



Description of the larva of *Ochthebius capicola* (Coleoptera: Hydraenidae) from marine rockpools of South Africa

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Abstract

Larval instars II and III of *Ochthebius* (*Ochthebius*) *capicola* (Péringuey 1892) from South Africa are described and illustrated by SEM, including a detailed analysis of their chaetotaxy and porotaxy. Specimens used in this study were collected with adults of the same species in marine rockpools. The larval morphology of *O. capicola* is compared to that of other members of the same genus occurring in this habitat, contributing to the current taxonomic and phylogenetic debate on the intrageneric taxonomy of Ochthebiinae.

Key words: Marine rockpools, Hydraenidae, Ochthebiinae, larval taxonomy, SEM, South Africa

Introduction

The genus *Ochthebius* (s.l.) represents the second largest group of hydraenid beetles, with nearly 400 species (Hansen, 1991), although the number of subgenera and their limits are still controversial. Recently, Jäch (2004) divided the genus into four subgenera: *Asiobates* C. G. Thomson 1859, *Calobius* Wollaston 1854, *Enicocerus* Stephens 1829 and *Ochthebius* s. str. Leach 1815. However, a previous subdivision of *Ochthebius* into nine subgenera (Knisch, 1924) is still followed by some authors (e.g. Delgado & Archangelsky, 2005). One relevant difference between the two classifications is that *Cobalius* Rey 1886, that following Knisch's classification was considered as a valid subgenus, is now included in the nominal subgenus *Ochthebius* (see Jäch, 2004). The latter, with nearly 280 species worldwide (Hansen, 1998), includes species associated with freshwater environments, such as mountain streams and springs, brackish lagoons, and also hyper-saline and saline waters. Some members of *Ochthebius* inhabit supralittoral marine rockpools, well defined patches of habitat in marine ecosystems, commonly found on rocky shores around the world (d'Orchymont, 1932a, b).

As in many other groups of Hydraenidae, the immature stages of *Ochthebius* s.str. are poorly known. To date, the larvae described for species belonging to this purported subgenus are those of *O. lejolisi* Mulsant & Rey, 1861 (d'Orchymont, 1913) from Atlantic coasts of Europe, *O. subinteger* Mulsant & Rey 1861 (Delgado & Soler, 1996) from North Mediterranean coasts, *O. auropallens* Fairmaire 1879 (Delgado & Soler, 1997b) from south-western Europe, *O. danjo* Nakane 1990 (Delgado & Matsui, 2000) from Japan, and *O. gonggashanensis* Jäch 2003 from China (Delgado, 2003). Additionally, larval instars of the closely related genus *Neochthebius* d'Orchymont 1932, have been recently described (Park & Ahn, 2008).

An hypothesis of phylogenetic relationships based on twenty-four larval characters, across most of the aforementioned species and other members of Ochthebiinae, was recently presented by Delgado and Archangelsky (2005). This work shows that the subfamily Ochthebiinae is clearly monophyletic, being likely subdivided into two clades: the first clade includes the species *O. quadricollis* and *O. subinteger*, while the second includes a polytomy of three representatives of the subgenus *Ochthebius* s. str., a clade with the two representatives of the genus

Meropathus plus a clade with representatives of the genera *Gymnochthebius* and *Aulacochthebius*. The authors suggest that the Palearctic species of *Calobius* and *Cobalius* (both 'subgenera' living in marine rockpools) could represent a distinct lineage within Ochthebiinae.

In this paper we describe the larval stages of *Ochthebius* (*Ochthebius*) *capicola* (Péringuey 1892) from South Africa. Described under the genus *Hydraena* Kugelann 1794 by Péringuey, this species was later ascribed to the genus *Ochthebius* by d'Orchymont (1933), who simultaneously described the new subgenus *Notochthebius* to include it.

For the closely related *Ochthebius rubripes* Boheman 1860 (coasts of Northern Province, South Africa), d'Orchymont (1933) established and described the additional new subgenus *Nyxochthebius*. These monospecific subgenera were later combined under the subgenus *Notochthebius* by Perkins and Balfour-Browne (1994) in recognition of the similarities between the two included species. Finally, Perkins (1997) reassigned both species to their present-day subgenus (*Ochthebius* s.str.).

Ochthebius capicola and *O. rubripes* are the only known African Hydraenids associated with marine rockpools, outside the Maghreb, Macaronesia, and the Cape Verde Islands, where other marine rockpools species are found (members of the above cited *Calobius* and *Cobalius* lineages).

Species of Ochthebiinae living in the same or in similar marine environments (members of the genus *Neochthebius* are associated with crevices of rocks along seashores, chiefly within empty barnacles; Perkins, 1980; Park & Ahn, 2008) are found also in Korea, Japan and surrounding islands [*Neochthebius granulosus* (Satô 1963); Satô, 1963; Perkins, 1980, 1997; Hansen, 1991; Park & Ahn, 2008; *Ochthebius danjo* Nakane 1990; Delgado & Matsui, 2000; Jäch, 2004], Australia and Tasmania (genus *Hugleechia* Perkins 1981; Perkins, 2007), and Western coasts of USA and Canada (California to Alaska) [*Neochthebius vandykei* (Knisch 1924); d'Orchymont, 1932a, b; Perkins, 2001; Park & Ahn, 2008].

The specific aims of the present paper are to: 1) describe the morphology and chaetotaxy of larval stages of *Ochthebius capicola*; 2) provide the first SEM illustrations of larvae in the genus *Ochthebius* in order to facilitate the identification of the main diagnostic characters; 3) compare larvae of this species with those of other marine rockpool members of the genus, in order to achieve additional insights into their phylogenetic relationships, and on the possible influence of convergent evolutionary phenomena associated with their shared peculiar lifestyle and environment.

Material and methods

Sampling. *Ochthebius capicola* (Fig. 1b) from South Africa (Cape Peninsula), was found in hypersaline pools in shallow depressions on rock surfaces above the high tide line (Fig. 1a), but within the splash zone. In addition to the unusual level of fine organic material found here, at the time partially attributed to the faecal deposits of the local population of African Penguin (*Spheniscus demersus* Linnaeus; also known as the Black-footed Penguin), a thin algal film covered the submerged rock surfaces as reported by Turner (2004). The pools contained variable densities of the beetles; they were usually found on the submerged rock surface of pools, in crevices of the rock or among submerged algae.

The larvae described below were collected with adults of the same species and identified *ex societate imaginis*. They were collected from the pools by hand with soft forceps or, after vigorous agitation of the water, from the water surface.

Examined material. A total of 12 larvae of *Ochthebius capicola* were examined: 4 second instars and 8 third instars (identification was based on absence of egg bursters and dimensions of the cephalic capsule). All larvae were initially preserved in 70% ethanol and deposited in the Sapienza University Zoological Collection (Rome, Italy).

Five specimens (3 second- and 2 third-instars) of *O. capicola* were rehydrated, cleared in 10% KOH, transferred to hot lactic acid, dehydrated through a series of EtOH baths of increasing concentration (10, 20, 50, 70, 90, 95 and 100%), left overnight in a clove oil bath, and mounted on slides with Canada balsam. They were studied and measured by using a light microscope Olympus BX51, equipped with a drawing tube (40/600X).

For SEM analysis, 3 specimens (1 second- and 2 third-instars) of *O. capicola* were dehydrated through a series of EtOH baths of increasing concentration (70, 80, 90, 95 and 100%), critical point dried (Bal-Tec CPD 030),

mounted on a stub (using self-adhesive carbon disks), sputtered with gold (Emitech k550 sputter coater), and observed with a Philips XL30 scanning electron microscope (L.I.M.E. laboratory, University “Roma Tre”, Rome).

In this paper the general terminology of larval structures follows Lawrence (1991) whilst the chaetotaxy follows Delgado and Soler (1996a, 1997a, b, c)

Results

Larval description of *Ochthebius (Ochthebius) capicola* (Péringuey 1892)

Diagnosis of second and third instars. The larva of *Ochthebius capicola* shows the following unique combination of characters: mandibles with one conspicuous triangular premolar tooth; prostheca without any basal denticle; second labial palpomere with medially directed elongate seta; thoracic tergites with Da1; one new subprimary seta L', lateral on sternum; pygopod without anal hooks.

Second instar. Habitus and colouration. Elongate, slender. Head and body sclerites moderately sclerotized. Colour of sclerites uniformly pale brown. Total body length about 3 mm.

Head. Head capsule width $0,36 \text{ mm} \pm 0,01$ (mean $\pm$ S.D.; $n = 3$); head transverse, slightly narrowed posteriorly and distinctly curved laterally. Ecdysial suture Y-shaped; five stemmata present on each ocular area. Chaetotaxy of head capsule as in Fig 3. Frontal region (Fig. 3a) with five setae on each side, two frontodorsal (Fd1, Fd2), two frontolateral (Fl1, Fl2), one frontomarginal (Fm1).



FIGURE 1. a) Hypersaline pool in shallow depression on rock surface, Boulders Beach, Simon's Town, Cape Peninsula, South Africa; b) Habitus of adult *Ochthebius capicola*; Scale bar: 1 mm.

Campaniform sensillum (FC1) present and clearly visible in all specimens. Frontoclypeal suture clearly distinct. Clypeus (Fig. 3a,c) with three setae on each side (Cl1–Cl3) transversally lined anteriorly, decreasing in length from medial (Cl1) to lateral (Cl3). Epicranial regions (Fig. 3a) each with two campaniform sensilla (EC1, EC2), one cephalic gland (CG) (one pair) and ten setae: a row of four minute posterior setae (P1–P4), two epicranial dorsal setae (Ed1, Ed2), two epicranial lateral setae (El1, El2) and two epicranial marginal setae (Em1, Em2). Temporal regions (Figs. 3a,d) each with four long setae (T1–T4). Lateral regions (Fig. 3d) each with one campaniform sensillum (LC1) and two setae (L1, L2). Ventral regions (Fig. 3b), each with two setae (V1 e V2); gula wider than long. Labrum cordiform (Fig. 4b) with the basic pattern of chaetotaxy of other hydraenid species, with two campaniform sensilla (C1, C2) on each side and seven setae arranged in two rows: two discal setae (Ld1, Ld2) and five marginal setae (Lm1–Lm5); setae Lm1, Lm3 and Lm5 situated dorsolaterally, Lm2 and Lm4

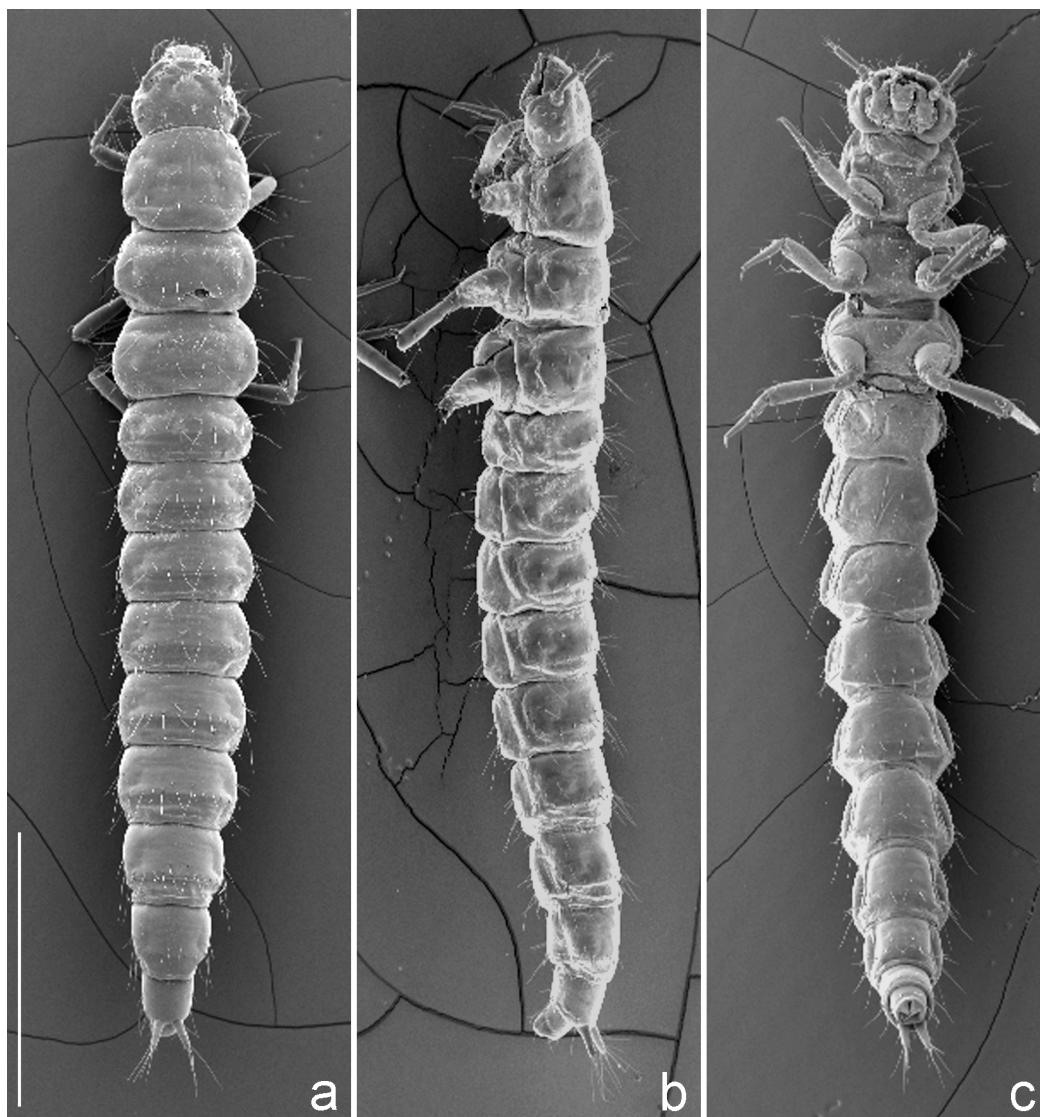


FIGURE 2. *Ochthebius capicola* larva. SEM micrographs of habitus: a) third instar, dorsal view; b) third instar, lateral view; c) second instar, ventral view. Scale bar: 1 mm.

ventrolaterally; setae Lm2 (Fig. 4b) pectinate. Antennae (Fig. 3a–c, 4a) 0,35x as long as head capsule width, antennomere II about 4x as long as antennomere I, with four setae (IIA1–IIA4) and two solenidia (IIS1 and IIS2); solenidium IIS1 long, slender, situated on distal end; solenidium IIS2 shorter, positioned ventrally on centre of antennomere; antennomere III 0.35x as long as II, with four setae (IIIA1–IIIA4), IIIA4 very small, subapical, and three apical solenidia (IIIS1–IIIS3); IIIS1 longer than IIIS2 & IIIS3. Mandibles (Figs. 3c, 4e,f) similar in size and shape, with two campaniform sensilla (C1 and C2) and 2 setae of different length, M1 shorter than M2; apex multidentate, with two major apical teeth (the dorsal one with distinct subapical pore) and dorsal row of four minor teeth; one conspicuous, triangular premolar tooth present, slightly curved toward base (Fig. 4f); both mandibles with a prostheca (Pr) long, slender and curved without any basal denticle, ending in four small teeth; penicillus extremely reduced; molar area with pointed, small denticulate microsculpture basally directed (Fig. 4f); fringe of minute hairs present at base of mola; outer edge of mandible with two setae; ventral part of mandibular base with a rounded condyle and without accessory process. Maxillae as in Figs. 3b–d, 4d: cardines longer than wide, transverse and widely separated from each other by submentum, each with one seta (Cdo1); stipes longer than wide, with four setae (Stp1–Stp4) and one campaniform sensillum; palpifer with a small clearly defined sclerite, and with one seta (Pf1); both galea and lacinia fixed; galea (Ga) hyaline, falciform and slender; lacinia slightly wider than galea, with six stout setae along outer edge and two elongate, dorsal, sub-basal setae; maxillary palp three-segmented: segment 1 with two campaniform sensilla, segment 2 with two setae (Pm1, Pm2), segment 3 with

a long, digitiform, sensorial appendage on external surface (SD) (Fig. 4d), and a small, complex sensorial structure on its apex. Labium (Figs. 3b,c) consisting of three sclerites: submentum (Smnt) with two setae, mentum (Mnt) with four setae and two campaniform sensilla, and prementum (Pmnt) with four setae as well as two inconspicuous campaniform sensilla; ligula (Lg) well developed composed by two globose lobes; bearing a number of small apical sensilla; labial palps, each with a cupuliform sensillum bearing several small papillae and pores and one rounded sensorial appendage as in Fig. 4c. Second labial palpomere with elongate seta medially directed.

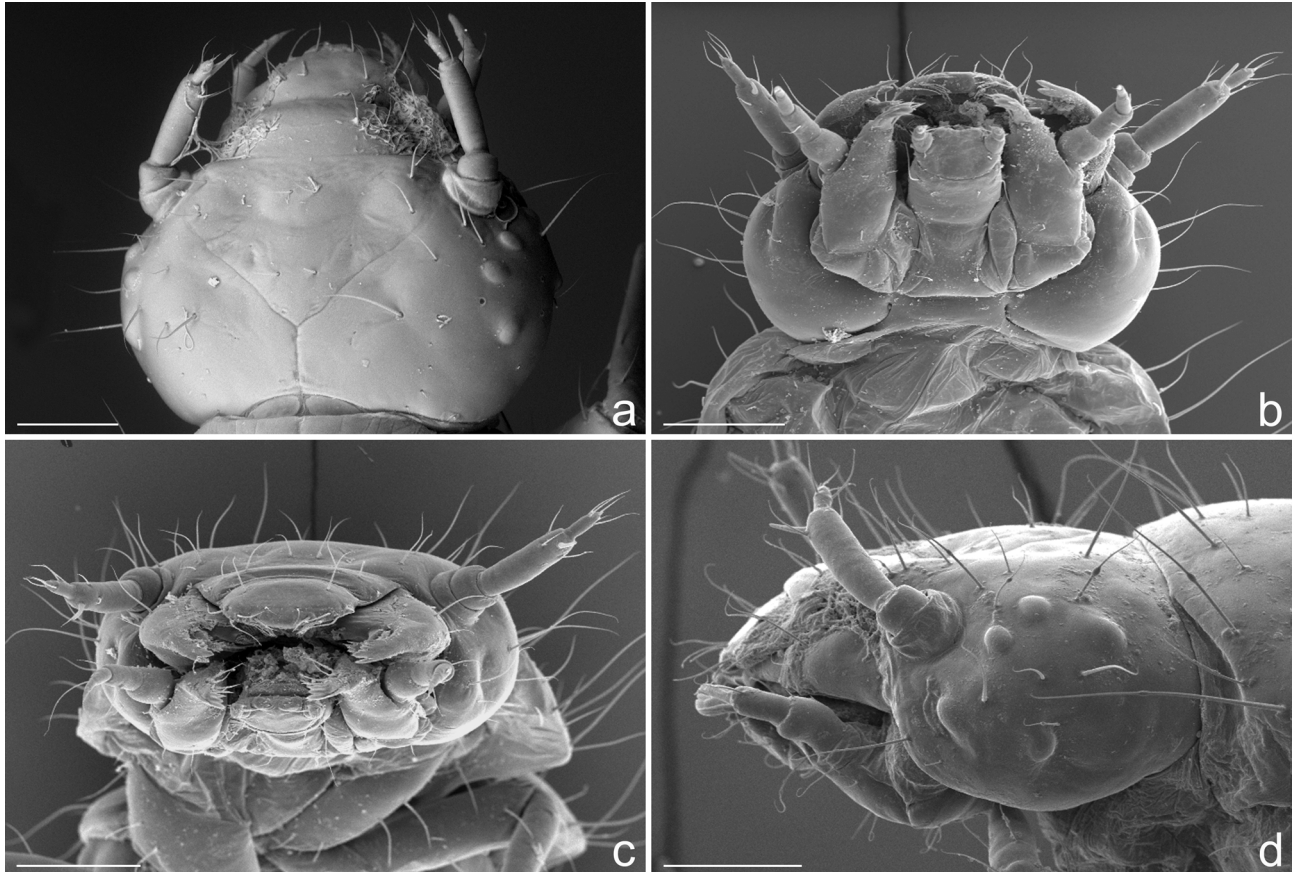


FIGURE 3. *Ochthebius capicola* larva. SEM micrographs of head capsule: a) third instar, dorsal view; b) second instar, ventral view; c) second instar, frontal view; d) third instar, lateral view. Scale bar: 100 μ m.

Thorax. Tergites transverse, similar in width, pronotum longer than meso- and metathorax; ecdysial suture present on all tergites. Pronotum (Figs. 2a,b, 5a) with fourteen setae and five campaniform sensilla on each side. Setae: four in anterior row A (A1–A4), A1 and A4 shorter, and one additional small setae posterior to A1; three in lateral row L (L1–L3), L2 shortest; four in posterior row P (P1–P4), P1 and P4 shorter; one in each of the three discal groups (Da1, Db1, Dc1); all discal setae well developed and similar in length, transversally lined. Pronotal campaniform sensilla C1 to C5 present. One tergal gland (Tg) on each side of the pronotum. Mesonotum (Fig. 2a,b) with fourteen setae and three campaniform sensilla (C3–5) on each side. Setae: four minute setae in anterior row A (A1–A4); three longer setae in lateral row L (L1–L3), L2 shortest; four in posterior row P (P1–P4); one in each of the three discal groups (Da1, Db1, Dc1) and one additional minute seta close to ecdysial line; discal setae on mesonotum not reduced. Mesonotal campaniform sensilla C1 and C2 absent. Metanotum similar to mesonotum. Legs: Prothoracic leg as in Fig. 2a,c. Coxa with 14 setae: 1D, 2 Ad, 4 Al, 1 Av, 1Pd, 4 PI and 1 Pv. Trochanter with 7 campaniform sensilla and 8 setae: 1 Ad, 2Al, 2 Av, 1 PI, 1 Pv and 1 V. Femur with 2 campaniform sensilla and 8 setae: 1 D, 1 Ad, 1 Al, 2 Av, 1 Pd, 1 PI and 1 V. Tibia with 1 campaniform sensillum and 8 setae: 2D, 1Al, 1Av, 2Pd, 1PI and 1Pv. Tibiotarsal setae Ad1 absent. Tarsungulus with 2 minute setae (Fig. 5d).

Abdomen. Subcylindrical, straight to slightly curved ventrally and tapering posteriorly. Abdominal terga and sterna I–VIII each with a well sclerotized plate; abdominal pleura with two small sclerites: a dorsopleural and a ventropleural sclerite on each side. Tergites I–VIII as in Figs. 2a–b, 5b. Number of setae and campaniform sensilla reduced: setae A2, Db1, Dc1, P2 and sensilla C1, C2, C4 absent. Remaining setae are arranged in a transverse row.

Dorsopleural sclerites each with a spiracle (SP) and two setae (DP1, DP2) and one subprimary setae (DP'). Ventropleural sclerites of segment I each with one seta: VP1. Ventropleural sclerites of segments II to VIII (Fig. 2c) each with two setae (VP1, VP2). Sternite I (Fig. 2c) with four setae on each side: one small presternal seta (PS1), one discal seta (D1), and two posterior setae (P1 and P2); one new subprimary seta L' lateral on sternum; additional seta (D2) absent. Segment IX bearing a pair of urogomphi, without dorsopleural nor ventropleural sclerites. Setal arrangements on segment IX and X as in fig 5e–f and with reduced chaetotaxy. Urogomphi (Fig. 5f) two-segmented: segment I (URI) mobile, not fused to tergite IX, with six setae (U1–U6) and four campaniform sensilla (C1–C4), seta U6 far from base of urogomphus; segment II (URII) 0.22x as long as segment I, with an apical seta (AS). Abdominal segment X as that shown in Fig. 5e–f, forming a completely sclerotized ring, with three long ventrolateral setae of unknown homology on each side. Pygopod (Fig. 5e–f) moderately developed, without anal hooks (AH), with three pairs of elongate setae.

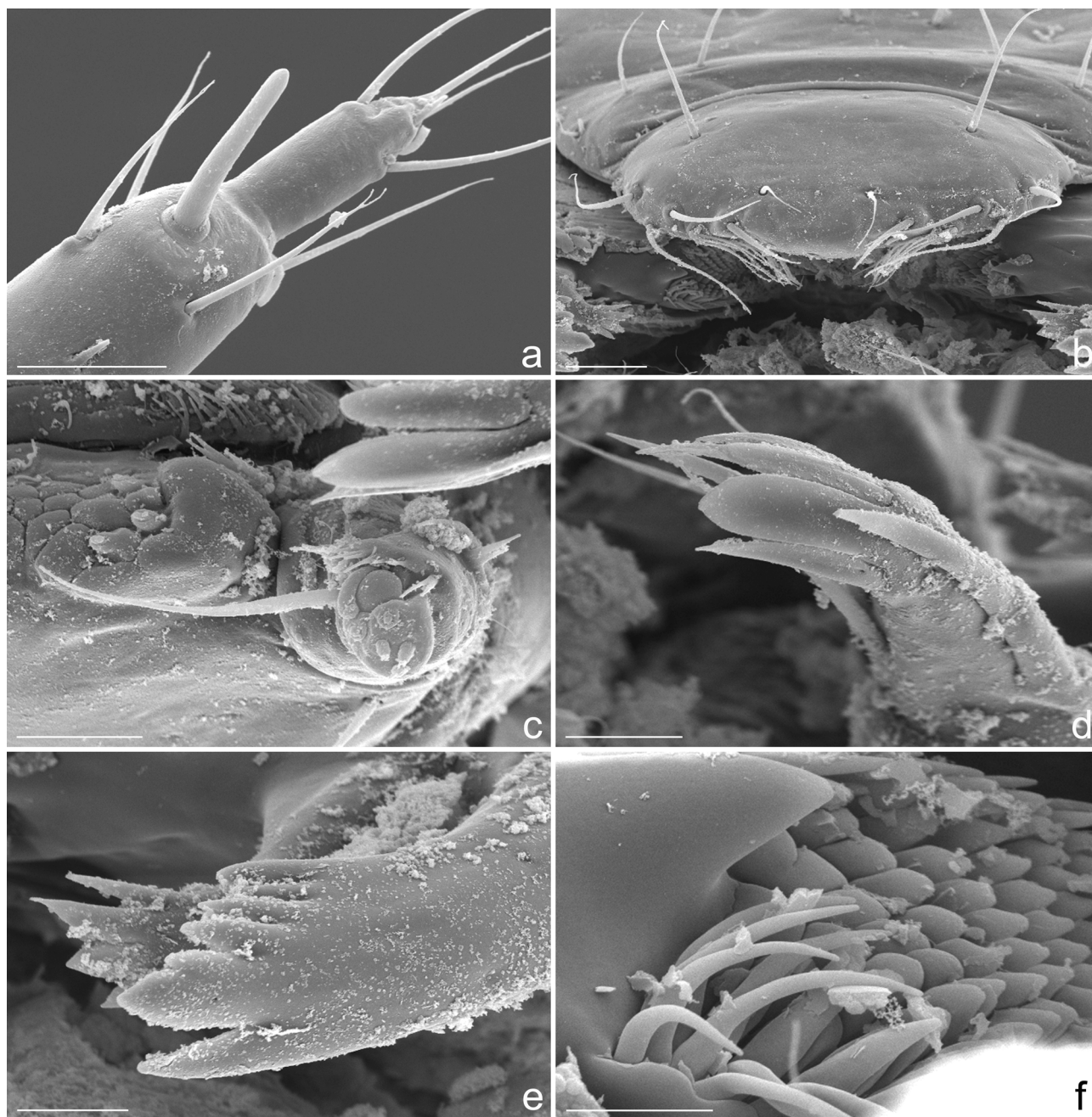


FIGURE 4. *Ochtthebius capicola* second instar larva, SEM micrographs of head appendages: a) apex of left antenna, ventral view; b) labrum, frontal view; c) left labial palp with medially directed elongate seta, frontal view; d) left maxilla, setiferous medial lobe; e) apex of left mandible; f) triangular premolar tooth and penicillus. Scale bars: a–b = 20 μ m; c–e = 10 μ m; f = 5 μ m.

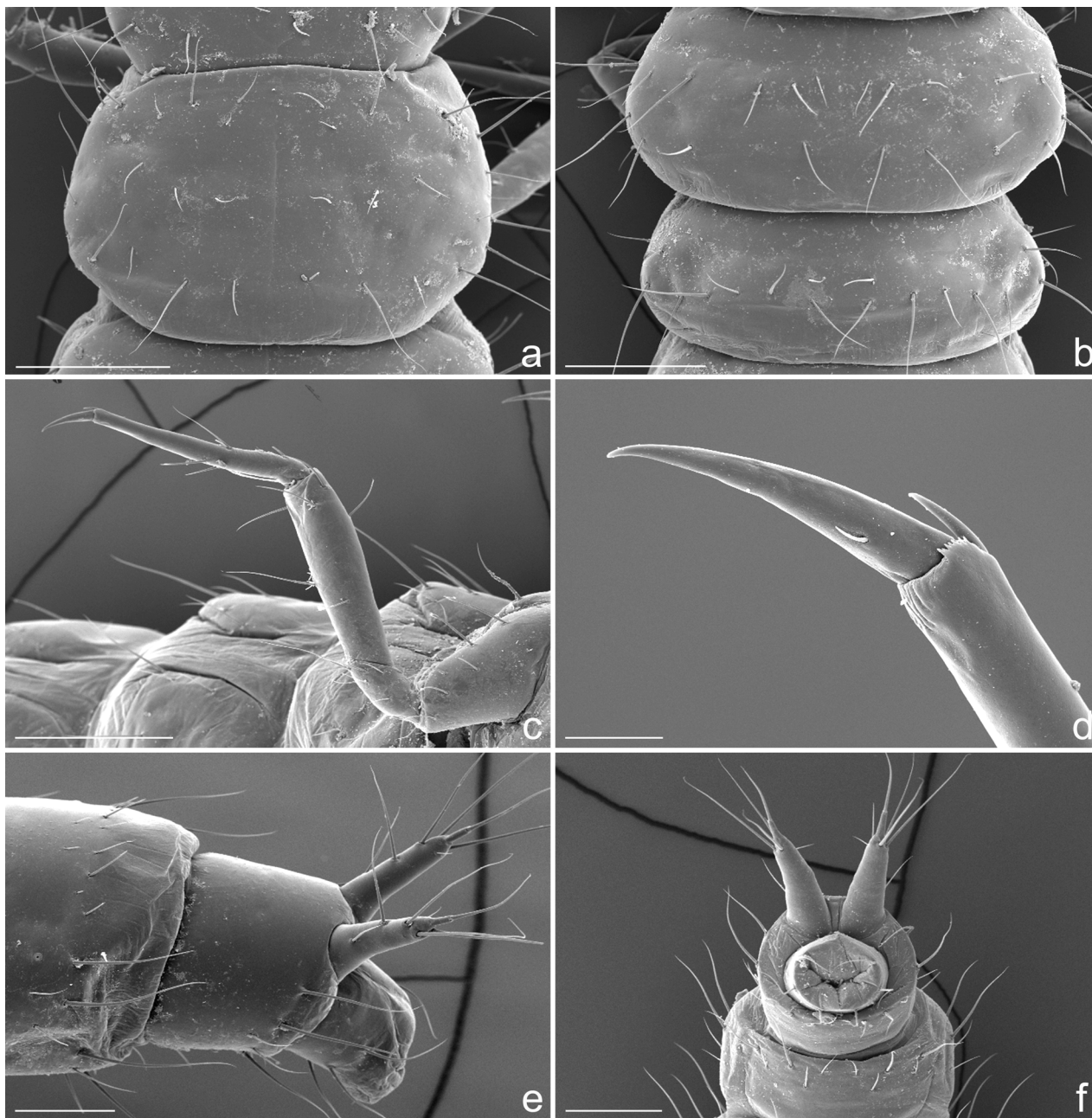


FIGURE 5. *Ochthebius capicola* larvae, SEM micrographs of: a) pronotum, third instar; b) tergites I–VIII, second instar; c) metathoracic leg in ventral view, third instar; d) metathoracic tarsungulus (close-up), third instar; e) abdominal segments IX and X of third instar larva, left lateral view; f) abdominal apex of second instar larva, ventral view. Scale-bars: a–c = 200 μ m; d = 20 μ m; e–f = 100 μ m.

Third instar. Body length 4 mm. Head capsule width: $0,45\text{mm} \pm 0,007$ (mean $\pm$ S.D.; $n=2$). Chaetotaxy identical to second instar except for an additional pair of setae on meso- and metanotum internal to Da1. Abdominal dorsopleurites and ventropleurites fused to dorsal and ventral sclerites.

Discussion

Larvae of *Ochthebius* (*Ochthebius*) *capicola* are characterized by the following autapomorphies: mandibles with one conspicuous triangular premolar tooth, slightly curved toward base; pronotum with one pair of additional setae posterior to A1; meso- and metanotum with a pair of additional setae close to ecdysial line; sternum with one new lateral subprimary seta L'.

We compared the larval stages of *O. capicola* with those currently known for the subfamily Ochthebiinae living in the same rockpool environment, using the set of characters selected in the recent work of Delgado and Archangelsky, (2005). Although *O. capicola* is currently included, on the basis of adult morphology, in the nominal subgenus, we could not detect any synapomorphies between its larva and those described for other species included in the same subgenus.

Larvae of *O. capicola* do not even bear the abdominal sternal setae D2 which represents the only synapomorphic character grouping *Ochthebius* s. str. (*O. auropallens*, *O. danjo* Nakane 1990 and *O. gonggashanensis* Jäch 2003), *Meropathus* (*M. campbellensis* Brookes 1951 and *M. zelandicus* Ordish 1984: tribe Meropathini) plus a clade with representatives of the genera *Gymnochthebius* (*G. jensenhaarupi*) and *Aulacochthebius* (*A. exaratus*).

Some characters which are considered phylogenetically informative are instead shared with species belonging to *Calobius* and *Cobalius* lineages (which also share the marine rockpool habitat with *O. capicola*). The following characters are considered synapomorphic: 1) presence of mandibular penicillum; 2) absence of tibiotarsal setae Ad1; 3) absence of anal hooks.

However, the larvae of *O. capicola* may be distinguished from larvae of *Calobius* by the normal shape of labral marginal setae Lm1 (strongly pectinate in *Calobius*), the presence of setae V1 on the ventral region, and the presence of abdominal sternal setae D1. Larvae of *O. capicola* differ from *Cobalius* in the globose shape of the ligula, the presence of cephalic temporal setae T2 and the presence of abdominal sternal setae D1.

For a rapid identification, larval stages of *O. capicola* can be distinguished from those of other *Ochthebius* (excl. *Cobalius*) by the absence of anal hooks. Additionally other minor differences are represented by: presence of mandibular penicillum, globose shape of the ligula, presence of medially directed elongate seta on second labial palpomere, absence of tibiotarsal setae Ad1 and absence of abdominal sternal setae D2.

Our results do not allow us to unequivocally assign *O. capicola* to the nominal subgenus or to other subgenera. However, the presence of synapomorphies shared with *Calobius* and *Cobalius* species, and in particular the absence of anal hooks, suggests a relationship between *O. capicola* and these last taxa.

The loss of the anal hooks does not seem to be related with adaptation to marine rockpool environments. The Japanese species *O. danjo*, which belongs to the nominal subgenus and bears well developed anal hooks, lives in the same habitat, for example (Delgado & Matsui, 2000). A future comparison of these larval morphological data, together with ongoing molecular analyses on the same target group (Sabatelli *et al.*, unpublished) may better clarify the position of *O. capicola* within the genus, and contribute to a more reliable definition of the subgenera in *Ochthebius*.

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References

- Delgado, J.A. & Soler, A.G. (1996) Descripción de la larva de *Ochthebius* (*Cobalius*) *subinteger* Mulsant & Rey, 1861 (Coleoptera, Hydraenidae). *Graellsia*, 51, 121–128.
<http://dx.doi.org/10.3989/graeellsia.1995.v51.i0.402>
- Delgado, J.A. & Soler, A.G. (1997a) Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) III: The genus *Calobius* Wollaston, 1854. *Aquatic Insects*, 19, 165–175.
<http://dx.doi.org/10.1080/01650429709361651>
- Delgado, J.A. & Soler, A.G. (1997b) Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) II: The subgenus *Ochthebius* s. str. Leach. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie*, 67, 45–55.

- Delgado, J.A. & Soler, A.G. (1997c) Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) I: genus *Limnebius* Leach, 1815 based on a description of *Limnebius cordobanus* d'Orchymont. *Aquatic Insects*, 19, 37–49.
<http://dx.doi.org/10.1080/01650429709361634>
- Delgado, J.A. & Matsui, E. (2000) Description of the larval stages of *Ochthebius* (s. str.) *danjo* Nakane (Coleoptera: Hydraenidae) from Japan. *Entomological Science*, 3, 125–130.
- Delgado, J.A. (2003) Hydraenidae: III. Description of the third instar larva of *Ochthebius* (s. str.) *gonggashanensis* Jäch (Coleoptera). In: Jäch, M.A. & Ji, L. (Eds.), *Water Beetles of China. Vol. 3. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein*. Wien, pp. 371–377.
- Delgado, J.A. & Archangelsky, M. (2005) Description of the larval stages of *Gymnochthebius jensenhaarupi* and phylogenetic analysis of the relationships with other species of the subfamily Ochthebiinae (Coleoptera: Hydraenidae). *European Journal of Entomology*, 102, 231–240.
- d'Orchymont, A. (1932a) Discours présidentiel: 'Des «rockpools» submarins et de leur population entomologique'. *Bulletin et Annales de la Société Entomologique de Belgique*, 72, 17–33 + 9 plates.
- d'Orchymont, A. (1932b) Notes sur certains sous-genres d'*Ochthebius* (*Calobius*, *Cobalius*, etc.). *Bulletin et Annales de la Société Entomologique de Belgique*, 72, 41–52.
- d'Orchymont, A. (1933) Au sujet de trois *Ochthebius* Africains. *Bulletin et Annales de la Société Entomologique de Belgique*, 73, 406–414.
- Hansen, M. (1991) A review of the genera of the beetle family Hydraenidae (Coleoptera). *Steenstrupia*, 17, 1–52.
- Hansen, M. (1998) *World Catalogue of Insects, Volume 2: Hydrophiloidea (Coleoptera)*. Apollo Books, Stenstrup, 416 pp.
- Jäch, M.A. (2004) Hydraenidae Mulsant, 1844, In Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palaearctic Coleoptera Vol. 2. Hydrophiloidea-Histeroidea-Staphylinoidea*. Apollo Books, Stenstrup, pp. 102–122.
- Knisch, A. (1924) Hydrophilidae. Chapter 79. In: Schenkling S. (Eds.), *Coleopterorum Catalogus*. W. Junk, Berlin, pp. 1–306.
- Lawrence, J.F. (1991) Order Coleoptera. Chapter 34. In: Stehr, F.W., (Ed.), *Immature Insects, Vol. 2*. Kendall/Hunt Publishing Company, Dubuque, Iowa, pp. 144–298.
- Park, S.-J. & Ahn, K.-J. (2008) Redescription of the littoral genus and species of *Neochthebius granulatus* (Satô), and the first larval description for the genus (Coleoptera: Hydraenidae: Ochthebiinae). *Journal of Natural History*, 42, 2501–2514.
<http://dx.doi.org/10.1080/00222930802354803>
- Péringuey, L. (1892) Fourth contribution to the South African Coleopterous fauna: description of new Coleoptera in the South African Museum. *Transactions of the South African Philosophical Society*, 4, 95–136.
<http://dx.doi.org/10.1080/21560382.1889.9526257>
- Perkins, P.D. (1980) Aquatic beetles of the family Hydraenidae in the Western Hemisphere: classification, biogeography and inferred phylogeny (Insecta: Coleoptera). *Quaestiones Entomologicae*, 16, 3–554.
- Perkins, P.D. (1981) *Hughleechia giulianii*, a new genus and new species of intertidal beetle from Australia (Coleoptera: Hydraenidae). *Pan-Pacific Entomologist*, 57, 295–302.
- Perkins, P.D. (1997) Life on the effective bubble: exocrine secretion delivery systems (ESDS) and the evolution and classification of beetles in the family Hydraenidae (Insecta: Coleoptera). *Annals of the Carnegie Museum*, 66, 89–207.
- Perkins, P.D. (2001) Hydraenidae. In: Arnett, R.H. Jr & Thomas, M.C. (Eds.), *American beetles. Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC press, Boca Raton, Florida, pp. 227–232.
- Perkins, P.D. (2007) A revision of the Australian intertidal water beetle genus *Hughleechia* Perkins (Coleoptera: Hydraenidae). *Zootaxa*, 1527, 17–29.
- Perkins, P.D. & Balfour-Browne, J. (1994) Contribution to the taxonomy of aquatic and humicolous beetles of the family Hydraenidae in southern Africa. *Fieldiana, Zoology (New Series)*, 77, 1–159.
<http://dx.doi.org/10.5962/bhl.title.3533>
- Satô, M. (1963) A new inter-tidal species of the genus *Ochthebius* Leach from Japan (Coleoptera: Hydraenidae). *Transactions of the Shikoku Entomological Society*, 7, 129–132.
- Turner, C.R. (2004) *Ochthebius* (s.str.) *capicola* (Coleoptera) re-discovered in the Cape Peninsula, South Africa. *African Journal of Aquatic Science*, 29, 271–273.
<http://dx.doi.org/10.2989/16085910409503820>