Rimutaka Forest Park, Wellington. **C.** *Asilis* sp. 3, Mt. Egmont Nat. Park, Taranaki. **D.** *Asilis* sp. 4, Franz Josef, Westland. **E.** *Asilis* sp. 5, Gertrude Valley, Fiordland. **F.** *Asilis* sp. 6, Rirongia Forest Park, Waikato. **G.** *Asilis* sp. 7, Kelly Creek, Westland. **H.** *Asilis* sp. 8, Tiropahi River, Buller. Scale bars: 1.0 mm.

Heteromastix Boheman

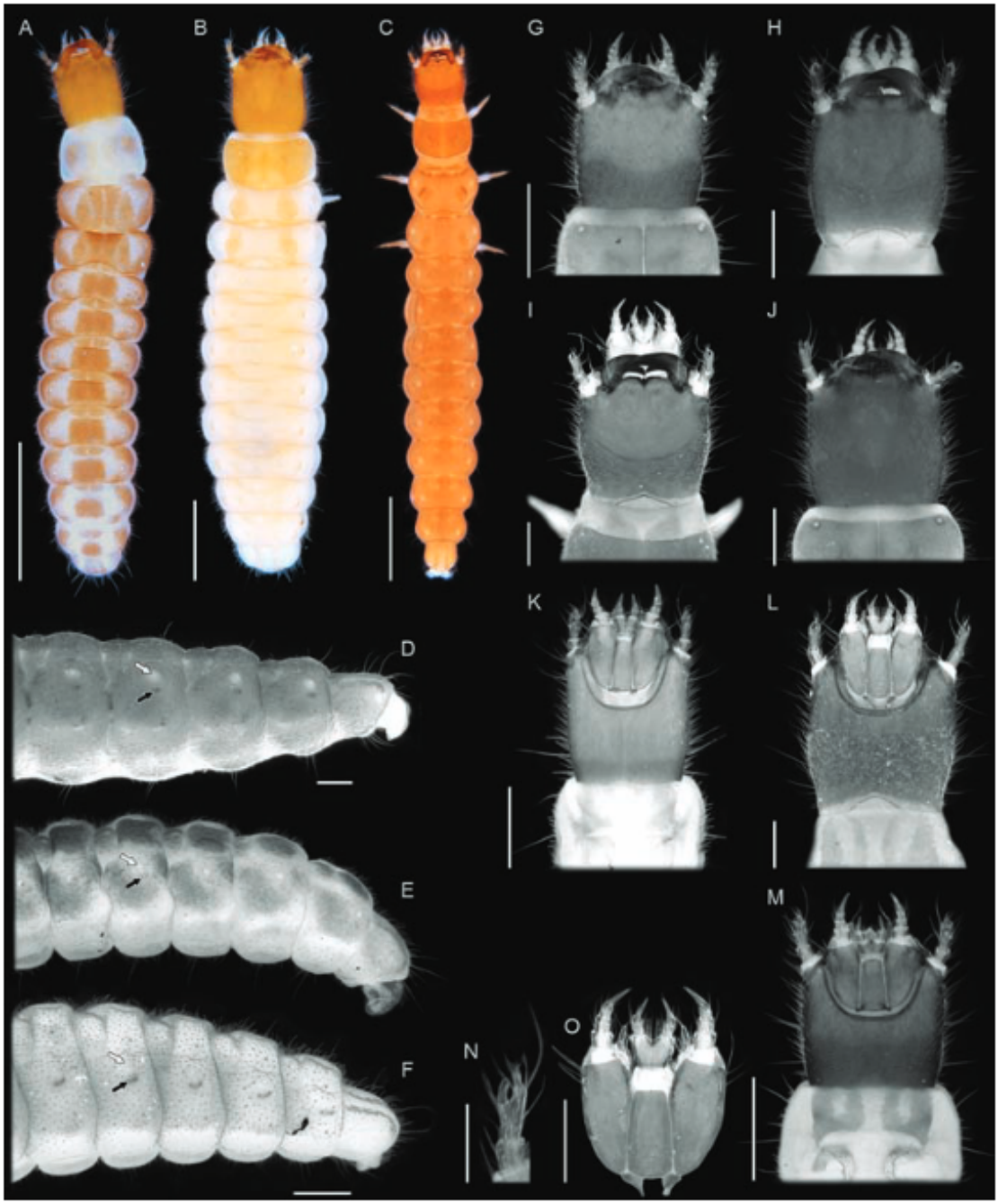

Figure 14. Morphology of *Heteromastix* species from Australia. **A.** *H.* sp1, from Queensland, dorsal habitus. **B.** *H.* sp 2, from Tasmania, dorsal habitus. **C.** *H.* sp 3 from Western Australia, dorsal habitus. **D–E.** Abdomen of *Heteromastix* species in lateral view; white arrows show the glandular openings and black arrows show the sensilla. **D.** *H.* sp 3. **E.** *H.* sp 1. **F.** *H.* sp. 2. **G–J.** Head of *Heteromastix* species in dorsal view. **G.** *H.* sp 4 from Far North Queensland. **H.** *H.* sp 5, from New South Wales. **I.** *H.* sp 3. **J.** *H.* sp 2. **K–M.** Head of *Heteromastix*

species in ventral view. **K.** *H.* sp 6, from Victoria. **L.** *H.* sp 3. **M.** *H.* sp 4. **N.** Left antenna of *H.* sp 6, dorsal view. **O.** Maxillo-labial complex of *H.* sp 3, ventral view. Scale bars: A–B = 0.5 mm, C = 1.0 mm, D–M, O = 0.2 mm, M = 0.1 mm.

In general, larvae of *Heteromastix* are more structurally and chromatically diverse than those of *Asilis* (Figures 9–10, 14A–C). The differences include the coloration of the integument, ranging from predominantly whitish to dark orange or with distinctive markings; the ratio of body length/width; size and ratios of head and prothorax; development of thoracic and abdominal ampullae; the outline of the nasale and paranasal lobes; the texture of the head capsule and the shape of the divisor line between the anterior smooth and posterior velvety regions; gular suture distinct or obsolete, among others. Notwithstanding, *Heteromastix* share features in common with some of the other members currently included in Dysmorphocerinae, such as the presence of an elevated median tooth on the nasale, antennomere II strongly constricted in the apex, bearing an elongate subterminal sensorium, and thoracic and abdominal ampullae with glandular openings flanked by single or groups of sensilla.

Afronycha picta (Wiedemann)

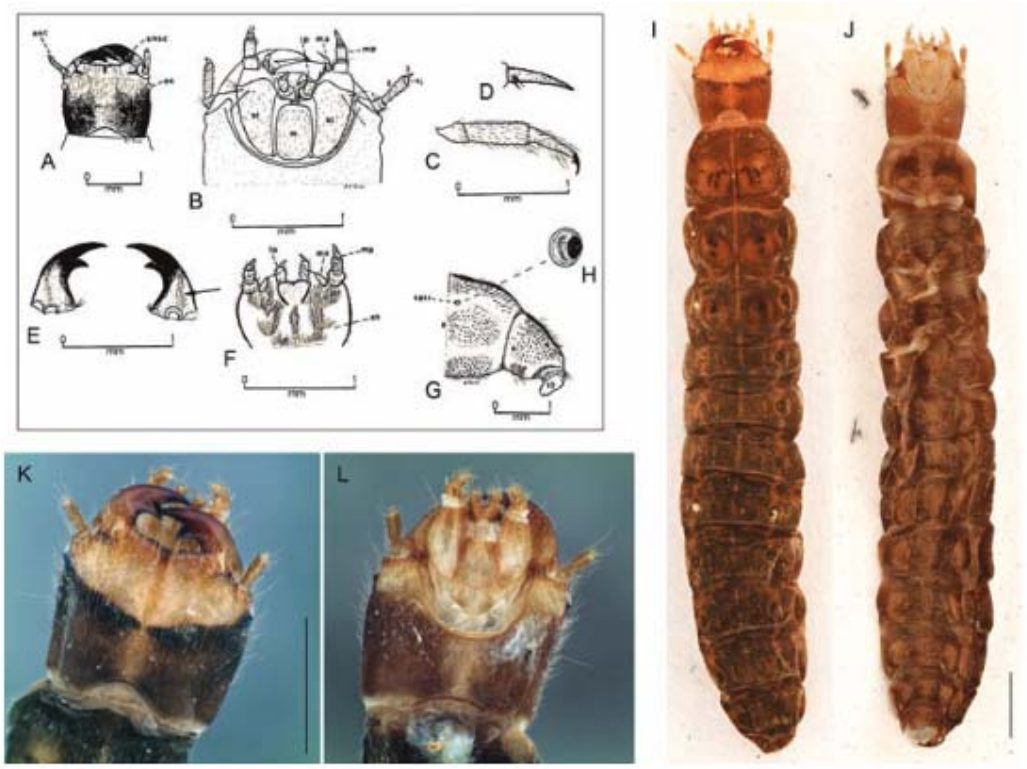

Figure 15. Morphology of *Afronycha* species from South Africa. **A–H.** *Afronycha picta* (Wiedemann, 1821), original figures adapted by Prins (1984). **A.** Head, dorsal view. **B.** Head and maxillo-labial complex, ventral view. **C.** Right mesothoracic leg, lateral view. **D.** Pretarsus. **E.** Mandibles, dorsal view. **F.** Hypopharinx. **G.** Apical abdominal segments, left lateral view. **H.** Abdominal spiracle**. I–L.** *Afronycha* sp. **I–J.** Habitus of larva in dorsal and ventral views. **K–L.** Head, dorsal and ventral views. Scale bars: 1.0 mm.

Description (adapted from Prins 1984): Total length. 17–18 mm. Coloration. Early instars greenish in colour, dotted with tiny black and larger dark-grey spots; later instars darker, head brownish, body velvety brown with somewhat bluish tinge on thoracic segments; each body segment with pale yellowish-brown marks and stripes and thin pale line on lateral margin. Head (Figure 15A–B) subquadrate, sides slightly rounded posteriorly, occipital region broad; one well-developed stemma on either side behind antennae; gula indistinct; nasale apparently straight, with short and rounded paranasal lobes and a median tooth. Antennae with three

antennomeres; antennomere I short, II twice as long as I, III very small; antennomere II with an apical sensorium. Mandibles (Figure 15E) falcate, nearly twice as long as wide, apex and retinaculum acute; each mandible with a dorsal longitudinal row of fine hairs extending from the acetabulum; lateral margin fairly strongly carinate; mesal side with well-developed channel. Maxillae (Figure 15B, F) well sclerotised, broadly rounded laterally; stipes elongate, narrowed basally, pubescent with sparse long setae apically; four-segmented maxillary palpi, palpomere I ring-like, II elongate, III very short, IV half as wide as III, tapering towards apex. Galea short, digitiform, with one long apical seta. Labial palpi two segmented, palpomere I elongate, II short, tapering apicad. Thorax and abdomen with gland openings on either side of each segment; legs (Figure 15C) well developed, pretarsus (Figure 15D) simple, long and acute, with two small setae near base on posterior side and one on anterior side; abdominal segment X (Figure 15G) membranous. Spiracles (Figure 15H) almost circular with black, triangular area anteriorly, opening furnished with fine hairs.

Pupa. Dimensions: 10.1 mm long and 4.6 mm broad across widest part. Coloration: whitish yellow with reddish eye-spots and extreme apices of mandibles reddish. Extreme apex of abdomen with two short spines or dents. Developing genital capsule visible as large convex or rounded tubercle.

Remarks: Early and mature larvae were collected during midwinter along the west coast of Cape Province, South Africa, in fresh and semi-fresh cow pats, and were observed to feed on coprophagous fly larvae. Pupae formed at the end of August and beginning of September from larvae collected in July and adults emerged in about 11 days in the laboratory (Prins 1984).

The original terminology used by Prins (1984) has been updated and characters he had not observed or mentioned in the original text, clearly seen in the figures (e.g., position of sensorium on the second antennomere and the proportion of maxillary and labial

Table 3. Comparative morphology of Cantharidae larvae. Data compiled from published descriptions and the present study. Chauliognathinae: 14 species in *Chauliognathus* Hentz, 1830, *Daiphron* Gorham, 1881, *Psilorrhynchus* Gemminger & Harold, 1869, *Macromalthinus* Pic, 1919 and *Belotus* Gorham, 1881; Malthininae: 8 species in *Malthinus* Latreille, 1806 and *Malthodes* Kiesenwetter, 1852; Dysmorphocerinae: 17 species in *Plectonotum* Gorham, 1885, *Heteromastix* Boheman, 1858, *Asilis* Broun, 1893, *Neoontelus* Wittmer, 1972 and *Afronycha* Wittmer, 1949; Cantharinae: 18 species in *Cantharis* Linnaeus, 1758, *Rhagonycha* Eschscholtz, 1830, *Podabrus* Westwood, 1838, and *Absidia* Mulsant, 1862; Silinae: 3 species in *Silis* Charpentier, 1825, *Autosilis* Kazantsev, 2011 and *Cordylocera* Guérin-Méneville, 1838. References of descriptions: Verhoeff (1917, 1923), Bøving & Craighead (1931), Larsson (1938), Gardner (1947), Striganova (1962), Janssen (1963), Fitton (1976), Gambardella & Vaio (1978), Costa et al. (1988), Gambardella & Gonzáles-Vainer (1991), Klausnitzer (1997), Biffi & Casari (2017), Biffi & Rosa (2019), Biffi et al. (2022).

Characters	**Chauliognathinae**	**Malthininae**	**Dysmorphocerinae**					**Cantharinae**	**Silinae**
			Plectonotum	***Heteromastix***	***Asilis***	***Neoontelus***	***Afronycha***		
Vestiture	two layers of simple setae: very dense and short pubescence, and sparse long setae	two layers of simple setae: very dense and short pubescence, and sparse long setae	two layers of simple setae: very dense and short pubescence and sparse long setae	two layers of simple setae: very dense and short pubescence, and sparse long setae	two layers of simple setae: very dense and short pubescence, and sparse long setae	scattered plumose and simple setae	'velvety'	two layers of simple setae: very dense and short pubescence, and sparse long setae	undescribed
Integument	smooth or finely punctate	smooth or finely punctate	smooth	smooth	smooth	densely covered with granules, denser and rougher at head	smooth	smooth	undescribed
Head capsule	divided into anterior smooth and posterior velvety regions	divided into anterior smooth and posterior velvety regions	divided into anterior smooth and posterior velvety regions	divided into anterior smooth and posterior velvety regions	divided into anterior smooth and posterior velvety regions	smooth area reduced to the nasal region	divided into anterior smooth and posterior velvety regions	divided into anterior smooth and posterior velvety regions	divided into anterior smooth and posterior velvety regions
Occipital foramen	broad	broad	broad	broad	broad	narrow	broad	broad	broad

Table 3. (*cont).*

Characters	Chauliognathinae	Malthininae	Dysmorphocerinae					Cantharinae	Silinae
			Plectonotum	***Heteromastix***	***Asilis***	***Neoontelus***	***Afronycha***		
Stemmata	present; rarely absent	present	present	present	present	absent	present	present	present
Nasale, anterior margin	straight, smooth or with short rounded teeth; paranasal lobes slightly projecting	straight, sinuous or angulate, paranasal lobes usually strongly projected laterally	sinuous, paranasal lobes usually strongly projected laterally	straight, sinuous or angulate, paranasal lobes slightly projected laterally	straight, sinuous or angulate, paranasal lobes slightly projected laterally	arched, paranasal lobes protruding, digitiform; small triangular teeth and tiny sharp teeth	straight to sinuous, paranasal lobes slightly projected laterally	straight to sinuous, paranasal lobes slightly projected laterally	straight to sinuous, paranasal lobes slightly or not projected laterally
Nasale, median tooth	absent	elevated, delimited (*Malthodes*) or not (*Malthinus*) by paramedian grooves	elevated, delimited by paramedian grooves	elevated, delimited by paramedian grooves	elevated, delimited by paramedian grooves	present, not distinctly prominent or projecting dorsally or anteriorly	elevated, delimited by paramedian grooves	elevated, delimited by paramedian grooves	elevated, delimited by paramedian grooves
Nasale, setae on median tooth	—	absent (*Malthodes*) or with one pair (*Malthinus*)	absent	absent	absent	absent	absent	absent	absent
Antenna, sensorium on antennomere II	apical	subapical	subapical	subapical	subapical	subapical	apical	apical	apical
Maxillary palps	3-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented

Table 3. (*cont).*

Characters	Chauliognathinae	Malthininae	Dysmorphocerinae					Cantharinae	Silinae
			Plectonotum	*Heteromastix*	*Asilis*	*Neoontelus*	*Afronycha*		
Maxillary palpomeres I–III, length	subequal	subequal	subequal	subequal	subequal	subequal	II very long, III very short	II very long, III very short	undescribed
Labial palpomere I	nearly as long as II	nearly as long as II	nearly as long as II	nearly as long as II	nearly as long as II	nearly as long as II	much longer than II	much longer than II	much longer than II
Galea	minute	elongate	elongate	elongate	elongate	elongate	elongate	elongate	elongate
Mandible, general shape	robust, arcuate	variable: robust, arcuate, slender or falciform	robust, arcuate	robust, arcuate	robust, arcuate	slender, falciform	robust, arcuate	robust, arcuate	robust, arcuate
Mandible, penicillus	absent or present as an elongate tuft	undescribed	absent or indistinct	absent or indistinct	present as a pubescent area	present as a fringe of fine setae	present	undescribed	undescribed
Mandible, retinaculum	present, sometimes bifurcate (*Macromalthinus*)	present (*Malthodes*, *Malthinus*) or absent (*Malthinus*)	present	present	present	present, small, barely projecting mesally	present	present	present, with a small additional tooth at base
Mandible, mesal channel	open	open, sometimes apparently closed (*Malthinus*)	open	open	open	open	open	open	open

Table 3. (*cont).*

Characters	Chauliognathinae	Malthininae	Dysmorphocerinae					Cantharinae	Silinae
			Plectonotum	***Heteromastix***	***Asilis***	***Neoontelus***	***Afronycha***		
Mandible, fringe of setae beneath mesal channel	present	absent	present	present	present	apparently absent	present	present	present
Glandular pores	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–VIII	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–IX	thoracic and abdominal terga I–IX
Glandular pores, paired sensilla	absent	absent	absent or indistinct	present posteriorly	present posteriorly	present anteriorly	absent	absent	undescribed
Glandular pit	absent	absent	absent	absent	present	absent	absent	absent	absent
Abdominal scoli	absent	absent	absent	absent	absent	present	absent	absent	absent
Abdominal segment X	membranous	membranous, sometimes with sclerotised hooks (*Malthinus seriepunctatus*)	membranous	membranous	membranous	membranous	membranous	membranous	undescribed

palpomeres) were added above. Characters listed in Table 3 (e.g., general pubescence and the absence of sensilla next to glandular pores) were observed in the fresh larva of *Afronycha* sp. (Figure 15I–L).

Discussion

Comparative morphology

In this section we examine ten character systems among Dysmorphocerinae larvae which are summarised for all of the cantharid subfamilies in Table 3.

Body vestiture: Fitton (1976) indicated that the relative length and pattern of setation on the thoracic and abdominal segments provides a reliable set of characters for discriminating amongst the genera of British Cantharinae and distinguishing species groups in *Cantharis* Linnaeus. However, shape of Cantharidae larval setae is not commonly mentioned in descriptions, and their fine structure has never been studied in detail. Nevertheless, the scattered plumose setae and dense granulation found on the integument of *Neoontelus* larva (Figures 7F, 8B) are unique and we would assume that these would not be overlooked in prior species descriptions. The integument of *P. laterale* is densely covered with very short fasciculate pubescence, especially on the head capsule (Figure 3F); upon closer examination, the pubescence is comprised of clusters of tiny simple setae (Figure 6E–G), giving the integument a grainy appearance.

Head capsule: In *Afronycha*, *Asilis*, *Heteromastix* and *P. laterale* larvae, the head capsules resemble most of the other cantharid larvae, being longer than wide, flattened dorso-ventrally, with lateral margins slightly arched, posterior foramen broadly open posteriorly, and dorsal surface with two well-delimited areas, almost smooth anteriorly, and with a

velvety appearance posteriorly. On the other hand, the head capsule of *Neoontelus* larva (Figure 7C–D) is remarkably different from all the other cantharid larvae. The dorsal and ventral surface are homogeneously covered with similar microsculpturation, and the distinct anterior smooth region is restricted to a small area right behind the nasale (Figure 7G). Furthermore, the lateral margins of the head capsule are constricted and membranous at the posterior fourth, without a clear distinction between the occipital foramen and the posterior phragma. Unlike many other Coleoptera larvae, cantharids lack the epicranial suture and ecdysial lines, and during moulting the head splits away from the exuvia through the broad occipital foramen (Lagoute 1966). We have observed that the exuvial head capsule often remains intact after ecdysis. In *Neoontelus*, it is possible that part of the broad membranous area in the constricted posterior region of head might rupture during moulting.

Nasale: The form of the nasale and the anterior angles of head are important characters for reliable separation of subfamilies, genera and species (e.g., Larsson 1938; Fitton 1976; Biffi & Casari 2017; Biffi & Rosa 2019). The nasale of Chauliognathinae differs from all other subfamilies by the numerous small teeth in the anterior margin and a median incision instead of a median projecting tooth. In the other four subfamilies, there is a strong median tooth flanked by variously shaped margins and paranasal lobes, which are more or less protruding anteriorly. The nasale of *Asilis*, *Heteromastix* and *Plectonotum laterale* larvae are more similar to those in the genus *Malthodes* Kiesenwetter, 1852 (Malthininae) for having the median tooth elevated, delimited by paramedian grooves, never with setae on the median tooth (Fitton 1976). Like in other genera, the outline of *Asilis* nasale is diagnostic for the different species (Figure 13). The nasale of *Asilis* have very large and thick sensilla directed anteriorly, seen from above (Figure 11A); in *P. laterale* they are much smaller and inserted in deep punctures (Figure 3G, I). In *Neoontelus*, the nasale (Figure 7G) differs from all the other known larvae. It is slightly arched, nearly straight, with a row of three small,

sharp triangular teeth on either side, and a larger triangular median tooth, not distinctly prominent or projecting dorsally or anteriorly; laterally, very small, digitiform paranasal lobes shorter than median tooth.

Stemmata: *Afronycha*, *Asilis*, *Heteromastix* and *Plectonotum laterale* larvae have one stemma on either side of the head placed behind the antennal insertion, like most larvae and instars of Cantharidae. The larvae of *Neoontelus* and *Macromalthinus brasiliensis* (Pic, 1906) (Chauliognathinae) are the only known larvae devoid of stemmata (Biffi & Casari 2017). In *Asilis*, the stemmata are pigmented and distinctive (Figure 10A–G), however, in one species, the stemmata lack pigment and a distinct lens (Figure 10H).

Mandibles: The mandibles of Dysmorphocerinae (except *Neoontelus*) do not differ from the general form in most other Cantharidae. They are arcuate, with the apex sharp or rounded, retinaculum acute or rounded, and an open mesal channel flanked by short fringes of setae below retinaculum. In *Asilis*, the penicillus is membranous and densely pubescent, with tufts of setae (Figure 11E–F). The mandibles of *Neoontelus* (Figure 7C–D, G), however, remarkably differ from other dysmorphocerines and resemble those described by Striganova (1962) for *Malthodes* sp., which are very slender, elongated and acute, and *Malthinus flaveolus* (Herbst, 1786), which is slender, very curved, without a retinaculum and having the channel opened at the apex and running internally along the entire length of the mandible.

Maxillo-labial complex: larvae of Dysmorphocerinae (except *Afronycha*) and Malthininae exhibit similar maxillo-labial complexes. In these subfamilies, the maxillary palpi have four palpomeres, with palpomeres I–III subequal in length, and galea very large, digitiform. The maxillary palpi of *A. picta* resembles those of Cantharinae, which have the palpomere III very short, II longer than I+III (cf., Bøving & Craighead 1931; Janssen 1963; Lagoutte 1966); Chauliognathinae have maxillary palpi with three palpomeres and a highly reduced galea (Biffi & Casari 2017); Silinae unknown.

Antennae: The antennae of Malthininae and Dysmorphocerinae (except *Afronycha*) are remarkable for the strong apical constriction on the antennomere II, bearing a large membranous subterminal sensorium, and antennomere III with long spine-like projections, inserted on the top of an inner prolongation of antennomere II. The length and shape of the inner projection of antennomere II and the size of the sensorium vary among malthinine and dysmorphocerine species. The antennae of *Afronycha picta* resemble those in all the other subfamilies, with the antennomere III and the sensorium inserted on the tip of antennomere II.

Legs: The legs of Cantharidae larvae are rarely described, so morphological comparisons are difficult. However, the ratios of length and width of podomeres, and the length and chaetotaxy of pretarsus might provide important diagnostic features that, at least, diagnose species groups (Fitton 1976; Biffi & Casari 2017; Biffi & Rosa 2019). In *Plectonotum laterale* (Figure 6A–D) the pretarsus bears two pairs of fine dorsal and ventral setae, whereas in *Asilis* sp. 1 (Figure 11P–Q) there are 12 thick setae mostly concentrated ventrally, and in *Afronycha picta* there are two small setae near the base on posterior side and one on the anterior side.

Thoracic and abdominal ampullae: Most cantharid larvae have well-defined lateral and transversal dorsal ampullae on the meso- and metathorax and abdominal segments 1–9. *Neoontelus* differs from all known larvae for having scoli present on the lateral abdominal ampullae (Figure 8B).

Glandular openings: All cantharid larva have one glandular opening on either side of thoracic and abdominal terga, while those of abdomen are usually present on lateral ampullae from segments I–IX (or I–VIII in Malthininae). According to Crowson (1972), the larvae of *Neoontelus* have ‘double glandular openings’ on either side of the terga of the mesothorax and abdominal segments I–VIII, with those of abdominal segment IX ventral

rather than dorsal. Those double glandular openings of *Neoontelus* (Figure 8C) are also present in the examined species of *Asilis* (Figure 12) and *Heteromastix* (Figure 14D–F), although with some differences in size and position, but are absent in the examined specimens of *Afronycha*. This feature may serve as a potential synapomorphy for part of the Dysmorphocerinae. Such an unusual trait prompted us to address the structure further: Are these two openings for the same gland, or openings of two independent glands?

Upon re-examination of Crowson's slide of *Neoontelus*, we confirm Crowson's (1972) observation that the glandular pore of abdominal segment IX is ventral while all other pores are dorsal, as in all other members of the family. The large cotyliform glandular pore (Figure 8F, G) is unique within the family while the supposed double pores are structurally different among *Neoontelus*, *Asilis*, and *Heteromastix*, suggesting that their functions might also differ. In *Neoontelus*, the abdominal 'pores' on segments I-VIII are juxtaposed, the posterior one is rounded, apparently forming a chamber opening, whereas the anterior one is a shallow hollow concavity surrounded by an oblong, rugous rim, with one adpressed seta (Figure 8C). The external structure of the former resembles an actual pore, whilst the latter resembles a tactile sensillum. By contrast, in *Asilis* and *Heteromastix*, the actual 'pore' is situated anteriorly, whereas the second so-called pore is posterior, alongside a shallow pit on the dorsal ampulla (Figures 12A–B, 14D–F), either large and single in *Asilis*, or arranged in groups of small punctures in *Heteromastix*. Cross-sectional images (Figure 12C–E) of an *Asilis* larva confirm that the anterior opening is a true pore connected to a rounded internal gland, whilst the posterior structure is not subtended by a gland and most likely has a sensorial function. Moreover, the pit beneath this putative sensorium is the insertion point of an oblique dorso-ventral muscle bundle, possibly associated with the extrusion of the glandular content. Such sensilla were not located in *P. laterale* and they are absent in Chauliognathinae and have not been observed in other described larvae.

We therefore conclude that the double gland openings observed by Crowson (1972) was slightly misinterpreted and represents a complex character involving a potential trigger mechanism that would function to release glandular secretions, perhaps in defence, as in other chemically protected beetle larvae (Lawrence & Ślipiński 2013).

Systematics and the characterisation of Dysmorphocerinae larvae

The subfamily Dysmorphocerinae was proposed to accommodate genera of cantharids that could not be reliably placed in any other subfamily with features that are similar to Silinae, Cantharinae, and Malthininae (Brancucci 1980). Furthermore, Brancucci (1980, p. 294) suggested that "subsequent studies are likely to subdivide this subfamily, which would be premature in the present state of our knowledge". Likewise, dysmorphocerine larval morphologies are diverse and are not sufficient for characterising the subfamily either. Within the Dysmorphocerinae, larvae of *Asilis* species, are more similar to *Heteromastix* and *P. laterale* than to their sympatric *Neoontelus*. *Afronycha picta* also resembles the former species, but differences in the form of the antennae and maxillary palpi differ from the remaining members.

None of the larval characters are uniformly present in the other the genera; including the glandular complex which is absent or indistinct in *P. laterale* and *A. picta,* and in *Asilis* and *Neoontelus* which are comparatively larger in size than they are in *Heteromastix* which have single or grouped sensilla. The antennae with a strong apical constriction on the antennomere II, bearing a large membranous subterminal sensorium is typical of Malthininae and most Dysmorphocerinae, except *A. picta*. The maxillary palpi of *A. picta* looks like those of Cantharinae and Silinae, with a very short third palpomere, whereas in the remaining dysmorphocerine genera, palpomeres I–III are subequal in length; other characters, which are

similar in *P. laterale*, *Asilis* and *Heteromastix*, are remarkably different from *Neoontelus*, like the shape of nasale and mouthparts.

The *Neoontelus* larva differs considerably from all other cantharid larvae. The shape of nasale and nasal teeth, the reduced labial palpomeres, the presence of abdominal scoli, and the reduction of body pubescence are unique features for the genus. Their extremely elongate and falciform mandibles are comparable, to some extent, to those of *Malthodes* species (see Striganova 1962; Crowson 1972). However, the larvae of *P. laterale*, *Asilis* and *Heteromastix* are more easily compared to other Cantharidae.

Among other characters, the larvae of Dysmorphocerinae, including *Neoontelus*, but excluding *A. picta*, readily differ from Cantharinae, Silinae and Chauliognathinae for having the antennae with subterminal sensorium on antennomere II, rather than terminal (Figures 4, 11C–D, 14N). *Asilis*, *Heteromastix*, *P. laterale* and *Neoontelus* larvae have characters in common with members of the remaining Cantharidae subfamilies but, in general, these larvae are more similar to those of Malthininae. The similarities between Dysmorphocerinae and Malthininae include the proportion of length of labial and maxillary palpomeres and the shape of the antennae. Within Malthininae, dysmorphocerines especially resemble members of the genus *Malthodes* by the shape of the nasale, with the median tooth elevated (i.e., delimited by paramedian groves), not projecting beyond paranasal lobes. In turn, Malthininae differ from Dysmorphocerinae and all other Cantharidae subfamilies for having glandular pores present only on abdominal segments I–VIII.

The systematic position of Cantharidae within the superfamily Elateroidea is unsettled. Some studies have placed cantharids amongst other groups with soft-bodied adults, such as Lampyridae, Lycidae, Omethidae and Phengodidae in a group formerly referred to as Cantharoidea, or more closely related to hard-bodied groups of Elateridae (e.g., Crowson 1972; Bocakova et al. 2007; Lawrence et al. 2011; Kundrata et al. 2014; McKenna et al.

2015, 2019; Zhang et al. 2018; Douglas et al. 2021; Kusy et al. 2021; Cai et al. 2022). However, recent molecular studies converge in results showing Cantharidae as sister to Elateridae (sometimes therein included 'lampyroid' lineages) (Zhang et al. 2018; Kusy et al. 2021; Douglas et al. 2021; Cai et al. 2022), with members of either Malthininae or Chauliognathinae as sister to the remaining cantharids. The uncertainty about the placement of cantharids impacts the interpretations on the evolution of morphological characters. Likewise, the systematic relationships of Cantharidae subfamilies are also controversial. Brancucci (1980) proposed an adults' morphology-based phylogeny of Cantharidae subfamilies in which Dysmorphocerinae is sister to Malthininae, supported by the lateral lobes of aedeagus strongly developed ventrally. In morphological phylogenies including extant and fossil species, Hsiao et al. (2021) and Zhao et al. (2022) recovered Dysmorphocerinae as sister to Malthininae + Tytthonyxini (currently classified in Silinae), although with a very reduced taxa sampling. The most comprehensive molecular phylogeny is Kundrata et al. (2014) and shows Malthininae as sister to the remaining subfamilies, however, the phylogeny did not include Dysmorphocerinae representatives. A similar topology was produced by Zhang et al. (2018), which includes at least one species of each Cantharidae subfamily, although with a much lower species representation. In their paper, one member of *Heteromastix* from Australia was included, and the topology shows Malthininae (Dysmorphocerinae (Chauliognathinae (Silinae + Cantharinae))). By contrast, the positions of Dysmorphocerinae and Malthininae in Cai et al. (2022) were inverted positions: Chauliognathinae (Malthininae (Dysmorphocerinae (Silinae + Cantharinae))).

The quite similar features found in the larvae of Dysmorphocerinae and Malthininae suggest that they are related. However, given the conflicting topologies, it is not possible to distinguish plesiomorphies and apomorphies for Dysmorphocerinae + Malthininae. Even though the larval characters of *Plectonotum laterale*, *Asilis*, *Neoontelus*, *Heteromastix* and

Afronycha picta are not sufficient to diagnose the subfamily Dysmorphocerinae or to establish their systematic position within Cantharidae, these characters suggest a close relationship of the latter four genera with respect to Malthininae and also add evidence of weak support of Dysmorphocerinae as a monophyletic group since *A. picta* shows more resemblance with Silinae and Cantharinae.

In some sense, larval characters corroborate the results based on recent molecular phylogenies (e.g., Bocak et al. 2018; Zhang et al. 2018; Kusy et al. 2021; Douglas et al. 2021; Cai et al. 2022) that show Cantharinae and Silinae as sister groups. The similarity of larval features between these subfamilies (Table 3) supports this hypothesis, despite the limited knowledge on Silinae larvae. Chauliognathinae, recovered as sister to the remaining subfamilies (e.g., Brancucci 1980; Cai et al. 2022), differ from all the other cantharids for exhibiting unique features, such as the absence of central tooth on nasale, extreme reduction of galea and 3-segmented maxillary palpi (Biffi & Casari 2017).

Crowson (1972) reckoned that adult members of *Neoontelus* are more similar to Omethidae than to other members of Cantharidae, but in recent phylogenetic studies (e.g., Zhang et al. 2018, Cai et al. 2022) Omethidae are more basal and Cantharidae are derived, and moreover *Neoontelus* adults share many features with some dysmorphocerine and other cantharids. Meanwhile, Crowson (1972) hypothesised that *Neoontelus* genus may represent "the oldest and most primitive surviving type of the family." While a thorough study of elateroid larvae is needed, a well-sampled phylogenetic study that includes *Neoontelus* and its potential relatives is also needed to test Crowson's assertion and determine if this strange larval type represents a highly derived cantharid or representing yet another unique higher taxon present only in New Zealand (Buckley et al 2015).

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