



South American terrestrial larva of Scirtidae (Coleoptera: Scirtoidea): the adaptation of Scirtidae larvae to saproxylic habitat is more common than expected

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Abstract

Terrestrial larvae of Scirtidae were found in southern South America (Chile) for the first time. The morphology of the larvae is described in detail and compared with terrestrial larvae known from Borneo, New Zealand and Australia. Special attention is paid to the prothoracic sclerites, which were examined for the first time in the family and compared with selected genera of Scirtidae. Large presternal sclerites seem to be a typical feature of terrestrial larvae of Scirtidae. Chilean saproxylic larvae seem to be specialised detritus feeders, feeding in water trapped in wood cavities.

Key words Chile, gut content, morphology.

INTRODUCTION

Scirtidae, the largest family of Scirtoidea, is a group of Coleoptera with 69 genera and over 1800 described species. The family occurs in all zoogeographic regions of the world, although its diversity is greatest in the tropics and in the temperate zone of the Southern Hemisphere. The great majority of Scirtidae larvae live in water bodies of various sizes and nature, like streams, lakes, ponds, peat-bogs and various kinds of phytotelmata (Kitching 2000; Lawrence 2016). They are readily distinguishable from other holometabolous insect larvae by their multisegmented antennae and are microphagous, feeding on various microorganisms filtered by dense maxillary or mandibular bristles or collected from the surface of decaying plant material and other substrates. These are subsequently sorted on a complex and highly modified hypopharynx (Lawrence 2016). The number of larval instars seems to be variable within the family. A total of five larval instars in the family had been widely accepted, until Zwick and Zwick (2010) estimated 9–12 larval instars in three European species in the course of detailed laboratory studies of Scirtidae. Pupation usually takes place in wet soil above the water surface, rarely also in air-filled cavities under submerged rocks. Adults are generally short lived, terrestrial and are often observed feeding on flowers of various families of plants (Lawrence 2016).

Phylogenetic analyses show that Scirtoidea is the sister group to all of the remaining polyphagan beetles (McKenna *et al.* 2015). Three subfamilies are currently included in the family Scirtidae: Nipponocyphoninae, Stenocyphoninae and Scirtinae

(Lawrence & Yoshitomi 2007). Both Nipponocyphoninae and Stenocyphoninae include a single, monotypic genus only. All the remaining species (currently over 1800) are classified within the Scirtinae. The knowledge of the phylogeny of Scirtinae is limited; only 20 genera out of 69 were studied in the only recent analysis (Lawrence & Yoshitomi 2007), and no subdivisions within the Scirtinae were proposed.

Records of scirtid larvae developing in terrestrial habitats, such as damp soil or tree logs, are rare, and such species are poorly studied. Until quite recently, data on terrestrial scirtid larvae were limited to early remarks by Hudson (1934), who described larvae of *Veronatus tricostellus* (White), and Crowson (1981), who found a larva in humus-rich damp soil in New Zealand. This larva was tentatively identified as *Veronatus* Sharp. Later, Hannappel and Paulus (1991) published descriptions of several undetermined larvae from Australia and New Zealand, including two identified by Watts (2014) as the saproxylic *Heterocyphon* Armstrong and *Prionocyphon insolitus* Watts. Recent research, focused mainly on Australian fauna, has provided more data on terrestrial larvae of Scirtidae. Klausnitzer (2006) provided the first detailed descriptions of two terrestrial larvae of Scirtidae, found in Borneo and New Zealand, and an important recent contribution by Watts (2014) includes data on numerous Australian scirtids that have saproxylic larvae. Interestingly, larvae developing in saproxylic habitats appear to belong to diverse genera, such as *Heterocyphon*, *Prionocyphon* Redtenbacher, *Macrodascillus* Carter and *Pseudomicrocara* Armstrong; although in some cases, their generic placements are somewhat tentative (Watts 2014). In other genera, of which adults were observed freshly emerging from saproxylic habitats, larvae are unknown but most

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likely also develop under these kinds of conditions (Watts 2014). It should be noted that genera, in which saproxylic habits of larvae were noticed, are not closely related (Cooper *et al.* 2014), and it seems that a shift to saproxylic larval habitat has taken place several times in the evolutionary history of the Scirtidae.

During recent expeditions to Chile, saproxylic larvae were collected for the first time in South America. The aim of the present paper is to provide a detailed description of newly found larvae and compare them with already known larvae of Scirtidae that develop under similar conditions. We were also able to compare these with previously known saproxylic larvae and evaluate morphological characters that seem to be adaptations to a terrestrial mode of life.

MATERIALS AND METHODS

Material was collected by Kirill Yuryevich Eskov under *Nothofagus* logs in moist soil in provinces Los Lagos and Aysen of Chile. In total, nine specimens were collected and stored in 70% ethanol. In Los Lagos, adults of '*Elodes*' *velutina* Solier were collected at the same localities where larvae were collected.

Single larvae were disarticulated and cleared in ~10% NaOH solution for about 3 h at room temperature. The specimen fragments were then rinsed in distilled water and transferred into glycerine and covered with cover slips as temporary slides. The morphological details were studied, measured and photographed under a Nikon Eclipse Ni compound microscope. Photographs were taken on Nikon D5100 and Leica DFC425 digital cameras in combination with compound or dissecting microscopes (Nikon SMZ 1500, Leica M165C, Stereo Discovery.V12 Carl Zeiss and Nikon Eclipse 50i). Images were generated by using Helicon FOCUS 5.3.14 software and enhanced by using PHOTOSHOP® CS4. Two specimens were studied with the use of scanning electron microscopes. One specimen was studied in field-emission SEM (Hitachi S-3400N) in the laboratory of the Museum and Institute of Zoology, Polish Academy of Sciences in Warsaw, Poland. The second one was gold coated with an ion coater (IB-3, Eiko Co., Japan) and observed under a JSM-6510VL (JEOL, Japan) in the Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences. The gut was removed prior to clearing of the specimen and its contents observed with a SEM and under a compound microscope. Terminology for the spiracle apparatus follows Watts (2014).

Comparisons with other terrestrial larvae were based on publications (Hannappel & Paulus 1991; Klausnitzer 2006; Watts 2014) and specimens kindly provided by C. H. S. Watts (South Australian Museum, Adelaide). The following alcohol-stored specimens were available for analysis:

- *Pseudomicrocara* sp. Watts (two specimens): Australia, Thungutti Camp, New England NP, 15/11/14, from log, leg. CHS Watts;
- *Pseudomicrocara* cf. *hylaiois* Watts (three specimens): Australia, Banksia Point, New England NP, 14/11/14, from eucalypt log, leg. CHS Watts; and

- *Prionocyphon* cf. *lamingtonensis* Watts (two specimens): Australia, Qld Morans Creek, Morans Falls Green Mts, 24.8.2004, leg. CHS Watts.

Depositories:

DBET	Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Wrocław, Poland
IBIW	Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Russia
MSPU	Moscow Pedagogical State University, Moscow, Russia
ZIN	Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia

Abbreviations for mouthpart morphology follow Hannappel and Paulus (1987, 1991). Newly introduced abbreviations are marked with asterisk:

Bf	bristle field
Bs	lateral row of bristles on the lacinia
Cb	chitin dent
Co	comb organ
Fb	feathered bristles
Ga	galea
Ka	claw apparatus
Kpl	comb plates
La	lacinia
Lf	field of lamellae
Lt	lacinian teeth*
Mk	T-shaped chitin prominence of the press apparatus
Mo	mola
Mp	maxillary palpus
Mpm	maxillary palpomere*
Ms	middle region of sclerites*
Mz	middle plug
P	cushion
Pf	cushion field
Pr	palpifer
Sf	sensory field*
Sk1	sclerite plate
Spl	lateral plate
St	stipes*
Stb	stalk comb bristles
Tz	terminal tooth
Vs	stiff plate
Z	teeth

TAXONOMY

Scirtidae, undetermined genus, cf. *Elodes velutina* Solier

(Figs 1–14)



Fig. 1. Terrestrial larva of Scirtidae: (a and b) total view of two specimens, dorsum and (c) venter. Scale bar: Figure 1 = 5.0 mm, Figure 3 = 2.0 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

Material examined

Eight specimens: ZIN (two specimens in alcohol), MSPU (one specimen in alcohol), DBET (one specimen, permanent slide), private collection of B. Klausnitzer, Dresden, Germany (one specimen in alcohol): Chile, Los Lagos, National Park Puyehue, Anticura Sector, 72°10'10"W 40°40'20"S, 400 m alt., 19 January 2014, Kirill Yu. Eskov. Depositories: IBIW (two specimens in alcohol, one permanent slide). One specimen: DBET (one specimen in alcohol): Chile, Aysen Prov., National Park Queulat, Ventisquero Colgante, S44°28'W72°33', ≥100 m alt., 29 December 2014, leg. Kirill Yu. Eskov.

Description

Body (Fig. 1) elongate, shiny, yellowish (only clypeolabrum, mandibles and claws darker, brownish), covered with sparse, long setae, 1/4–1/3 width of widest thoracic segment. Thoracic segments wider than abdominal ones, abdominal segment eight subtriangular, pointed at apex. Body length 17.7 mm.

Head capsule transverse, width 2.4 mm (Fig. 2). Setaion of head. 20–30 long setae on lateral margins, 1/4 width of head; setae on dorsum 4–10× shorter than longer, lateral setae, consisting of rows of >30 setae along frontal arms of epicranial suture, large group of ~10 relatively longer setae situated close to

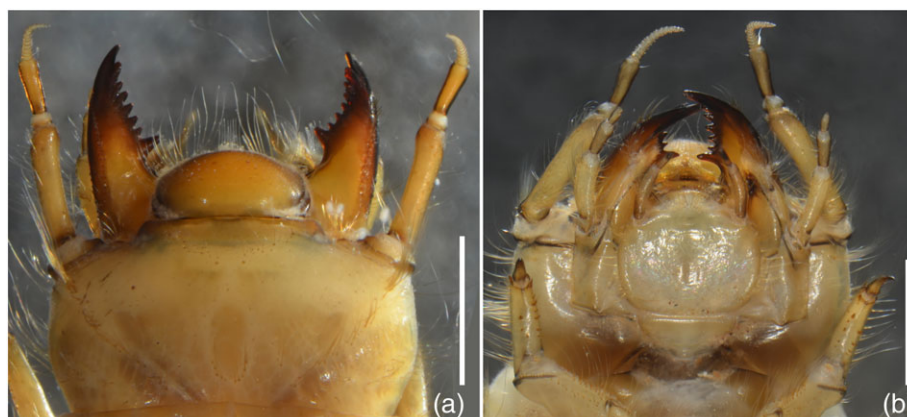


Fig. 2. Head: (a) dorsal view and (b) ventral view. Scale bars = 1.0 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

antennal base, sparse group of about 30 setae on epicranial plates and >30 short setae in frontal region. Eyes absent. Antennae short (Fig. 3), slightly longer than mandibles, reaching prothorax; scape long, subcylindrical, covered with long, straight setae; pedicle approximately half as long as scape, somewhat thinner than scape, with single sensorium at apex, ~1/3 length of pedicel; flagellum short, 13–15 secondary segments. Flagellomeres with numerous sensory organs.

Mandibles (Fig. 4), strongly projecting forward, narrowly subtriangular, tips not divided; apical half with 7–8 denticles

on mesal edge; basal half of mesal edge with two bristle fields: one located closer to apical portion, consisting of small group of long feather-like bristles and shorter bristles hooked apically, the other located close to comb organ consisting of more numerous but shorter bristles, hooked apically. Comb organ well developed; mola pronounced, smooth, without lamellae. Outer margin of mandibles with row of about 20 long setae on dorsal portion. Ventral portion of mandibles without setae.

Maxillae (Fig. 5) elongate; lacinia with very well pronounced three lacinial teeth at apex, mesal ridge covered with very short

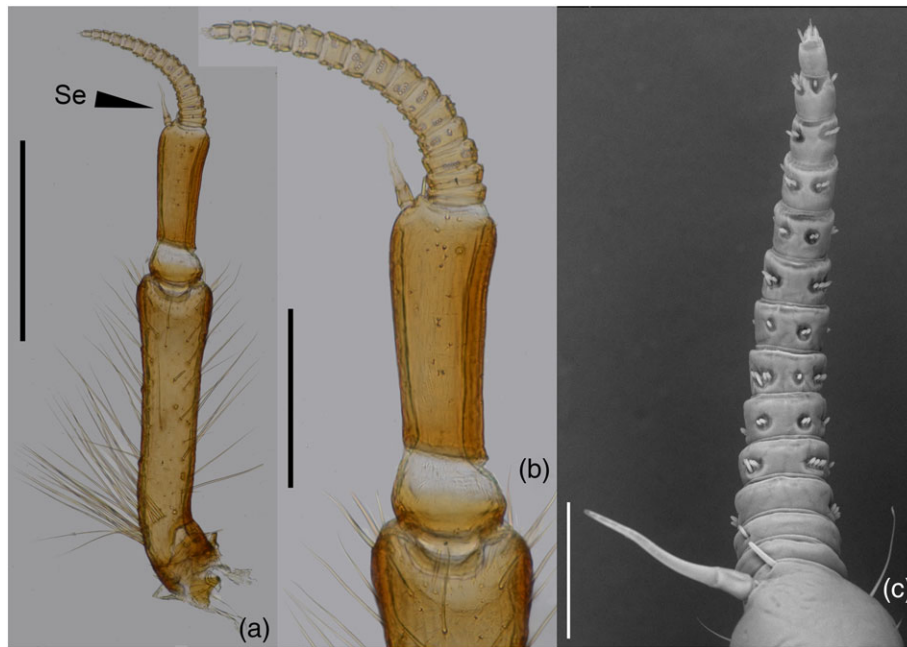


Fig. 3. Antenna: (a) total view, scale bar = 0.5 mm; (b) pedicle and flagellum, close-up, scale bar = 0.25 mm; (c) flagellum, SEM micrograph; Se, sensorium; scale bar = 0.1 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

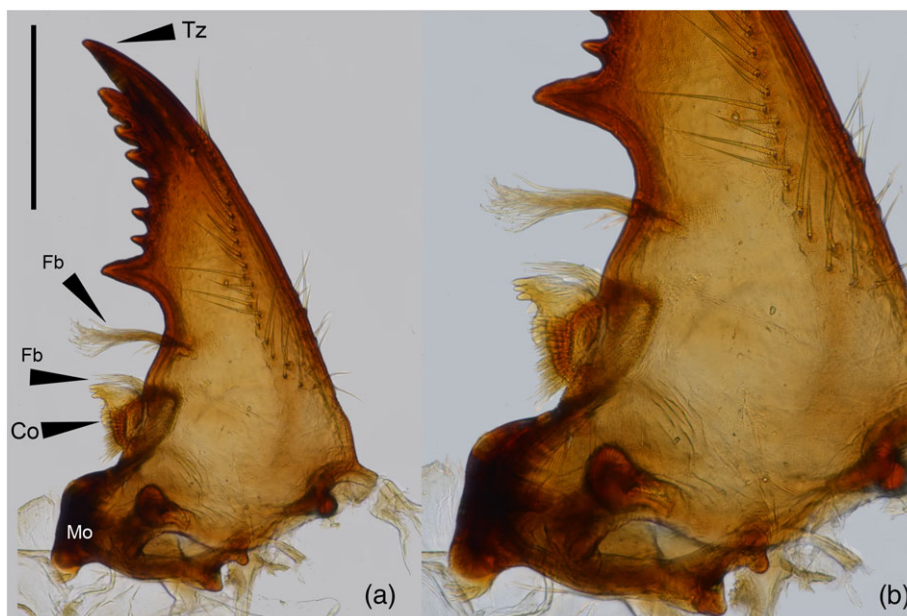


Fig. 4. Mandible, dorsal: (a) total view, scale bar = 0.5 mm; (b) close-up. [Colour figure can be viewed at wileyonlinelibrary.com]

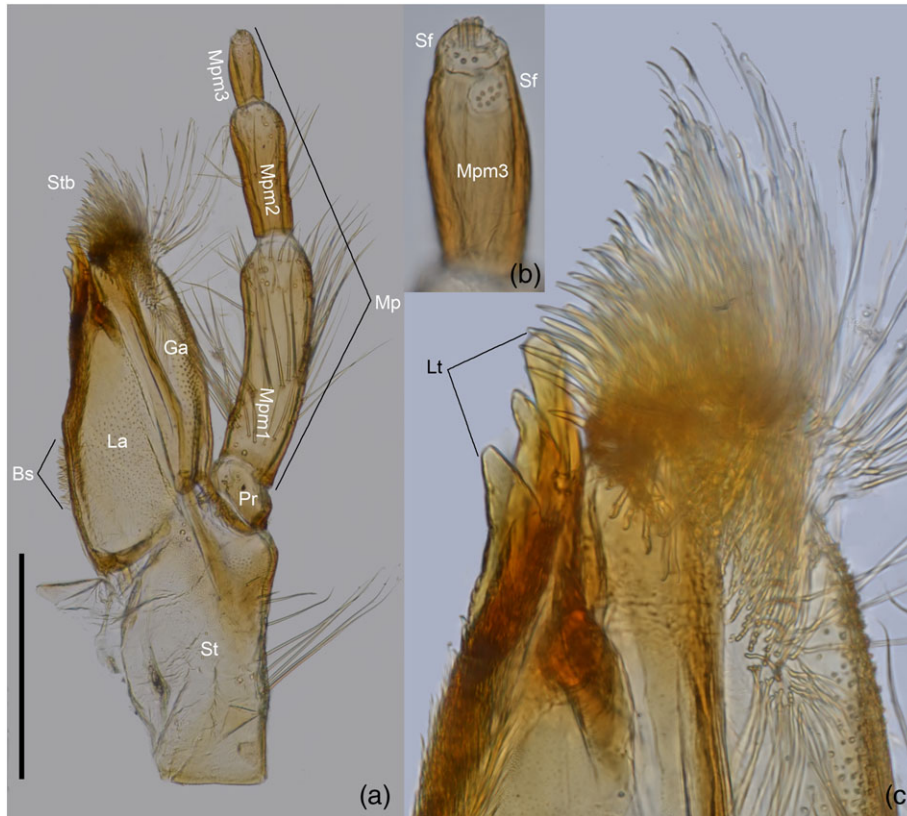


Fig. 5. Maxilla: (a) total view (cardo is missing), scale bar = 0.5 mm; (b) apical maxillary palpomere, close-up; (c) galea and lacinia, close-up of apical portion. [Colour figure can be viewed at wileyonlinelibrary.com]

setae (Fig. 5a: Bs); galea with group of dense setal brushes, setae long, longer than width of galea, simple, not feather-like. Maxillary palpus moderately long, three-segmented; palpomere 1 long, subcylindrical, densely covered with long setae, palpomere 2 $\sim 0.7\times$ as long as palpomere 1, with long setae in its middle length, palpomere 3 $\sim 0.6\times$ as long as palpomere 2, with two fields of sensory organs: apical and subapical one (Fig. 5b).

Clypeolabrum (Fig. 6) large, transversely oval, clypeolabral wall reduced, lobes not developed; anterior margin triangularly

extended in the middle, with ~ 30 long, soft setae strongly differing in length; dorsal portion not setose. About 10 shorter, straight, subparallel palisade setae (sensu Watts 2014) present in central portion of anterior margin of clypeolabrum; inner and basal setae distinctly longer. Lateral portions of anterior margin with a row of more adherent setae, $\sim 8\times$ shorter than long setae. Mesal portion of anterior margin of clypeolabrum with two rows of teeth: first row with four teeth, located laterally, second row with six teeth, located mesally. Epipharynx (Figs 6, 7) with well-developed middle plug and large cushion fields surrounded

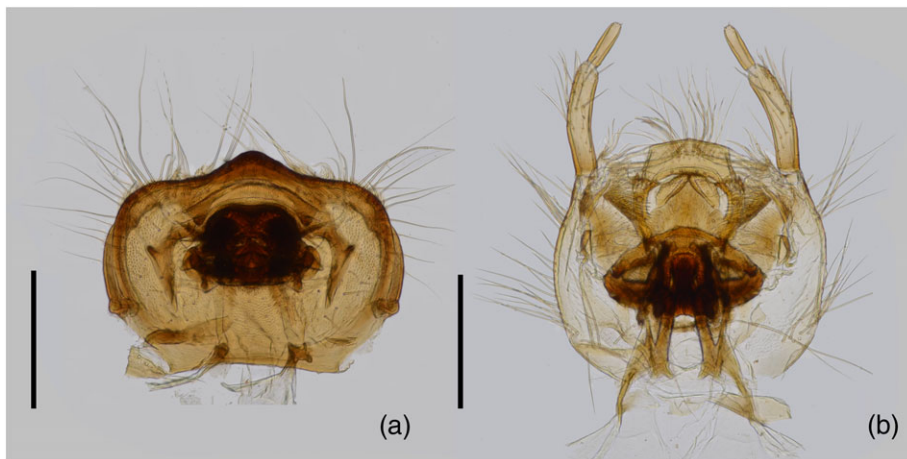


Fig. 6. Mouthparts: (a) clypeolabrum and epipharynx; (b) labium and hypopharynx. Scale bars = 0.5 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

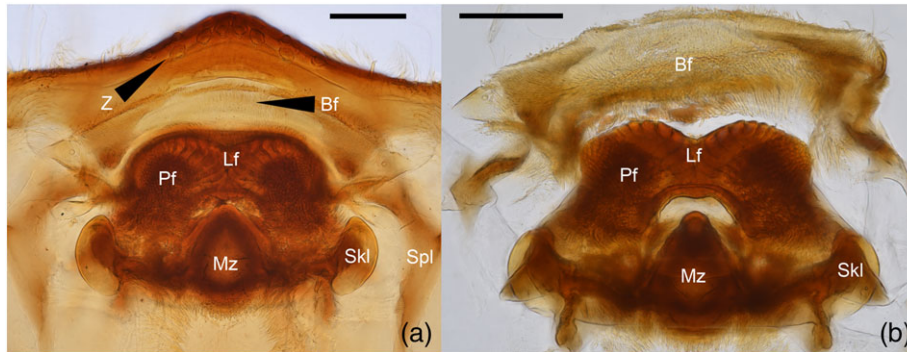


Fig. 7. Epipharynx, ventral view: (a) not separated from clypeolabrum; (b) separated from clypeolabrum. Scale bars = 0.1 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

by lamellae. Bristle field relatively large, separating epipharynx from clypeolabrum.

Labium (Fig. 6b) suboval, with long setae on lateral margins and two-jointed labial palpi. Hypopharynx (Fig. 8) with large press apparatus and well-developed cushion area. Stiff plate greatly reduced, keel sclerite and socket sclerite absent. Basal portion of stiff plate with structures resembling digitiform sensillae. Claw apparatus small, composed of rows of subtle bristles present in lateral portions of hypopharynx. Middle region of sclerites and bristles well developed, with numerous long bristles. Comb plates reduced, with ~10 teeth, stalk of comb plate with round and sensory structure.

Tergites with diverse setation consisting of long, sparse setae, minute, straight setae and microtrichia which are distributed

regularly on the cuticle (Fig. 9). Prothorax with a pair of well-developed lateral presternal ('cervical') sclerites. Legs relatively long (Fig. 10), longer than 0.7–0.8 width of widest thoracic tergites; coxa sparsely covered with long setae; trochanters narrow and elongate; femora with row of short, strong spines on inner edge and sparse, long setae; tibiotarsi relatively long, with strong spines on inner edge, pretarsi moderately long with two small setae in the middle of their length. Forelegs without tibiotarsal organs (sensu Zwick 2008).

Abdominal segments gradually elongated and narrowed till apex, with sparse long setae on lateral sides, dorsal and ventral surfaces covered with microtrichia. Tergite 8 subtriangular (Fig. 11), with four long setae along lateral margin, covered with microtrichia, apex pointed. Tergite 9 with very narrow apical



Fig. 8. Hypopharynx: (a) total view, scale bar = 0.5 mm; (b) close-up of central portion with probable sensory structures (Se?) on comb plates; (c) close-up of stiff plate with digitiform sensillae (Ds). [Colour figure can be viewed at wileyonlinelibrary.com]



Fig. 9. Thoracic segments and first abdominal segment. Scale bar = 2 mm. [Colour figure can be viewed at wileyonlinelibrary.com]



Fig. 10. Fore leg: (a) total view; Cx, coxa; F, femur; Tr, trochanter; Tt, tibia; Pt, pretarsus; scale bar = 0.5 mm. (b) Close-up of tibia and pretarsus, scale bar = 0.25 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

half, lateral margins with single long seta. Sternite 8 with arcuate margin and long marginal setae. Spiracle apparatus with subtriangular apical lobes, covered with reticulate microsculpture; inner atrium narrow. Five anal papillae present.

Variation

Body length 15.0–20.4 mm (mean 18.0, $n = 6$). We were unable to determine if larvae represent the same instar, but no significant morphological differences were noticed. The number of flagellomeres differed from 13 to 16.

Biology

Analysis of gut contents showed the presence of plant material mixed with mineral particles, diatoms, fungal hyphae and possibly bacteria (Figs 12, 13). The apex of the abdomen of one larva was covered with ciliates (cf. *Vorticella* L.; Fig. 14).

Remarks

Larvae were identified as Scirtidae on their multisegmented antennae, which are a unique feature not only in Coleoptera but also in all Holometabola. All studied larvae shared identical morphology of mouthparts, including the epipharynx and hypopharynx, which are species-specific structures. In this study, we were working with a small number of larvae, and the determination of instar stage proved to be impossible. We concluded that the larvae collected were late instar but not necessarily the final on the basis of differences in body length, head width and the number of flagellomeres.

The identity of the described larvae is unknown, but it is highly plausible that it belongs to *E. velutina*, as adults of this species were collected at the same locality. When Solier worked on the Chilean Scirtidae, a very broad concept of *Elodes* Latreille was commonly adopted (Solier 1849). As a result, numerous species were classified under this 'waste-basket' taxon containing many unrelated species. Today, *Elodes* is regarded (Klausnitzer 2009) as a primarily Eurasian genus which does not occur in the Neotropics. *Elodes* s. str.

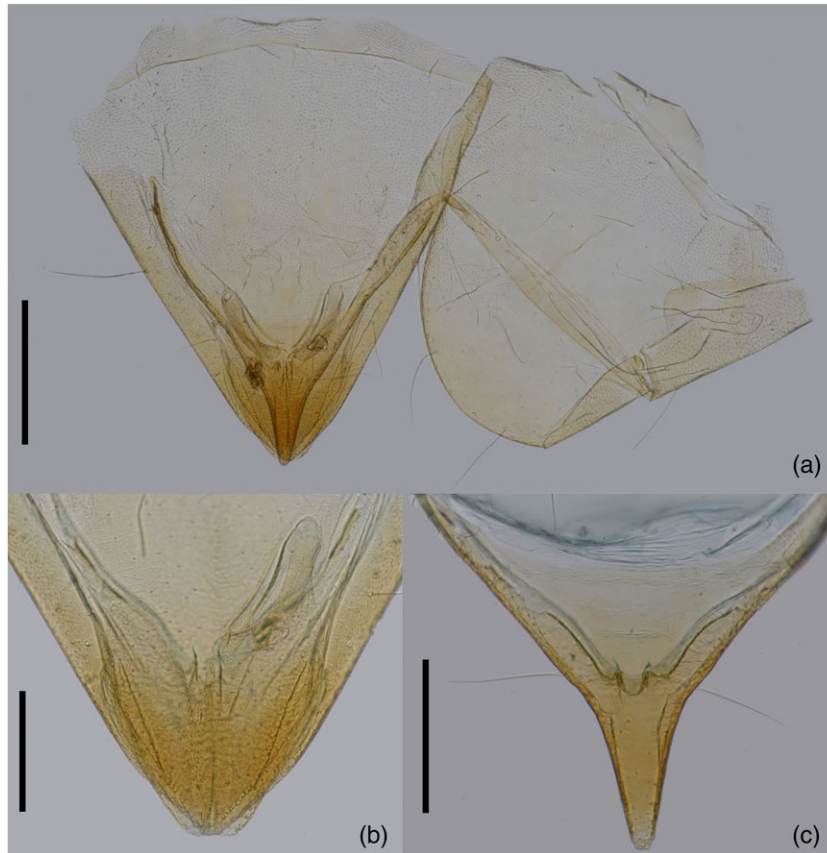


Fig. 11. Abdominal segments 8 and 9: (a) tergites and sternites 8 and 9, scale bar = 0.5 mm; (b) tergite 8 (tergite 9 removed), scale bar = 0.25 mm; (c) tergite 9, scale bar = 0.25 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

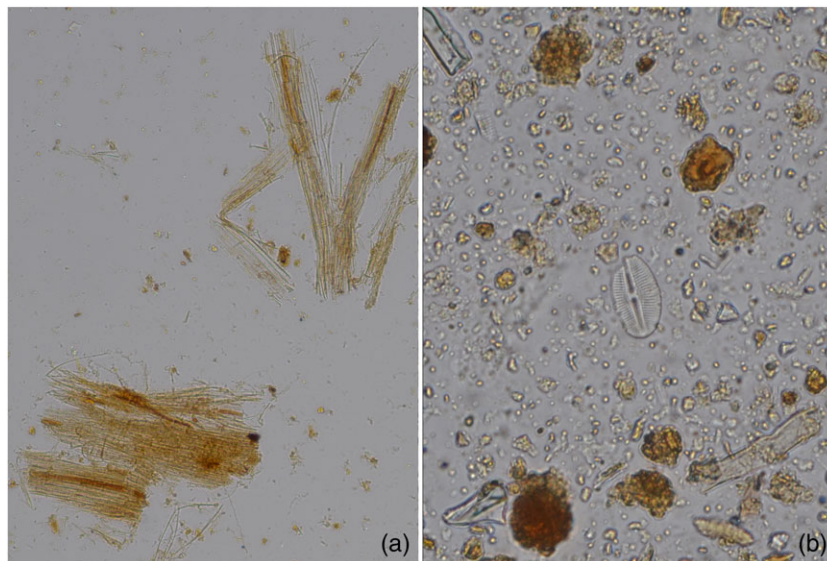


Fig. 12. Gut contents, light microscope view: (a) wood particles and (b) organic and mineral debris, a diatome visible in central portion of the photograph. [Colour figure can be viewed at wileyonlinelibrary.com]

share several features, such as a semicircular pronotum with no marked anterolateral angles and contiguous mesocoxal cavities, which are absent in *E. velutina*. In fact, *E. velutina* belongs to an undescribed genus (Ruta 2011), which will be described in a separate paper (Ruta *in prep.*).

Morphological features of saproxylic larvae of Scirtidae are listed in Table 1. Some characters are common to all known larvae, but others are found only in selected taxa. The most striking example of the latter is projections on the anterior portion of the head, close to the antennal base (Fig. 15), in some of Australian

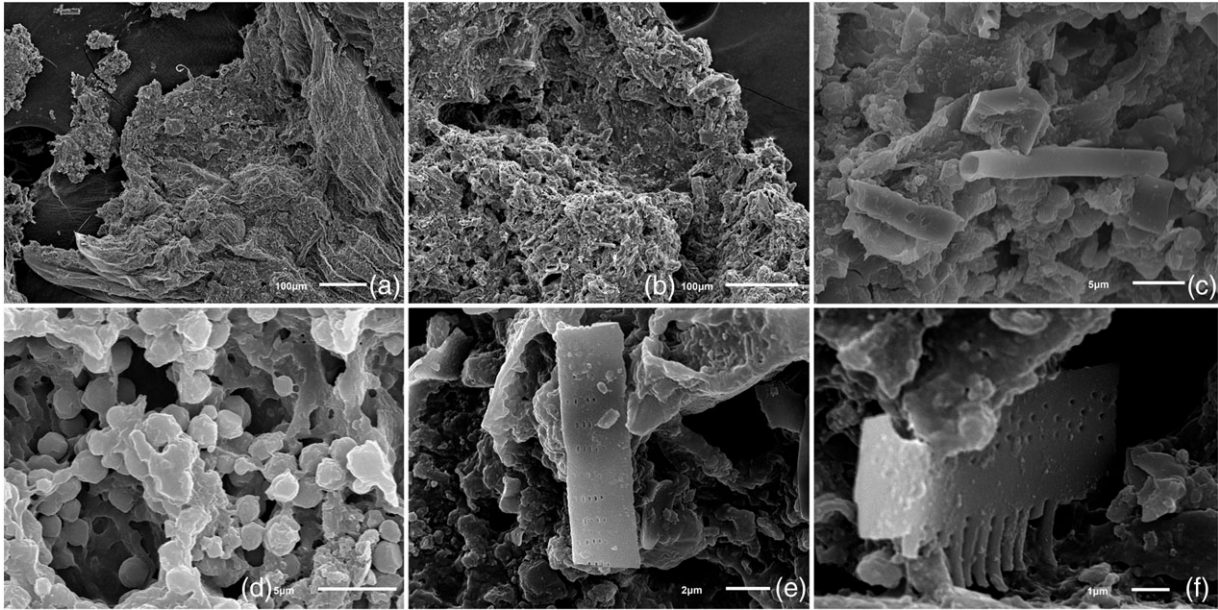


Fig. 13. Gut contents, SEM: (a) peritrophic membrane and (b–f) organic material with presence of (c) fungal hyphae, (d) supposed bacteria and (e and f) diatoms.

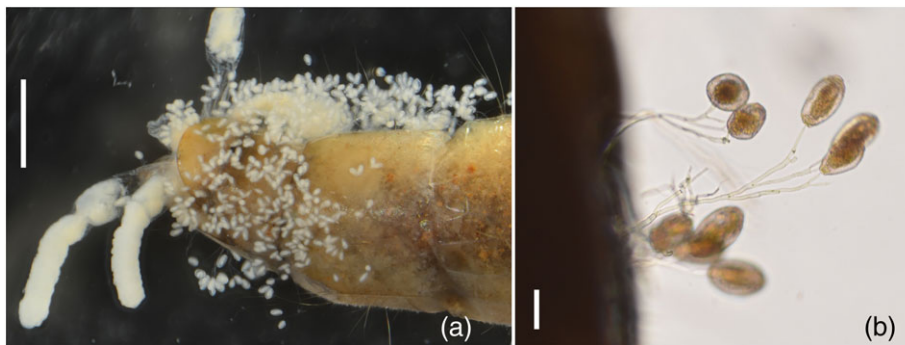


Fig. 14. Ciliates on caudal portion of larva: (a) caudal portion with anal papillae and ciliates visible, scale bar = 1.0 mm; (b) enlarged photograph of ciliates, scale bar = 0.1 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

larvae. This feature of unknown function is not shared by other known larvae of Scirtidae (Watts 2014). Apart from the light body colour and shortened antennae, features listed in Table 1 are unique to terrestrial larvae. There are also several features that were found in Chilean specimens that are rare or absent in other terrestrial larvae of Scirtidae. The significant reduction of the mouthparts of the Chilean larva, in which the clypeolabral lobes are not developed, is also known in New Zealand larvae (Klausnitzer 2006) and *Macrodascillus scalaris* (Lea) (Watts 2014). Features that appear unique to the Chilean larva are a total reduction of the keel sclerite and socket sclerite, and sensory structures (digitiform sensillae) usually present in the basal portion of keel sclerites are present on the stiff plate. Knowledge of the morphology and function of prothoracic structures, including presternal sclerites ('cervical sclerites' according to Lawrence & Ślipiński 2013) in Scirtidae is scarce. According to the authors' observations, they are present in most genera, including those inhabiting aquatic habitats (Fig. 16b,d), but are exceptionally well developed in saproxylic larvae (Figs 1, 16a).

It seems plausible that these sclerites play an important role in supporting the muscles that execute feeding movements. Similar sclerites occur in other groups of Coleoptera, e.g. in Helophoridae (Fikáček *et al.* 2012).

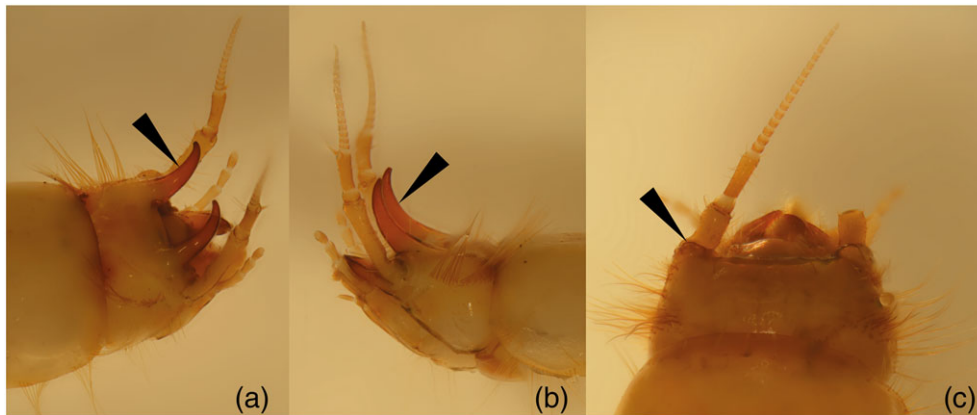
The described Chilean larvae share most similarities with New Zealand larvae of '*Veronatus*' (Klausnitzer 2006), especially in the following morphological characters: reduction of the comb plates in the hypopharynx (unknown in other saproxylic larvae), clypeolabrum with projecting anterior portion and subconical middle plug, and mandibles with distinct mola, similar feathered bristles and a comb organ.

DISCUSSION

It has only recently become widely known that saproxylic scirtid larvae inhabiting water-saturated logs are relatively common in austral and tropical regions (Watts 2014). The present study shows that adaptation to terrestrial habitats has also evolved in

Table 1 Morphological features of terrestrial larvae of Scirtidae (X, present; —, absent; ?, unknown)

Feature	Larva							
	Chile (present paper)	<i>Heterocyphon</i> (Watts 2014)	<i>Macrodascillus</i> (Watts 2014)	<i>Prionocyphon</i> <i>insolitus</i> Watts (Watts 2014)	<i>Pseudomicrocara</i> <i>cincta</i> species group (Watts 2014)	<i>Pseudomicrocara</i> '?sp. 'thungutti' (Watts 2014)	New Zealand (Klausnitzer 2006)	Borneo (Klausnitzer 2006)
Light body colour	X	X	X	X	X	X	X	X
Sparse setation	X	X	X	X	X	X	X	X
Eyes reduced or absent	X	X	X	X	X	X	?	?
Short antennae	X	X	X	X	X	X	X	X
Mandibles strong, projecting, apex pointed	X	—	X	X	—	X	X	X
Feather bristles on mandibles reduced	X	—	—	X	—	—	X	X
Mesal edge of mandibles with sharp denticles or tubercles	X	—	X	—	—	—	X	X
Tibiotarsal organ absent	X	X	X	X	X	X	X	X
Apical half of tergite 9 strongly narrowed, elongated, pointed	X	X	—	X	X	X	X	X
Projections on the anterior portion of the head	—	—	—	—	X	X	—	—

**Fig. 15.** Head projections of Australian Scirtidae: (a and b) '*Pseudomicrocara*' sp., posterolateral and lateral views and (c) '*Pseudomicrocara*' sp. cf. *hylaios* Watts. [Colour figure can be viewed at wileyonlinelibrary.com]

Neotropical Scirtidae. Although knowledge of the phylogeny of the Scirtidae is limited, recent molecular studies suggest that the saproxylic mode of life evolved independently at least five times in Australian taxa (Cooper *et al.* 2014; Watts 2014). The present finding suggests that shifts to terrestrial habitats may have occurred multiple times in the evolution of various lineages of Scirtidae.

Gut content analysis seems to support the hypothesis on the feeding of saproxylic larvae presented by Watts (2014), who suggested that larvae are specialised detritus feeders like most aquatic Scirtidae larvae. Larvae reared by Watts formed cells in wood debris in which water collected. This watery environment facilitated the scraping of the cell walls by the larvae. The presence of well-developed anal papillae in described specimens suggests that larvae spend at least some time in water, as papillae can only function properly as osmoregulatory organs in aquatic conditions (Wichard & Komnick 1974). Also, ciliates found on the abdominal segments of a single specimen suggest that the

larva was living in aquatic conditions or at least by using capillary water in the feeding process.

This research shows that the Chilean saproxylic larvae of Scirtidae seem to be most closely related to the New Zealand forms on morphology. This may be another example of links between South American and Australian/New Zealand Scirtidae. Previous research showed close relations among South American, New Zealand and Australian Scirtidae, members of Stenocyphoninae have been recorded in all of these regions, a single species is known from Chile (another one from New Zealand), and there are also undescribed females known from Australia (Ruta *et al.* 2011). *Pseudomicrocara* is another genus of Scirtidae which shows similar distributional pattern: 40 species were recorded in Australia (Watts 2007), and 7 species are known from Argentina (Libonatti & Ruta 2013). According to Cooper *et al.* (2014), Australian species of *Pseudomicrocara* are not monophyletic; resolution of the genus needs further studies focused on relationships between South

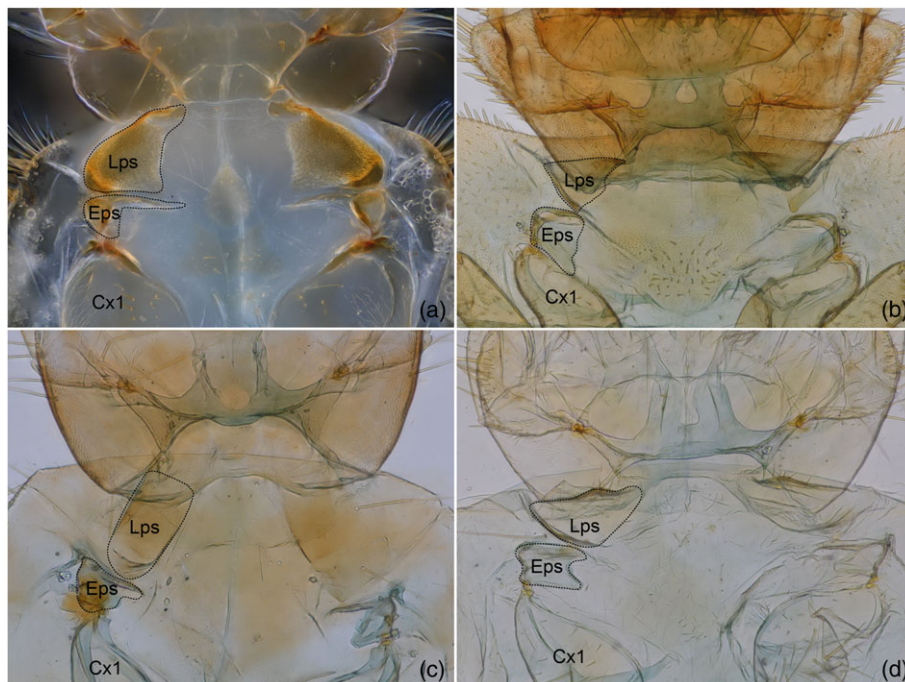


Fig. 16. Prothoracic sclerites in Scirtidae, Cx1, procoxa; Eps, episternum; Lps, lateral presternal sclerite: (a) '*Pseudomicrocara*' sp. cf. *hylaios* Watts; (b) *Elodes* cf. *minuta*; (c) *Contacyphon* sp.; (d) *Prionocyphon serricornis* (Müller). [Colour figure can be viewed at wileyonlinelibrary.com]

American and Australian species currently included in *Pseudomicrocara*.

Although our knowledge of terrestrial larvae of Scirtidae has greatly improved recently, further research is needed to provide certain identification of larvae and to verify hypotheses on the evolution of a terrestrial mode of life in Scirtidae larvae. Association of New Zealand, Bornean and Chilean larvae with adults may be possible with the aid of DNA barcoding of properly preserved specimens. Future phylogenetic studies should provide more data on the independent evolution of terrestrial larvae in several lineages of Scirtidae. Another interesting question concerns the possibility of finding saproxylic Scirtidae larvae in other geographical areas. Close biogeographical connections between SE Asia, where saproxylic larvae have been recorded, and Africa suggest that the occurrence of terrestrial larvae of Scirtidae is plausible in tropical Africa.

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