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Immature stages of Euchirinae (Coleoptera : Scarabaeoidea): genera *Cheirotonus* and *Propomacrus* with comments on their phylogeny based on larval and adult characters

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Abstract. We report the discovery of the larvae of *Propomacrus bimucronatus* (Pallas, 1781) in their natural habitat; providing notes on their biology based on field observations and laboratory-bred specimens. We give a detailed description of *Cheirotonus formosanus* Ohaus, 1913 and *P. cypriacus* Alexis & Markis, 2002 larvae as well as a redescription of the immature stages of *P. bimucronatus* and present the first diagnosis of larval Euchirinae. Based on 105 morphological and ecological characters of adults and larvae in 24 taxa of Scarabaeoidea, we discuss the phylogenetic relationships of Euchirinae within the group. Our results corroborate Euchirinae monophyly, supported by two larval synapomorphic characters; however, no adult autapomorphic characters were detected. The results of 15 separate phylogenetic analyses (differing in the set of terminalia, characters and in the optimality criteria) indicate a possible sister group relationship between Euchirinae and a clade comprising Melolonthinae + Rutelinae + Dynastinae, with Cetoniinae being a sister group to the whole clade. Larval characters represent a valuable source of information for the systematics of Scarabaeoidea; however, special effort should be paid to improve the still unsatisfactory sampling of immature data.

Additional keywords: larvae, Melolonthinae, morphology, Oriental and Palaearctic region, pupae, Scarabaeidae.

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Introduction

The Euchirinae are considered to be an under-studied, somewhat mysterious group within the family Scarabaeidae with an uncertain subfamiliar status (see Young 1989; Scholz and Grebennikov 2005; Smith *et al.* 2006). The group consists of three genera primarily confined to the highland areas of Asia, the Near East and south-east Europe. In insular and continental Asia, species of *Cheirotonus* Hope, 1841, *Euchirus* Burmeister & Schaum, 1840 and *Propomacrus* Newman, 1837 are distributed approximately between the province of Nanjiang in China in the north and island of Sulawesi in the south. The westernmost extension of the distribution of Euchirinae, represented by two species of the genus *Propomacrus*, reaches to Iran, Syria, Turkey, the Balkan Peninsula and Cyprus. The total number of described species in the subfamily is 16 (Young 1989; Bezděk 2006; Fujioka 2007; Muramoto 2008). The occurrence of Euchirinae is usually associated with densely forested highlands covered with old-growth broadleaved trees, alluvial forests and growths around small streams and rivers, all with an abundance of trees with holes required for the survival of both immature stages and adults. Papers dealing with the immature stages of this group are sparse. Photos of all larval instars, pupae and pupal cases of *Cheirotonus jambar* Kurosawa, 1984 have been published (Mizunuma 1984), but they are not useful for purposes of comparative morphology. Only third instar larva of *Propomacrus bimucronatus* (Pallas, 1781) has been described so far (Lumaret and Tauzin 1992).

A phylogenetic study of Euchirinae has never been conducted, and similarly, their classification on subfamiliar level remains doubtful. Traditionally, the group is considered as being one of several separate subfamilies of pleurostict (or phytophagous) Scarabaeidae on the same level as Melolonthinae, Rutelinae, Dynastinae or Cetoniinae (Young 1989; Scholz and Grebennikov 2005; Bezděk 2006), for example. Lumaret and Tauzin (1992) found Euchirinae to be a subfamily closely related to Melolonthinae (particularly Melolonthini), whereas Iablokoff-Khnzorian (1977) had no doubt about their close relation to Dynastinae, Rutelinae and Cetoniinae. However, recent studies focusing on the phylogeny of the phytophagous scarab lineage have shown that the situation is more complicated. Similarly, Ahrens (2006) and Smith *et al.* (2006) have not found support for Euchirinae being a separate subfamily, discussing its affinities to the Melolonthinae (Smith *et al.* 2006) or to the clade composed of several representatives of Melolonthinae (excluding Sericini, Ablaberini and representatives of fauna primarily confined to southern continents), Rutelinae, Dynastinae and Cetoniinae (Ahrens 2006). On the other hand, Šípek *et al.* (2009) found *Propomacrus* to be a sister group to all other pleurostict scarabs.

The aim of this paper is: (1) to describe or redescribe the little known immature stages of the genera *Cheirotonus* and *Propomacrus*, (2) to report field and laboratory observations of Euchirinae biology and ecology, (3) to provide a diagnosis of Euchirinae based on larval characters, and (4) to hypothesise about the phylogenetic position of Euchirinae.

Materials and methods

The studied larvae were partly obtained from beetle breeders and partly field collected by the authors (for further details see descriptions).

Some of the obtained larvae of both species of *Propomacrus* were reared to adulthood to observe their life cycle, verify the identification and to gain first and second instar larvae. Reared larvae were kept in plastic breeding boxes appropriate for their size, filled with a mixture of *Fagus* leaf litter and large pieces of soft decayed wood (~40% of the container's volume) and crushed decayed wood of deciduous trees of various genera (*Fagus*, *Quercus*). The temperature was maintained between 24 and 26°C in summer months and was lowered gradually to 8−12°C between November and March. Adults were kept in insectaria with a 20 cm layer of organic matter of the same composition as for larvae. Ripe fruits, such as bananas or apples, were provided as food and the insectaria were moistened regularly.

Based on Švácha and Danilevsky (1986), the larvae used for morphological studies were killed by immersion in boiling water for 20 s, subsequently the cuticle was perforated with a slender, sharp pin before fixing in Pampel's fluid. Mouthparts were dissected and, if necessary, mounted on slides in Liquide de Swan. Morphological analyses and measurements were carried out using an Olympus SZX 9 and Olympus BX 40 light microscope both equipped with an Camedia 5060 digital camera (Olympus, Tokyo). Drawings were made on the basis of a photograph or using a camera lucida. Structures examined using the scanning electron microscope (model 6380, JEOL, Tokyo) were cleaned in 10% lactic acid for 24 h and submerged into a Sonorex ultrasonic bath (Bandelin electronics, Berlin) for 30 s, dried in a heating chamber or using critical point drying and mounted on aluminium plates. Drawings were made on the basis of photographs, all pictures were enhanced using Photoshop (Adobe Systems, San Jose, CA), and plates were mounted together using the CorelDRAW program (Corel, Ottawa).

The morphological terminology used in the present study is adopted from Böving (1936), Ritcher (1966), Lawrence (1991) and Šípek *et al*. (2008). Material for the phylogenetic analyses originated from the authors' collections and the collection of the late professor Karel Hůrka. All material is deposited in the Charles University Collection, Prague, Czech Republic.

Morphological datasets and analyses of phylogeny

One hundred and five morphological and ecological characters were selected for analysis; characters 1–54 are of larval morphology, 56–103 are of adult morphology, and the few remaining characters are of larval and adult ecology (characters 55 and 104–105, respectively). In total, 15 heuristic parsimony analyses were performed with PAUP version 4.0b10 (Swofford 2002) using 1000 random taxon additions and tree bisection–reconnection branch swapping; missing data were coded with a question mark (?), inapplicable characters as 'en' dash (–). The data matrix was prepared using Nexus data editor software. Branch support was assessed by bootstrapping 1000 randomly selected trees (Felsenstein 1985). The TreeView and Winclada (Nixon 2002) programs were used to visualise the trees and character state optimisation.

The initial analyses were performed on combined (characters 1–105) and larval (characters 1–55) datasets of 24 terminal taxa, with all characters unordered and under the Fitch criterion (equal weights; Fitch 1971). The subsequent analyses (referred to in the text as analyses 1–12) were performed including only 22 terminal taxa (excluding *Xylotrupes gideon* (Linné, 1767) and *Oryctes nasicornis* (Linné, 1758) from the dataset). Both taxa were excluded due to several common derived characters leading to long branches, suggestive of possible artificial attraction (see 'Discussion'). In analyses 1–12 we analysed three different morphological datasets: larval (characters 1–55), adult (56–105) and combined (characters 1–105), for each dataset four possible combinations of ordering and successive weighting (Farris 1969) parameters were used (Table 1). In these analyses, characters 7, 11, 15, 21, 23, 24, 31, 34, 35, 36, 37, 41, 43, 46, 64, 78, 82, 87, 95 and 102 were analysed as being either ordered (analyses 3, 4, 7, 8, 11 and 12) or unordered (analyses 1, 2, 4, 5, 9 and 10), and all others were treated as unordered. Finally, a 50% majority rules consensus tree was obtained from each of the 12 analyses. The results of analyses 1–12 and the 50% majority rules analyses are summarised in Table 1 (see below). Partitioned Bremer support (PBS) (Bremer 1994) was calculated for all internal branches using Nona (Goloboff 1994).

Relative support value and relative resolution value

Relative support value (RSV) and relative resolution value (RRV) recently introduced by Grebennikov and Newton (2009) were used to evaluate the strength of the support for each of the 10 clades highlighted in Table 1 and to measure how each of the 12 analyses contributes to resolving the clades. The values were calculated as a ratio of the obtained support values (SV) for clades and resolution values (RV) for analyses of their possible maxima (see below), respectively. Support values and RV were calculated as the sum of horizontal (SV) and vertical (RV) individual cell scores varying from 0 (clade unsupported, i.e. absent on the strict consensus tree and bootstrap <50%; white cells in Table 1) to 1 (clade moderately supported, i.e. present on the strict consensus tree and bootstrap <50% or absent on strict consensus tree, but bootstrap equal or >50%; grey cells in Table 1) to 2 (clade strongly supported, i.e. present on strict consensus tree and bootstrap equal or >50%; black cells in Table 1). Maximum possible values for SV and RV (Table 1) for 12 analyses focusing on 10 clades, were 24 and 20, respectively. A maximum possible RSV of 100%, as observed in Euchirinae (Table 1), indicates that this clade was strongly supported by all 12 analyses, while the lowest RSV of 25%, as observed in the clade of Melolonthinae, indicates that it was recovered only a few times. The maximum possible RRV of 95%, as observed in analyses 10 and 12, indicates that these

Table 1. Results of analyses 1–12 performed with different datasets and analytical strategies

Results of 12 phylogenetic analyses of the Scarabaeidae phylogeny (columns 1–12) and the results of a 50% majority rules analysis of strict consensus trees obtained in analyses 1–12 (last column: '50% maj. rule'); 'dataset' row indicates three datasets used in analyses 1–12 (larvae, adults and their combination; characters 1–55, 56–105 and 1–105, respectively); 'ordered/unordered' row indicates whether some multistate characters (7, 11, 15, 21, 23, 24, 31, 34, 35, 36, 37, 41, 43, 46, 64, 78, 82, 87, 95 and 102) were ordered. 'Successive weighting' row indicates whether successive approximation was used for character weighing. The next three rows indicate tree length, consistency (ci) and retention (ri) indexes, and the number of the shortest (= most parsimonious) trees obtained; Euch, Euchirinae; Dyn, Dynastinae; Rut, Rutelinae; Mel, Melolonthinae (Melolonthini+Rhizotrogini); Ser, Sericini; Cet, (Cetoniinae inclusive *Valgus*); Cet(–), Cetoniinae without *Valgus*. Cell values: clade presence (+) or absence (–) on strict consensus tree followed by bootstrap value, if applicable. Cell colour: black (branch highly supported: present on the strict consensus tree and bootstrap value 60% and higher); grey (branch moderately supported: present on the strict consensus tree and bootstrap value less than 50%); white (branch not supported: absent on the strict consensus tree and bootstrap less than 50%). Column SV/RSV (support value/relative support value) is designed to demonstrate how strongly a given clade was supported throughout all 12 analyses; SV value is the sum of horizontal cell scores (0 for white cells, 1 for grey cells, 2 for black cells) with a maximum of 24 for clades fully supported in all 12 analyses; RSV value is the ratio of actual SV to its maximum of 24; expressed in %. RV/RRV (resolution value/relative resolution value) is designed to demonstrate how effective each of the 12 analyses was to resolve phylogeny of Scarabaeidae; RV value is the sum of vertical cell scores (0 for white cells, 1 for grey cells, 2 for black cells) with a maximum of 20 for an analysis giving fully resolved and strongly supported Cetoniinae and all its selected internal branches; RRV value is the ratio of actual RV to its maximum value of 20; expressed in %. Alternative groupings recovered in the analyses are highlighted in italics. (Table after Grebennikov and Newton 2009, reproduced with permission)

Analysis ###	SV/RSV	1	2	3	4	5	6	7	8	9	10	11	12	50% maj. rule
Dataset		larvae	larvae	larvae	larvae	adults	adults	adults	adults	comb.	comb.	comb.	comb.	Contree 1–12
Ordered/unordered		unord.	unord.	order.	order.	unord.	unord.	order.	order.	unord.	unord.	order.	order.	
Successive weighting		no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	
Tree length		160	85,5	167	85,5	149	73,7	151	73,7	320	158	329	159,5	
CI/RI		51/69	62/78	48/70	60/77	45/57	55/67	44/57	55/67	46/62	58/72	45/62	57/72	
# of shortest trees		12	6	4	4	17	6	17	6	3	1	9	2	
Euchirinae	24/100%	+/99	+/99	+/98	+/99	+/83	+/83	+/83	+/85	+/100	+/100	+/100	+/100	+
Euch+(Dyn+Rut+Mel+Ser)	16/67%	+/76	+/85	+/71	+/82	–/na	–/na	–/na	–/na	+/68	+/83	+/60	+/79	+
Cet+(Euch+(Dyn + Rut+Mel+Ser))	14/58%	–/na	+/77	+/57	+/79	–/na	–/na	–/na	–/na	+/57	+/76	+/61	+/82	+
Rut	22/92%	+/69	+/76	+/81	+/87	+/<50	+/55	+/<50	+/57	+/72	+/81	+/81	+/90	+
Mel	6/25%	–/na	–/na	–/na	–/na	–/na	–/na	–/na	–/na	+/<50	+/56	+/<50	+/58	–
Ser	22/92%	+/71	+/76	+/77	+/84	+/<50	+/70	+/<50	+/72	+/82	+/93	+/84	+/94	+
Dyn+Rut	13/54%	+/60	+/85	+/74	+/91	–/na	–/na	–/na	–/na	–/na	+/73	+/ <50	+/85	–
(Rut+Dyn)+Mel	10/38%	+/<50	+/51	+/<50	+/57	–/na	–/na	–/na	–/na	–/na	+/<50	+/ <50	+/ <50	–
((Rut+Dyn)+Mel)+Ser	13/54%	+/<50	+/83	+/72	+/90	–/na	–/na	–/na	–/na	–/na	+/80	+/58	+/85	–
Cet	21/88%	–/na	+/50	+/<50	+/67	+/71	+/90	+/71	+/90	+/81	+/96	+/85	+/97	+
RV/RRV		12/60%	18/90%	16/80%	18/90%	6/30%	8/40%	6/30%	8/40%	13/65%	19/95%	17/85%	19/95%	
Alternative groupings recovered in the analyses														
Dyn+(Rut+(Ser+Mel))	*2/8%*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*+/53*	*–/na*	*–/na*	*–/na*	–
Euch+Rut+Mel+Ser	*2/8%*	*–/na*	*–/na*	*–/na*	*–/na*	*+/<50*	*–/na*	*+/<50*	*–/na*	*–/na*	*–/na*	*–/na*	*-/na*	–
Euch+(Rut+Mel+Ser)	*2/8%*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*+/<50*	*–/na*	*+/<50*	*–/na*	*–/na*	*–/na*	*–/na*	–
Cet+Dyn+(Euch+Rut +Mel+Ser)	*2/8%*	*–/na*	*–/na*	*–/na*	*–/na*	*+/<50*	*–/na*	*+/<50*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	–
(Cet+Dyn)+(Euch+ Rut+Mel+Ser)	*2/8%*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*+/<50*	*–/na*	*+/<50*	*–/na*	*–/na*	*–/na*	*–/na*	–
Rut+Ser+Mel	*3/12,5%*	*–/na*	*–/na*	*–/na*	*–/na*	*–/na*	*+/<50*	*–/na*	*+/<50*	*+/<50*	*–/na*	*–/na*	*–/na*	–
Cet(–)	*8/33%*	*+/55*	*+/81*	*+/60*	*+/58*	*–/na*	*–/na*	*–/na*	*–na*	*–/na*	*–/na*	*–/na*	*–/na*	–

analyses were capable of resolving all 10 clades and each clade was strongly supported, while the lowest observed RRV of 30%, as recorded for analyses 5 and 7 (Table 1), indicates that they were only partly consistent with the most supported and fully resolved topology (Fig. 7). For more details on RSV and RRV see Grebennikov and Newton (2009) and Šípek *et al.* (2009).

To give a complete and unbiased view, we also included alternative groupings recovered in analyses 1–12 in Table 1 (cells in *italics*). For these alternative groupings only RSV was calculated and the values were not used for the calculation of the RRV of each of the 12 analyses.

Results

Morphology

Subfamily **EUCHIRINAE** Hope, 1840

(Figs 1*G*, 2–6)

Diagnosis of Euchirinae based on larval characters

Larvae C-shaped, grub-like, large. Cranium brownish-yellow to brown, with numerous setae. Stemmata absent. Labrum

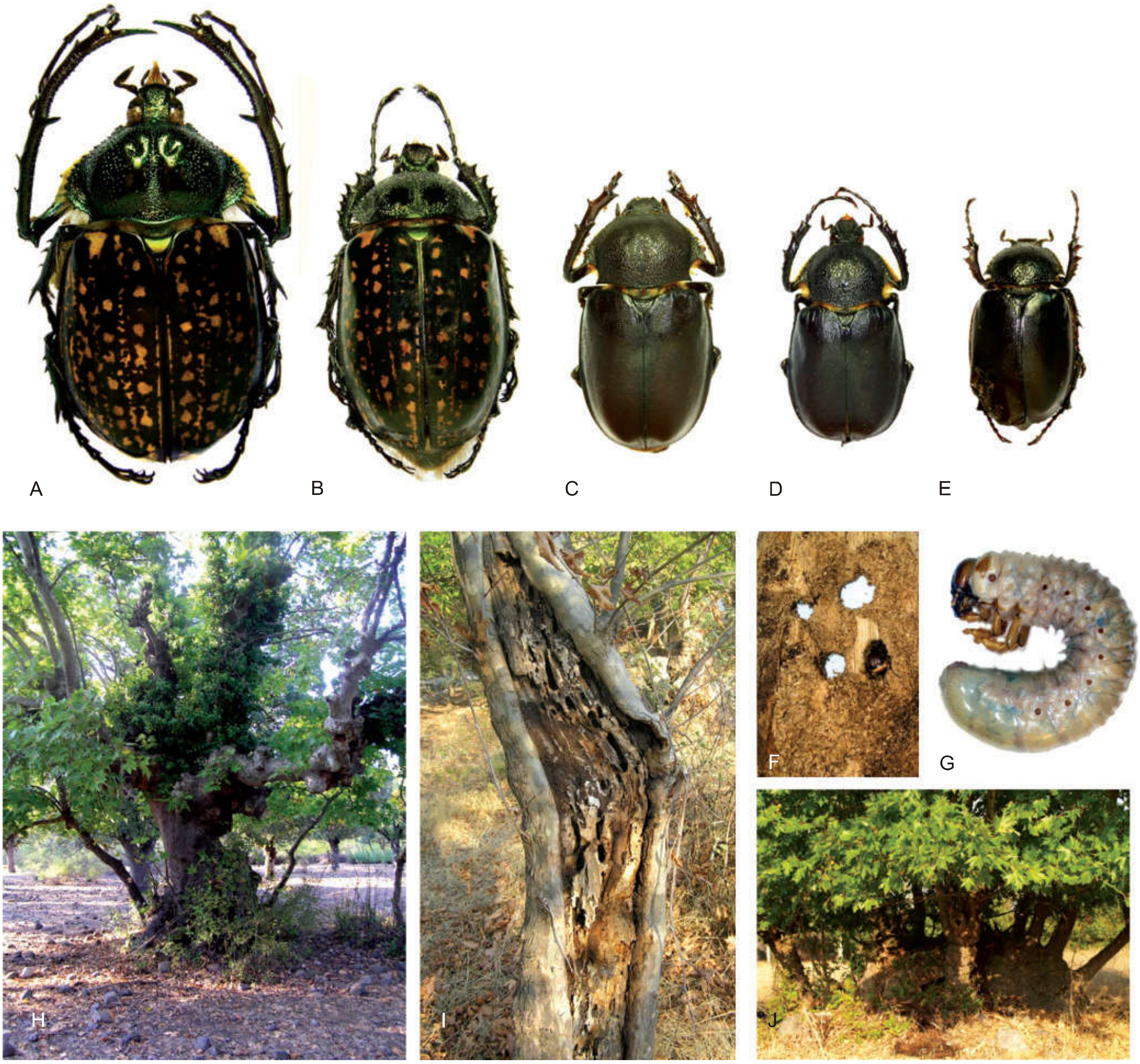


Fig. 1. Adult and larval Euchirinae (*A*–*E*, *G*), habitat (*H*–*J*) and frass (*F*) of *Propomacrus bimucronatus*. *Cheirotonus gestroi* Pouillaude, 1913 (a close relative species to *C. formosanus*): (*A*) male, 85 mm; (*B*) female, 63 mm. *Propomacrus bimucronatus* (*C*) medium-sized male (41 mm) and (*D*) small male (30 mm). (*E*) *Propomacrus cypriacus* (male, 35 mm). (*F*) Rotten piece of *Quercus* spp. wood with holes and frass of *P. bimucronatus* larvae with a freshly emerged adult (laboratory reared). (*G*) Fully grown last instar larva of *C. formosanus*. Natural habitat of *P. bimucronatus* in western Turkey, larvae were found (*H*, *J*) in old, as well as (*I*) in slender rotten trunks of *Platanus orientalis*.

semi-oval, anterior margin trilobed. Groups of anterior and exterior epicranial setae fused, forming a row. Acanthoparia with minute setae in basal two thirds and with long setae in the apical third. Plegmata and proplegmata present, haptomeral region without epizygum, heli or haptomeral process, clithra either present or absent. Sense cone low, with four pores. Sclerotised plate absent, crepis reduced. Scissorial area of mandibles with two teeth. Stridulatory area of mandibles without transverse ridges, only with fine microsculpture. Maxillar stridulatory teeth conical surrounded by large membranous basal area. Galea and lacinia fused basally, apical part separate, fitting tightly together. Pronotum with lateral sclerite. Claws equal in all pairs, cylindrical, with two apical setae and a small pointed tip. Abdominal segments IX and X separated; anal slit Y-shaped; palida absent; tergites with numerous spiny setae. Diagnostic characters of genera *Cheirotonus* and *Propomacrus* are listed in Table 2.

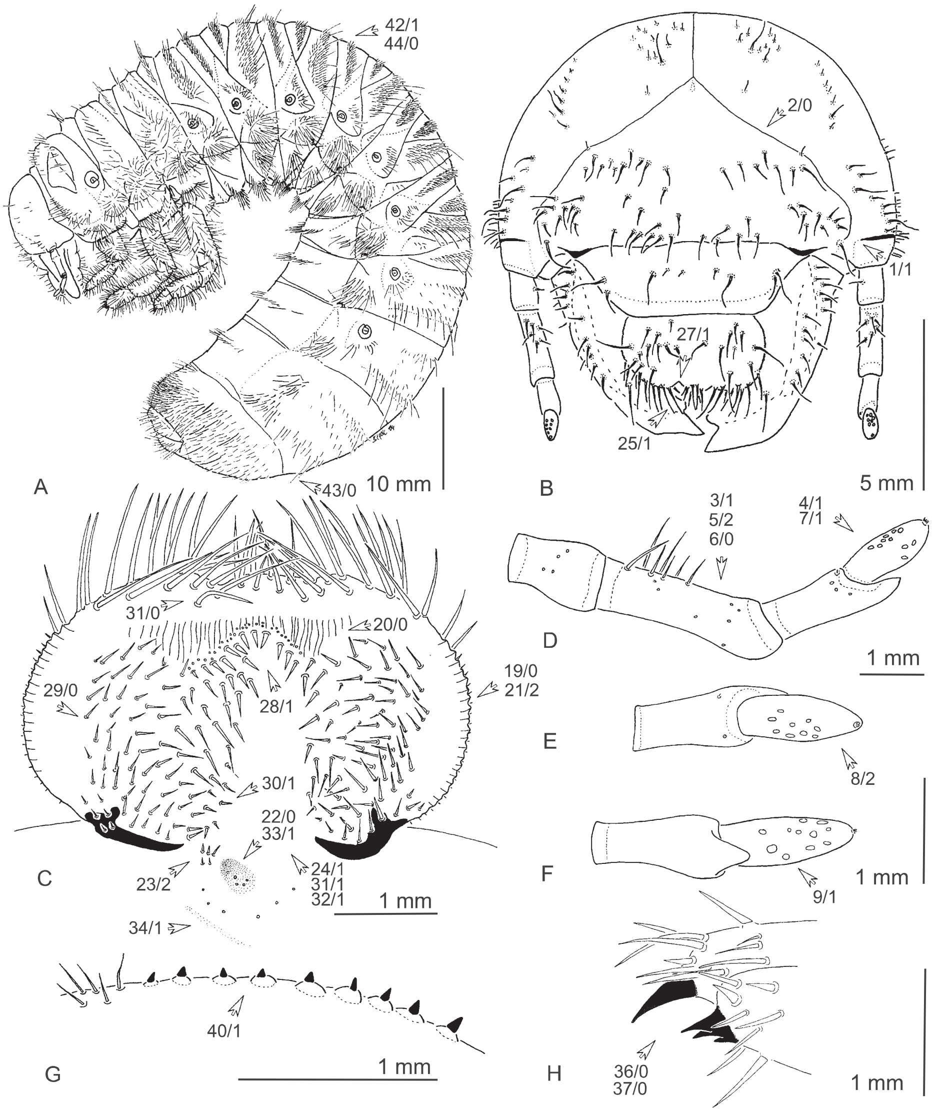


Fig. 2. *Cheirotonus formosanus*, third instar larva. (*A*) Habitus of fully grown larva; (*B*) cranium (*C*) epipharynx; (*D*) antenna, lateral view; (*E*, *F*) penultimate and ultimate joint of left antenna, (*E*) dorsal and (*F*) ventral aspect; (*G*) maxilla, stridulation area, dorsolateral aspect; (*H*) right maxilla, unci of galea and lacinia, dorsolateral aspect.

Descriptions of immature stages

Genus ***Cheirotonus*** Hope, 1841

Cheirotonus formosanus Ohaus, 1913

Material examined

Five third instar larvae were obtained from beetle breeder František Bačovský (Brno, Czech Republic). The larvae were reared from eggs laid by determined adults collected by Lin Kuang-Fang in Taiwan, NP Yangmingshan env., during May and June 2005 (F. Bačovský, pers. comm.). Another four third instar larvae and two second instar larvae were obtained in January 2002 from beetle breeder Roman Kocina (Praha, Czech Republic). Larvae were reared from eggs laid by determined adults, collected in July 2001 by a local collector, Tao-Yuan, in Taiwan (Paliang) (R. Kocina, pers. comm.).

Third instar larva (Figs 1*G*, 2, 3, 5*A*–*E*)

Body (Figs 1*G*, 2*A*). Length of full-grown larvae 120–155 mm.

Head capsule (Fig. 2*B*). Maximal width 10.35–11.80 mm. Cranium with irregular texture, anterior part of frons pitted. Epicranium, posterior part of frons, preclypeus and anterior part of labrum brownish-yellow to brown. Antennifer, anterior parts of frons, postclypeus, posterior part of labrum, mandibles and precoilae dark brown or black. Chaetotaxy of head capsule summarised in Table 3. Frontal sutures lyriform, posterior frontal

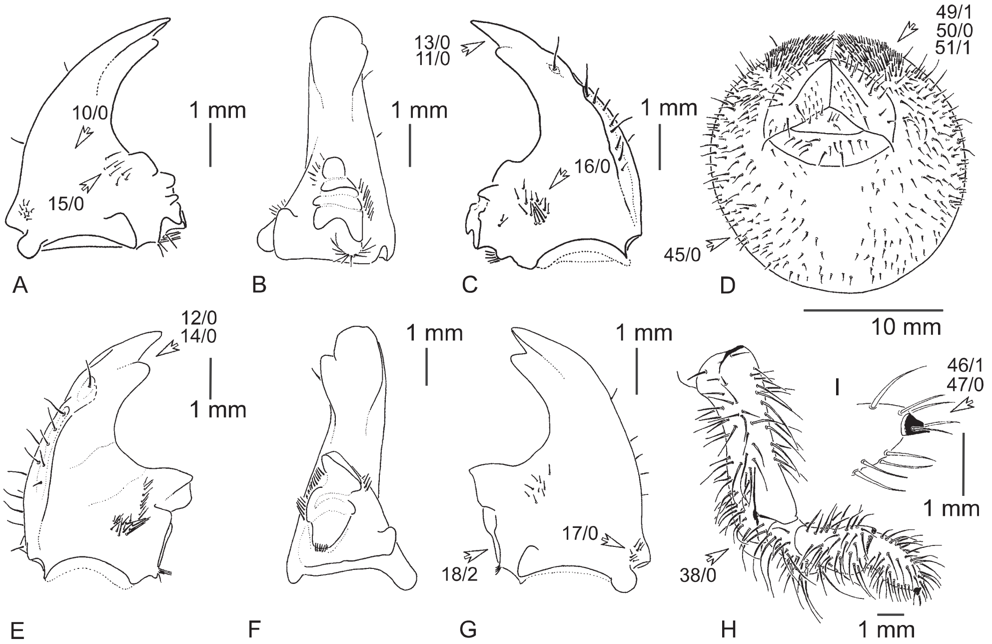


Fig. 3. *Cheirotonus formosanus*, third instar larva. Right mandible, (*A*) ventral, (*B*) medial and (*C*) dorsal aspect; left mandible, (*E*) dorsal, (*F*) medial and (*G*) ventral aspect; (*H*) metathoracal leg; (*I*) claw of metathoracal leg; (*D*) last abdominal segment, anal slit and raster.

angle with a straight shallow depression. Clypeus trapezoidal, preclypeus weakly sclerotised. Antenna (Fig. 2*D–F*) with four antennomeres (AN I–IV). Length of antennomeres: AN II > AN III > AN IV ≥ AN I. Antennomere III with ventral and apical protruding portion bearing one to three sensoric spots (Fig. 2*D*). Ultimate antennomere (AN IV; Fig. 2*E, F*) with 6–10 dorsal, 8–14 ventral sensoric spots and one apical field with minute sensilla.

Lateral margins serrated with minute setae (Fig. 2*C*). Clithra present in six out of eight specimens studied.

Epipharynx (Fig. 2*C*). Corypha distinct. Zygum transverse, faintly sclerotised with 30–35 pore-like sensilla, an arcuate irregular row of 13–14 spine-like setae and eight spine-like setae beneath the row. Proplegmatium with15–20 proplegmata on each side. Acanthoparia with 21–26 setae and 17–26 plegmata. Posterior setae of acanthoparia minute or almost indistinct, increasing in size anteriorly, last two to six setae very long. Gymnoparia present (Fig. 2*C*). Chaetoparia consisting of 75–93 hair-like setae on each side. Dexiotorma long, narrow. Laeotorma long and narrow, medial end curved anteriorly towards pedium. Pternotormae absent. Haptolachus: sense cone faintly sclerotised with four sensilla in basomedian area. Crepis reduced to two faintly sclerotised oblique sclerites. Distad to crepis two oblique groups of three pore-like sensilla. Mandibles (Fig. 3*A–C*, *E–G*) asymmetrical. Scissorial area nearly symmetrical, scoop-like in medial aspect (Fig. 3*B, F*), with two scissorial teeth distad to a single anterior mandibular seta. Scrobis with 6–14 setae, dorsal groove deep with five to eight setae. Stridulation area (Figs 3*A*, *G*, 6*E*) indistinct, with numerous microridges and tubercles on a broad pale brown field. Dorsomolar area with 15–30 setae. Seven to eight ventromolar setae present in two rows or irregularly scattered. Molar area of right mandible (Fig. 3*A–C*). Distal molar lobe with two low transverse sub-lobes. Proximal molar lobe with a single sub-lobe and calyx. Calyx bilobed in medial aspect. Brustia with 5–10 setae. Basolateral region of ventral face with 6–12 setae. Left mandible (Fig. 3*E–G*). Distal molar lobe transverse. Proximal molar lobe with two sub-lobes and calyx. Calyx flattened, sub-triangular. Acia absent, brustia with five to six setae. Basolateral region of ventral face with 12–15 setae.

Maxilla (Figs 2*G*, 2*H*, 6*B*, 6*C*). Cardo dorsal with 42–50 setae, labacoparia membranous with 45–63 setae on dorsal face. Stipes dorsal with 29–37 setae. Maxillary stridulatory area (Figs 2*G*, 6*C*) with 7–11 stridulatory teeth. Stridulatory teeth subequal in size, conical, well sclerotised, with a membranous basal area. Blunt tubercle absent. Galea and lacinia as in Figs 2*H* and 6*B*, galeo-lacinial sulcus well distinct. Galea with a falcate uncus (Fig. 2*H*) and 19–26 setae, apical setae stout. Lacinia with 50 to 61 setae and three unci fused at base, decreasing in size posteriad (Fig. 2*H*). Maxillar palpus four jointed, first palpomera with one or two, second with four to eight and third palpomera with two to three setae.

Labium and hypopharynx (Fig. 6*A*). Hypopharyngeal sclerome asymmetric, with large truncate process, lateral lobes of hypopharynx less sclerotised, with numerous setae. Tufts of tegumentary expansions (= phoba *sensu* Böving 1936) absent. Ligula with 49–61 setae on each side. Anterior margin of ligula with four very long setae. Dorsal face of ligula with 13–24 campaniform sensilla organised in a transverse row, 6–11 pores scattered proximad to the anterior margin and a medial pit-like structure. Labial palpi two jointed.

Thorax (Figs 1*G*, 2*A*). Size of legs (Figs 2*A*, 3*H*) increasing posteriorly. Claw (pretarsus) as in Fig. 3*I*. Thoracic spiracle

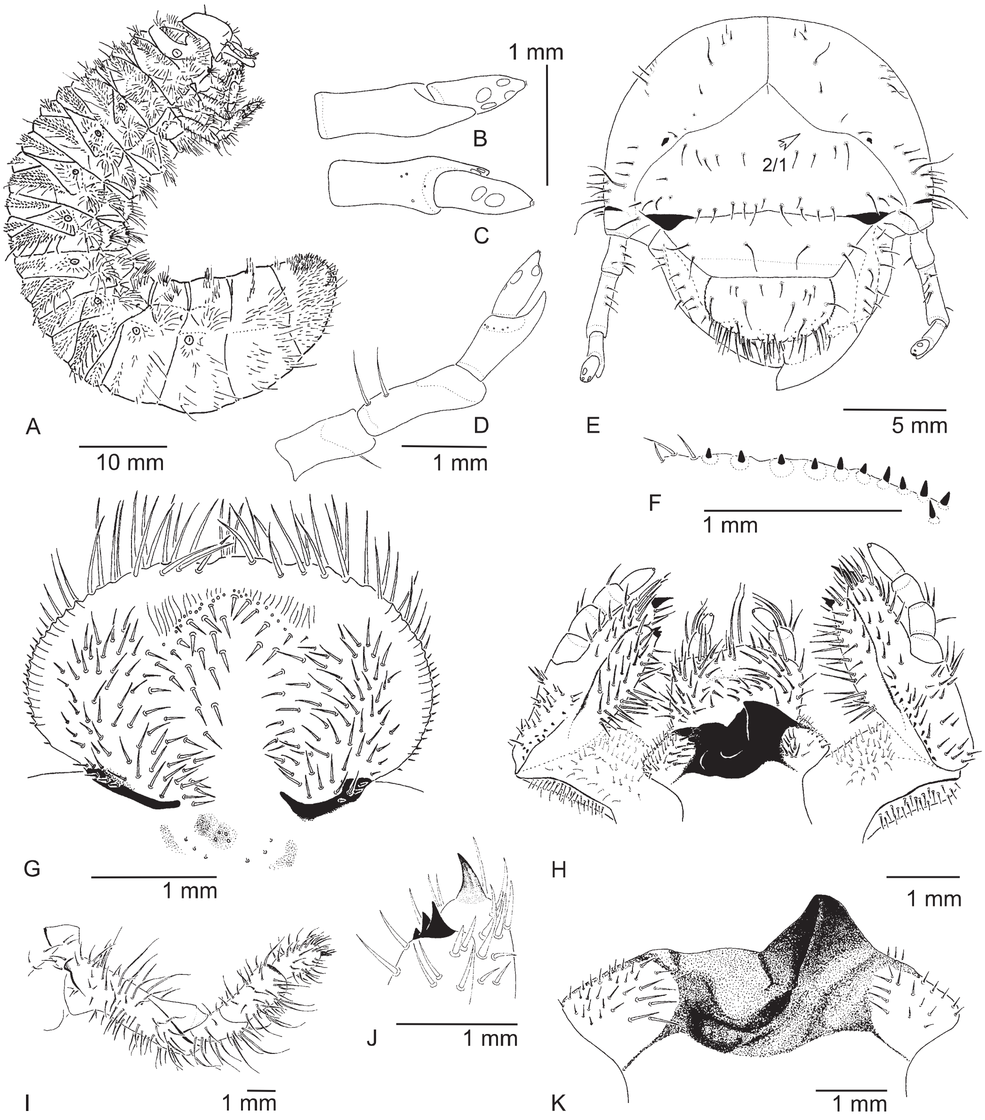


Fig. 4. *Propomacrus bimucronatus*, third instar larva. (*A*) Habitus of fully grown larva; penultimate and ultimate joint of right antenna, (*B*) ventral and (*C*) dorsal aspect; (*D*) right antenna, lateral view; (*E*) cranium, (*F*) maxilla, stridulation area, dorsolateral aspect; (*G*) epipharynx; (*H*) labio–maxillar complex, dorsal aspect; (*I*) metathoracal leg; (*J*) right maxilla, unci of galea and lacinia, dorsolateral aspect; (*K*) hypopharyngeal sclerome.

(Fig. 6*D*) 1.625–1.75 mm × 1.2–1.275 mm in diameter; larger than abdominal spiracles, respiratory plate C-shaped with concealed arms and 50–60 holes across diameter. Dorsa of each sub-lobe of thoracic segments with three to six rows of short setae, last rows with a few medium long setae (Fig. 2*A*).

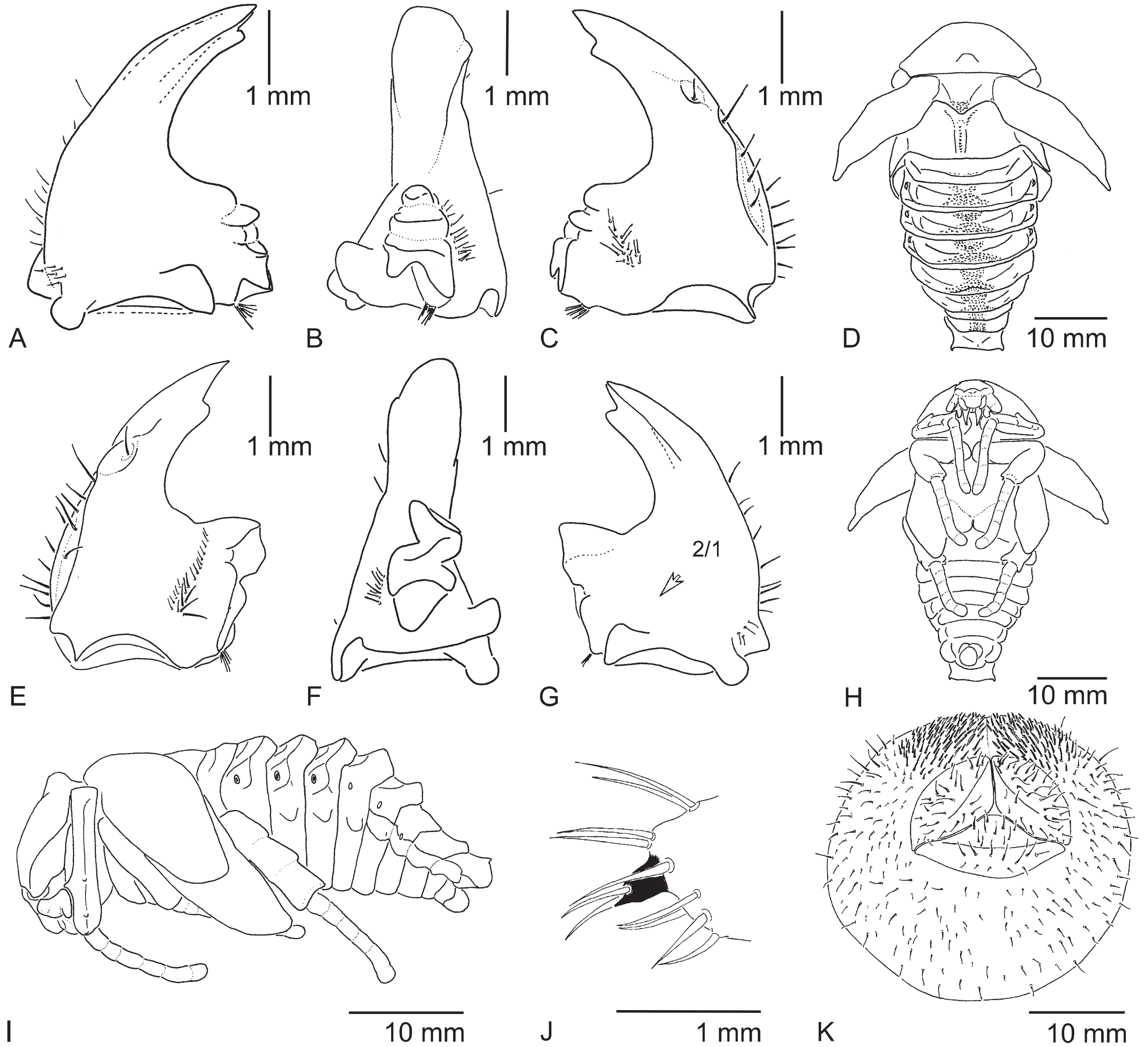
Abdomen (Figs 1*G*, 2*A*, 3*D*). Ten-segmented. Abdominal spiracles similar to thoracic; abdominal spiracles I–V elliptical, spiracles VI–VIII almost circular. Size of spiracles gradually decreasing, spiracle V–VI smallest, abdominal spiracles VII–VIII larger than previous, spiracle VIII about the size of the first abdominal spiracle. Dorsal chaetotaxy of abdominal segments I–VI similar to chaetotaxy of thorax (Fig. 2*A*). Segments VII–IX with a few setae, forming isolated patches or rows, the entire dorsum of last segment with numerous setae. Raster (Fig. 3*D*): palida absent, tegites with dense, spiny medioposteriad oriented setae, separated by a narrow septula. Anal slit Y-shaped, the ventral stem of anal slit slightly shorter than the arms. Lower anal lip transversally divided into two parts, each part with 35–51 setae. Dorsal anal lobe with 23–32 setae. Dorsal anal lobe divided by a longitudinal sulcus.

Second instar larva

The second instar larva of *C. formosanus* is similar to the third instar larvae except for the following features.

Body. Length of studied larvae 61 mm, maximal width of head capsule 6.7–6.85 mm.

Head capsule. Cranium brown to dark brown, anterior parts of frons pitted. First antennomere shorter than the ultimate. Ultimate antennomere with 11–16 ventral, 7–9 dorsal sensoric



Figs 5. *Propomacrus bimucronatus*, (*A–C*, *E–F*, *J*, *K*) third instar larva and (*D*, *H*, *I*) male pupa. (*A–C*) Right mandible, (*A*) ventral, (*B*) medial and (*C*) dorsal aspect; (*D*) male pupa, dorsal aspect; left mandible, (*E*) dorsal, (*F*) medial and (*G*) ventral aspect; male pupa, (*H*) ventral and (*I*) lateral aspect; (*J*) claw of metathoracal leg; (*K*) last abdominal segment, anal slit and raster.

spots and one apical sensoric field. Clithra present. Chaetoparia with 108–112 hair-like setae on each side. Chaetotaxy of cranium in Table 3.

Genus ***Propomacrus*** Newmann, 1837

Propomacrus bimucronatus (Pallas, 1781)

Material examined

Twenty-five mature third instar larvae, 15 second instar and 30 first instar larvae collected by the authors in north-west Turkey, Çanakkale province, Ayvaçik env. 24.–29.ix.2006, all larvae were found in hollows of *Platanus orientalis* trees of various ages. Part of the collected material was reared to adulthood. One mature third instar larva, one pupa, two second stage larvae collected in Bulgaria, m. occ. Lebnica, Ograzhden Mts, vi.1988 Jiří Mička legit., in hollows of *P. orientalis*. Ten last instar larvae and four second instar larvae were obtained in the years 2004 and 2005 from beetle breeder Oldřich Jahn (Sušice, Czech Republic), five larvae were reared to the adult stage to observe their life cycle. The origins of the parental generations are presumed to be Turkey or Syria, but no further data are available (O. Jahn, pers. comm.).

Third instar larva (Figs 4, 5, 6*F–J*)

Body. Length of fully grown third instar larvae 71–95 mm (Fig. 4*A*).

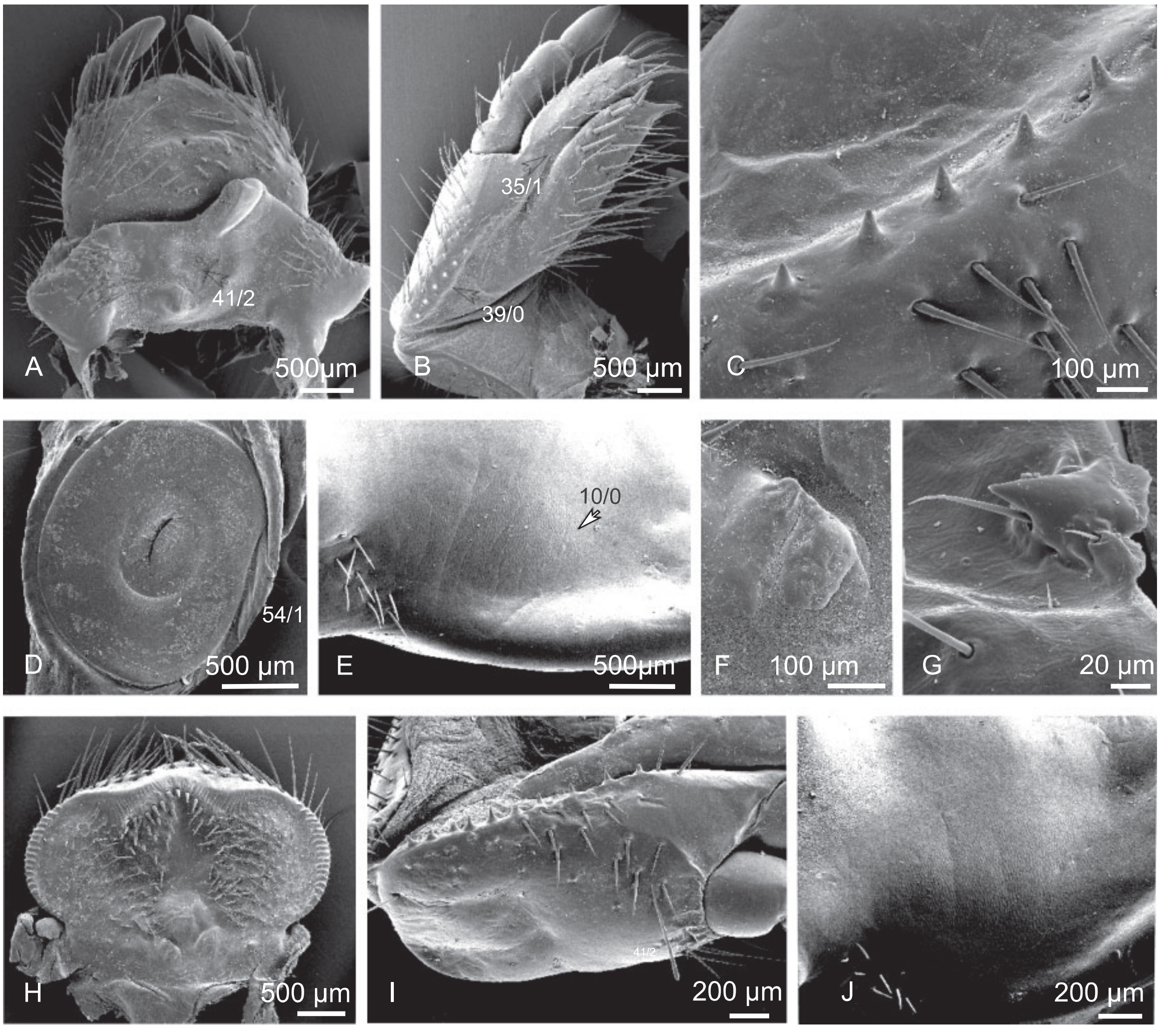


Fig. 6. *Cheirotonus formosanus*, (*A–E*) third instar larva, *Propomacrus bimucronatus*, (*F*, *H–J*) third instar larva, *P. bimucronatus*, (*G*) first instar larva. *Cheirotonus formosanus*, third instar larva: (*A*) labium and hypopharynx, dorsal aspect; (*B*) left maxilla, dorsal aspect; (*C*) maxilla, detail of stridulation teeth; (*D*) thoracic spiraculum; (*E*) right mandible, ventral aspect, detail of stridulation area with microridges. *Propomacrus bimucronatus*, third instar larva (*F–J*, except *G*): (*F*) sense cone of epipharynx; (*G*) metathoracal egg burster (first instar larva); (*H*) epipharynx; (*I*) right maxilla, stridulation teeth, laterodorsal aspect; (*J*) left mandible, ventral aspect, detail of stridulation area.

Head capsule (Fig. 4*E*). Maximal width 8.0–9.1 mm. Cranium yellowish brown, with fine irregular texture, anterior part of frons sparsely pitted. Antennifer, anterior parts of frons, postclypeus and posterior part of labrum brown. Mandibles dark brown to black. Chaetotaxy of head capsule summarised in Table 3. Frontal sutures bisinuated, posterior frontal angle with shallow depression. Clypeus trapezoidal (Fig. 4*E*). Lateral margins of labrum serrate with minute setae (Fig. 4*G*). Antenna (Fig. 4*B–D*) with four antennomeres (AN I–IV); length of antennomeres: AN II > AN III > AN I ≥ AN IV. Antennomere III with ventral and apical protruding portion bearing one or two sensoric spots. Ultimate antennomere (AN IV; (Fig. 4*B*, *C*) with one or two (three) dorsal and three to four (five) ventral sensoric spots and one apical sensoric field with minute sensilla.

Epipharynx (Figs 4*G*, 6*F*, *H*). Corypha distinct. Clithra absent, present as two faintly sclerotised spots or prolonged and fused posteriorly. Zygum transverse, faintly sclerotised, with 21–27 pore-like sensilla, an arcuate row of 9–13 stout, spine-like setae and 10–13 spine-like setae beneath the row (Fig. 6*H*). Proplegmatium with 15–21 proplegnata. Plegmatiun with 14–22 plegmata. Acanthoparia with 14–22 setae, posterior setae of acanthoparia minute, increasing in size anteriorly. Chaetoparia with 55–68 setae on each side. Dexiotorma long, narrow, right pternotorma only indicated or absent. Laeotorma long narrow, medial end curved towards pedium, left pternotorma absent. Sense cone (Fig. 6*F*) faintly sclerotised, low and obtuse. Crepis reduced to two faintly sclerotised sclerites. Distad to crepis two groups of three pore-like sensilla.

Table 2. Diagnostic characters of the genera *Cheirotonus* and *Propomacrus*

Character	*Cheirotonus*	*Propomacrus*
Last instar cranium width (mm)	10.4–11.8	8.0–9.0
Last instar body length (mm)	120–150	71–95
Frons	Almost entire frons dark brown to black, densely pitted	Only anterior half dark brown, punctuation of frons less dense
Number of dorsal sensoric spots of antenna (Figs 2*E*, 4*C*)	6–10	1–2 (rarely 3)
Number of ventral sensoric spots of antenna (Figs 2*F*, 4*B*)	8–14	3–4 (rarely 5)
Number of ventromolar setae (Figs 3*A*, *G*, 5*A*, *G*)	7–8	absent

Mandibles (Fig. 5*A–C*, *E–G*). Generally asymmetrical. Scissorial area almost symmetric, broad, scoop-like in medial aspect, with two teeth distad to a single anterior mandibular seta, scissoral notch absent. Scrobis with four to eight setae, dorsal groove deep, with five to six setae. Stridulation area indistinct, with numerous microridges (Fig. 6*J*). Ventromolar setae absent (Fig. 5*A*, *G*), 11–24 dorsomolar setae organised in row widened posteriorly. Molar area of right mandible (Fig. 5*A–C*): distal molar lobe with two distinct transverse sub-lobes. Proximal molar lobe with a single sub-lobe and calyx. Calyx in medial aspect bilobed into two subtriangular lobes. Brustia with 9–12 setae. Basolateral region of ventral face with six to nine setae. Left mandible (Fig. 5*E–G*): distal molar lobe transverse; proximal molar lobe with two more or less distinct sub-lobes and calyx. Calyx flattened, sub-triangular. Acia absent. Brustia with six to nine setae. Basolateral region of ventral face with 5–13 setae.

Table 3. Chaetotaxy of head capsule of *Cheirotonus formosanus*, *Propomacrus bimucronatus* and *P. cypriacus*

AAS, anterior frontal angle setae; ACS, anterior clypeal setae; AES + EES, anterior epicranial and exterior epicranial setae; AFS, anterior frontal setae; AN I, setae of antennomera I; AN II, setae of antennomera II; DES, dorsoepicranial setae; ECS, exterior clypeal setae; EFS, exterior frontal setae; ELS, exterior labral setae; LLS, setae of lateral labral lobe; MLS, setae of medial labral lobe; PES, posterior epicranial setae; PFS, posterior frontal setae; PLS, posterior labral setae; PMS, paramedial labral setae; numbers in brackets indicate a rarely occurring stage

	Epicranium			Frons				Clypeus				Labrum			Antenna	
Setae	DES	PES	AES + EES	PFS	EFS	AFS	AAS	ACS	ECS	PLS	PMS	ELS	LLS	MLS	AN I	AN II
Third instar								*Cheirotonus formosanus*								
Long setae	0–2	(1)	0–2	0–4	0–6	0–2	1	1	2–3	–	1	2–4	18–20	10–11	–	–
Medium setae	2–5	1–4	28–49	3–10	3–9	5–9	–	–	–	3–4	1–3	0–3	–	–	0–3	6–9
Minute setae	5–14	5–14	0–9	0–5	–	2–9	–	(1–2)	–	0–2	0–2	–	–	–	–	–
Second instar																
Long setae	–	0–1	3–4	2–3	2–3	6	1	1	2–3	–	1	2	16–17	10	–	–
Medium setae	1–2	1	22–25	4–6	5	0–2	–	–	–	2–3	2–4	2	–	–	–	3–7
Minute setae	1	6–8	8–9	0–2	0–2	–	–	–	–	–	0–1	–	–	–	0–3	–
Third instar								*Propomacrus bimuconatus*								
Long setae	1–2	0(1)	1–7	0–2	0–1	1	1	1	2	–	1	2	15–17	9–10	–	0–2
Medium setae	4–6	1–3	26–35	3–7	2–6	3–6	–	–	–	2–4	1–4	0–1	–	–	2–5	1–5
Minute setae	0–7	3–8	3–10	0(2)	0	0	–	–	–	1–2	–	(1)	–	–	0–3	0–1
Second instar																
Long setae	1–2	–	3–4	1–2	1	0–2	1	1	2	–	1	2	15–18	10	–	–
Medium setae	2–5	1–3	15–18	1–3	1–4	2–4	–	–	–	1–4	1–4	0–1	–	–	1–3(0)	2–3
Minute setae	2	3–5	6–10	0–2	0–2	3	–	–	–	–	–	(1)	–	–	0–5	0–3
First instar																
Long setae	1	0–2	3–5	1–3	0–1	1–2	1	1	2	–	1	2	15–18	9–10	–	–
Medium setae	1–3	1–3	16–24	1–2	1–2	2–5	–	–	–	0–4	2–4	0–1	–	–	–	2
Minute setae	3–7	2–4	3–10	0–2	0–2	0–3	–	–	–	–	–	–	–	–	–	–
Third instar								*P. cypriacus*								
Long setae	1–2	0(1)	1–7	0–2	0–1	1	1	1	2	–	1	2	15–17	9–10	–	0–2
Medium setae	4–6	1–3	26–35	3–7	2–6	3–6	–	–	–	2–4	1–4	0–1	–	–	2–5	1–5
Minute setae	0–7	3–8	3–10	0(2)	0	0	–	–	–	1–2	–	(1)	–	–	0–3	0–1
Second instar																
Long setae	1–2	–	3–4	1–2	1	0–2	1	1	2	–	1	2	15–18	10	–	–
Medium setae	2–5	1–3	15–18	1–3	1–4	2–4	–	–	–	1–4	1–4	0–1	–	–	1–3(0)	2–3
Minute setae	2	3–5	6–10	0–2	0–2	3	–	–	–	–	–	(1)	–	–	0–5	0–3
First instar																
Long setae	1	0–2	3–5	1–3	0–1	1–2	1	1	2	–	1	2	15–18	9–10	–	–
Medium setae	1–3	1–3	16–24	1–2	1–2	2–5	–	–	–	0–4	2–4	0–1	–	–	–	2
Minute setae	3–7	2–4	3–10	0–2	0–2	0–3	–	–	–	–	–	–	–	–	–	–

Maxilla (Figs 4*F, H*, 6*I*). Cardo dorsal with 30–40 setae, labacoparia membranous with dorsal 35–51 slender setae. Stipes dorsal with 25–34 setae. Maxillary stridulatory area (Figs 4*F*, 6*I*) with a row of 10–15 sclerotised, conical stridulatory teeth surrounded by a broad membranous area. Blunt tubercle absent. Galea and lacinia as in Fig. 4*H, J*. Galea with a pointed uncus and 16–23 setae, apical setae stout. Lacinia with 39–45 long stout setae and three unci fused at base (Fig. 6*J*). Maxillar palpus four jointed, first three joints with several setae: first palpomera with one seta, second palpomera with five to six setae and third palpomera with two setae. Labium and hypopharynx (Fig. 4*H, K*). Hypopharyngeal sclerome asymmetric, with large truncate process, lateral lobes of hypopharynx less sclerotised, with numerous setae. Tufts of tegumentary expansions (= phoba *sensu* Böving 1936) absent. Ligula with 38–52 setae on each side, anterior margin with two very long paramedian setae. Dorsal surface of ligula with numerous hair-like sensilla, 24–30 campaniform sensilla organised in a transverse basomedian row, four to six pore-like sensilla scattered near the anterior margin and a medial pit-like structure. Labial palpi two jointed, basal palpomera with four to eight long hair-like setae.

Thorax (Fig. 4*A*). Size of legs (Fig. 4*A, I*) increasing posteriorly. Claw (pretarus) as in Fig. 5*J*. Thoracic spiracle larger than abdominal spiracles, respiratory plate C-shaped with almost concealed arms. Dorsi of each sub-lobe of thoracic segments with three to six rows of short setae, last rows with few medium length setae.

Abdomen (Figs 4*A*, 5*K*). Ten-segmented. Abdominal spiracles elliptical or almost circular (spiracles on segments VI–VIII), the arms of respiratory plate almost concealed with the exception of the first abdominal spiracle where the arms are well separated. Spiracles of abdominal segments I–VI gradually decreasing in size, spiracles VII–VIII larger than previous, but about the size of the first abdominal spiracle. Chaetotaxy of dorsi of abdominal segments I–VI similar to chaetotaxy of thorax (Fig. 4*A*). Segments VII–IX with few setae forming only isolated patches or rows, entire dorsum of last segment with numerous setae. Raster (Fig. 5*K*): palida absent, venter of last abdominal segment with two groups of dense, spiny medioposteriad oriented setae, septula narrow. Anal slit Y-form, the stem of anal slit slightly shorter than the arms. Lower anal lip transversally divided into two parts, each part with 18–27 short or medium length hair-like setae, and 15–22 long setae. Dorsal anal lobe with 23–38 hair-like setae. Dorsal anal lobe divided by a longitudinal sulcus.

Second instar larva

The second instar larva of *P. bimucronatus* is similar to the third and first instar larvae, except for the following features.

Body. Maximal body length of a fully grown second stage larvae 44–52 mm, maximal width of head capsule 5–5.4 mm.

Head capsule. Chaetotaxy of head capsule summarised in Table 3. Cranium smooth, anterior parts of frons without punctuation. Relative length of antennomeres: AN II > AN III > AN IV > AN I. Ultimate antennomere (AN IV) with two (three to five) dorsal, three to four ventral sensoric spots and one apical sensoric field. Clithra either slightly developed, or present, prolonged medio-posteriorly and fused, separating corypha by a sclerotised ring. Apex of mandibles with a prominent anterior mandibular seta and two pores. Maxillary stridulatory teeth surrounded by membranous area.

First instar larvae (Fig. 6*G*)

The first instar larva of *P. bimucronatus* is similar to the third and second instar larvae, except for the following features. Length of a first instar larva 11 mm (newly enclosed larva) to 31 mm (fully grown). Chaetotaxy of head capsule summarised in Table 3. Cranium pale yellow, smooth. Maximal width of head capsule 2.55–2.83 mm. Relative length of antennomeres: AN II > AN III ≥ AN IV > AN I. Ultimate antennomere (AN IV) with two (three to five) dorsal, three to four ventral sensoric spots and one apical sensoric field.

Epipharynx. Clithra absent or present as two faintly sclerotised spots, sometimes prolonged and fused posteriorly. Heli absent. Zygum transverse, faintly sclerotised, with an arcuate row of 9–13 stout, spine-like setae and numerous pore-like sensilla distad to the row. Plegmata present. Proplegmata indistinct, but present. Chaetoparia asymmetric with ~50–80 setae on each side. Rudiments of crepis absent.

Mandibles. stridulation area indistinct. Ventromolar setae absent. Dorsomolar setae present. Basolateral region of ventral face with 5–11 setae. Acia absent. Brustia present.

Maxilla. Stipes dorsal with 18–21 setae. Maxillary stridulatory area with a row of 10–11 conical stridulatory teeth, membranous area absent. Blunt tubercle absent. Galea and lacinia fitting tightly together, fused basally, apical part separate. One galear and three lacinial unci fused at base present.

Spiracles. Respiratory plate oval, bula and ecdysial scar absent. Metathorax lateral with a single spine-like egg burster (Fig. 6*G*).

Male pupa (Fig. 5*D, H, I*)

Body. Length 42.5 mm, maximal width 24 mm. Pupa exarate, testaceous, surface glabrous except the dorsa of abdominal tergites.

Head. Bent ventrally. Mouthparts and antenna well separated. Labrum tumid, clypeus slightly concaved. Maxilla elongated conical. Compound eyes distinct.

Thorax. Pronotal disk convex with a distinct median tubercle proximal to basal margin. Lateral margins of pronotal disc distinct, posterior angle of pronotal disc with shallow depression. Meso and metanota differentiated. Mesonotum with a triangular posterior projection. Pterotecae free, closely compressed around body and almost equal in length. Protibia with typical spines, meso and metatibia with distinct spurs, tarsomeres more or less well defined.

Abdomen. Dioneiform organs absent. Terga I–VI with distinct transverse towards ends anteriorly bent carina. Carina of tergum I lower than the subsequent. Surface of medial portion of terga and carina with asperate structures, on terga I–IV with minute spines. Urogomphi present, apically pointed and bent posteriorly, with a small sclerotised tip. Spiracles of first four abdominal segments with an oval sclerotised ring-like peritreme and open atrium, placed on area dorsally and posteriorly bordered by a carina. Spiracles of abdominal segments V–VIII with closed atrium, without sclerotised peritreme. All spiracles slightly elevated. Genital amupula large, protruding, with rounded apex.

Propomacrus cypriacus Alexis & Markis, 2002

Material examined

Seven mature third instar and four second instar larvae were obtained from an anonymous beetle breeder. Larvae were collected in 2004 in Cyprus, no further data are available. Four larvae were reared to adulthood to observe their life cycle and verify the identification. Six first instar larvae were obtained by breeding the hatched adults.

Third instar larva

Last instar larvae of *P. cypriacus* resembling those of *P. bimucronatus*, no clear differential character could be observed. Larvae of *P. cypriacus* generally tend to have fewer setae on most parts of the body than *P. bimucronatus*. But due to the relatively small sample size studied, and the fact that the number of setae observed in both species often overlap, this feature cannot be considered as a differential character. Maximum length of studied larvae 82–92 mm, maximal width of head capsule 8.2–8.7 mm. Length of antennomeres: AN II > AN III > AN I > AN IV. Chaetotaxy of head capsule is summarised in Table 3.

Second instar larva

Similar to the third instar larvae except of the following features.

Body length 24–26 mm (early second stage larvae), maximal width of head capsule 4.6–5.0 mm. Cranium smooth, anterior parts of frons without punctuation. Relative length of antennomeres: AN II > AN III > AN IV ≥ AN I. Ultimate antennomere with one or two (three to four) dorsal, three ventral sensoric spots and one apical sensoric field. Clithra present, extending medio-posteriorly and fused, separating corypha by a sclerotised ring. Apex of mandibles with a prominent anterior mandibular seta and two pores. Chaetotaxy of head capsule is summarised in Table 3.

First instar larva

Larvae similar to the first instar larvae of *P. bimucronatus*, length of a first instar larva varies from 14 mm (newly enclosed larva) to 29 mm in fully grown larva. Cranium pale yellow, smooth maximal width of head capsule 2.63–2.9 mm. Chaetotaxy of head capsule summarised in Table 3. Relative length of antennomeres: AN II > AN IV > AN III > AN I. Ultimate antennomere with two to three (five) dorsal sensoric spots, three (four to five) ventral sensoric spots and one apical sensoric field.

Epipharynx. Clithra absent or present. Zygum transverse, faintly sclerotised, with an arcuate row of about 9–11 stout setae and numerous pore-like sensilla. Plegmata present. Proplegmata indistinct, but present. Chaetopariae asymmetric with ~50–70 setae on each side.

Mandibles. Asymmetrical, scissorial area with two scissorial teeth. Apical half of mandible with a prominent anterior mandibular seta and two pores on dorsal face. Stridulation area indistinct. Ventromolar setae absent.

Maxilla. Maxillary stridulatory area with a row of 9–14 stridulatory teeth, membranous area absent. Galea and lacinia fit tightly together, fused basally, apical part separate.

Spiracles. respiratory plate oval, bula and ecdysial scar absent. Metathorax lateral with a single spine-like egg burster.

Biological comments

Habitat of Propomacrus *and collection circumstances*

Larvae of *P. bimucronatus* were found by the authors in September 2006 in several living *Platanus orientalis* (Fig. 1*H–J*) trees surrounding a small river in the vicinity of Ayvaçik (Çanakkale province, north-western Turkey). The larvae fed on decayed soft wood in the hollow trunks and dead roots of *Platanus* trees, leaving characteristic frass accumulation, tunnels and holes in the soft but still compact wood. We found larvae of all stages including freshly emerged first instar larvae and eggs, indicating the late summer (August to the first half of September) activity of the females reported also by Onucar and Ulu (1986). However, no adults and only very few remains of adults were found. Most surprising was the fact that a reasonably high number of larvae was collected in slender trees with a trunk diameter of not more than 40 cm at the base of the tree (Fig. 1*I*).

Another observation of first instar *P. bimucronatus* larvae was made by the authors in April 2009 in north-eastern Greece next to the small village of Avas (Alexandroupoli env., Thrakia province). Approximately 10 second instar larvae were excavated from a hollow branch of *P. orientalis* at a height of about 3 m.

Observations on the life cycle of Propomacrus

The life cycle under laboratory condition took between one and two years. The length of the second and third instar was the most variable. After emergence, the adults were active for approximately two or three weeks, the females usually lived longer and laid eggs soon after their emergence. Larvae hatched after 3 weeks. The first instar lasted for about three to four weeks, the second between 21 and 170 days and the third instar for more than 205 days, but several larvae remained in the last instar for over a year. The last instar larvae fed mainly on bulky pieces of decayed wood, and made deep burrows into soft wood (Fig. 1*F*). The pupal phase was short – about two or three weeks. Pupating occurred in a pupating cell made from wooden debris either inside of the compact rotten wood or at the side of the container. Adult beetles spent much time buried in the substrate, and were active mainly during afternoon and evening hours. Ripe bananas were used as food and mating often occurred at the food source.

Larval stridulation

When the mature larvae were disturbed (e.g. by digging them out of the substrate or by handling) stress stridulation was observed in the form of a light repeated ‘buzz’. The vibrations were accompanied by clearly visible contractions of the meso and metathoracic segments (so that a transversal depression occurred for a moment). The ‘buzz’ strongly resembled the stridulation of Lucanid larvae. However, no external structure on the legs or elsewhere was observed, nor was any intense movement of maxillae or mandibles detected. Stridulation was observed several times in all mature larvae of both *Propomacrus* species but was not observed in *Cheirotonus* larvae.

Result of the cladistic analysis

The parsimony analysis of the 105 morphological and ecological characters of larvae and adults resulted in six equally parsimonious trees (length 347, CI 0.43, RI 0.62). However, the trees deviated in their topology significantly. Three of them showed an overall similarity with only minor differences, the others were inconsistent, mainly with respect to the position of the Dynastinae and Euchirinae clade (see the majority rules consensus tree shown in Fig. 8). Subsequent larvae-only analysis yielded 32 equally parsimonious trees (tree length 176, CI 0.46, RI 0.68) that are congruent with the three similar trees mentioned above (see Fig. 9), with the exception of the position of *Valgus*. Searching for the source of inconsistency in the original analysis, we excluded two representatives of Dynastinae (*Xylotrupes gideon* (Linné, 1767) and *Oryctes nasicornis* (Linné, 1758)) from the dataset, which led to topologies identical with the three trees from the original analysis and also with the larvae-only analyses. Having identified the source of instability, we excluded the above-mentioned species from all following analyses.

The results of the 12 parsimony analyses are summarised in Table 1; the most consistently resolved topology inclusive of the relative support value of scarab beetle taxa in our analysis is show in Fig. 7. Based on the data source, the analyses are grouped into three sets: larval (1–4), adult (5–8) and combined (9–12); the former two are also termed 'partial'. The 'contree' column in the table represents a 50% majority rules consensus tree obtained from the strict consensus trees of each of the 12 analyses.

Discussion

Analytical strategy and the exclusion of Xylotrupes *and* Oryctes *from the dataset*

Based on a set of 105 morphological and ecological characters of larvae and adults from 24 taxa, we have not been able to establish a consistent phylogenetic hypothesis, as three out of the six most parsimonious trees were not of congruent topology and the phylogenetic position of Euchirinae remained ambiguous. While searching for the source of such inconsistency, we performed several subsequent analyses; first with a partial

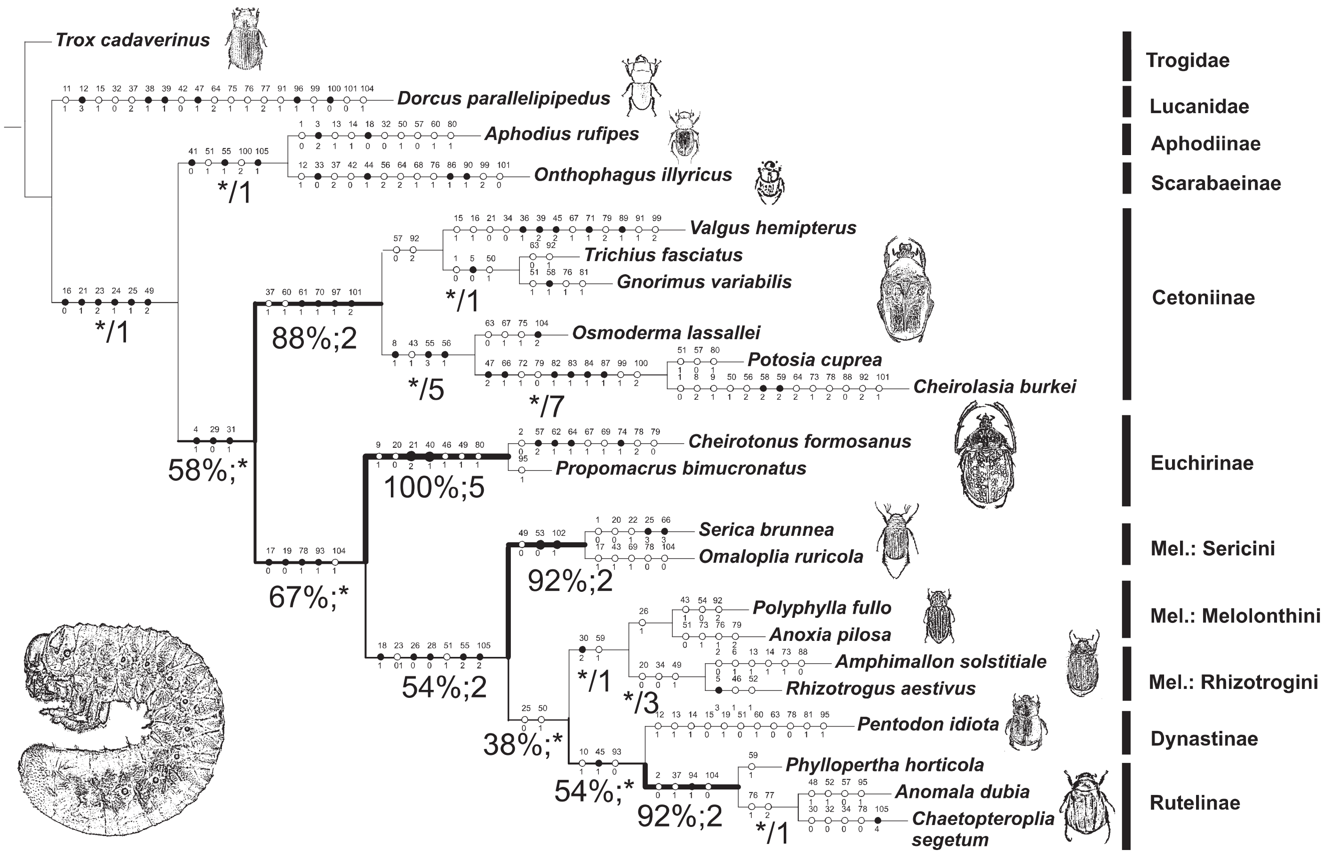


Fig. 7. Strict consensus topology of Scarabaeidae with the position of Euchirinae based on combined data of larval and adult morphology, with some characters ordered and all characters successively weighted (analysis 12); character stages are marked on clades, character numbers are above the circle, numbers of stages are below circles; black circle indicates unique evolutionary events, white circles denote reversals or parallelisms. Relative support value (RSV; in percentage) and partitioned Bremer support (PBS) values are indicated. The RSV is proportional to the width of internodes and indicates how strongly each clade was supported thought analyses 1–12. An asterisk (*) indicates RSV below 25% or a missing Bremer support.

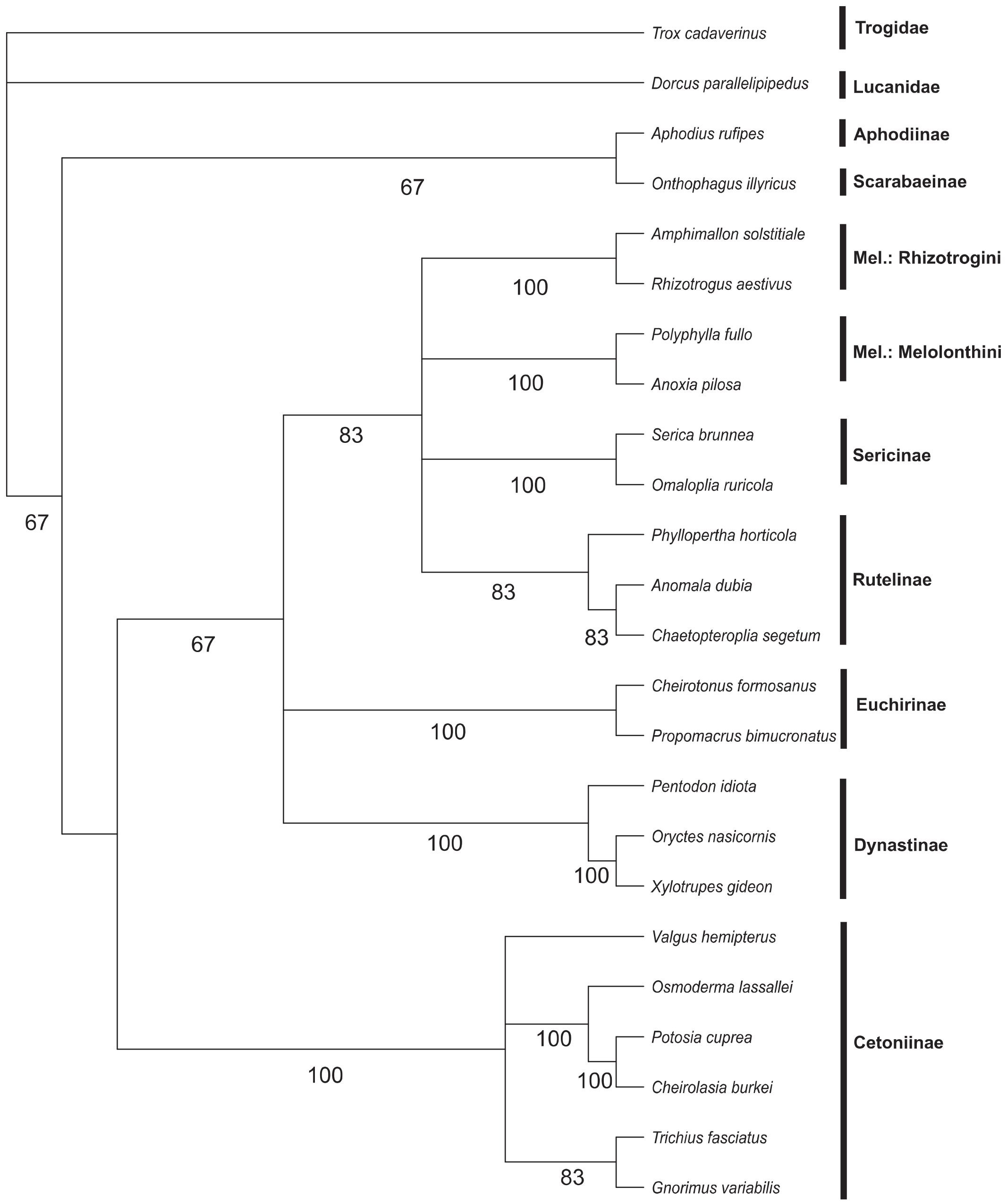


Fig. 8. Majority rules consensus tree obtained from six most parsimonious trees in the analysis of 105 morphological and ecological characters in 24 taxa of Scarabaeoidea (including *Xylotrupes gideon* and *Oryctes nasicornis*). Majority rule values over 50% are indicated below branches.

larvae-only dataset and a full set of terminalia, second with a full set of characters, but with the exclusion of taxa suspected of causing long-branch attraction effect. We focussed on the representatives of the Dynastinae clade, exhibiting the most unstable position in the initial analysis. Although the phylogeny of Dynastinae as yet remains unresolved (Scholz and Grebennikov 2005; Ratcliffe and Cave 2006; Smith *et al.* 2006), we excluded the taxa *Xylotrupes gideon* and *Oryctes nasicornis*, which form a long-branch clade with a high number of common derived characters (mostly related to pronounced sexual dimorphism). Results of these analyses justified the exclusion of the two taxa, as the resulting strict consensus topologies were congruent with the three trees from the initial analysis.

Position of Euchirinae and the Euchirinae–Melolonthinae relationship

Although we could not include representatives of nominotypic genus in our study, we consider our data informative enough to

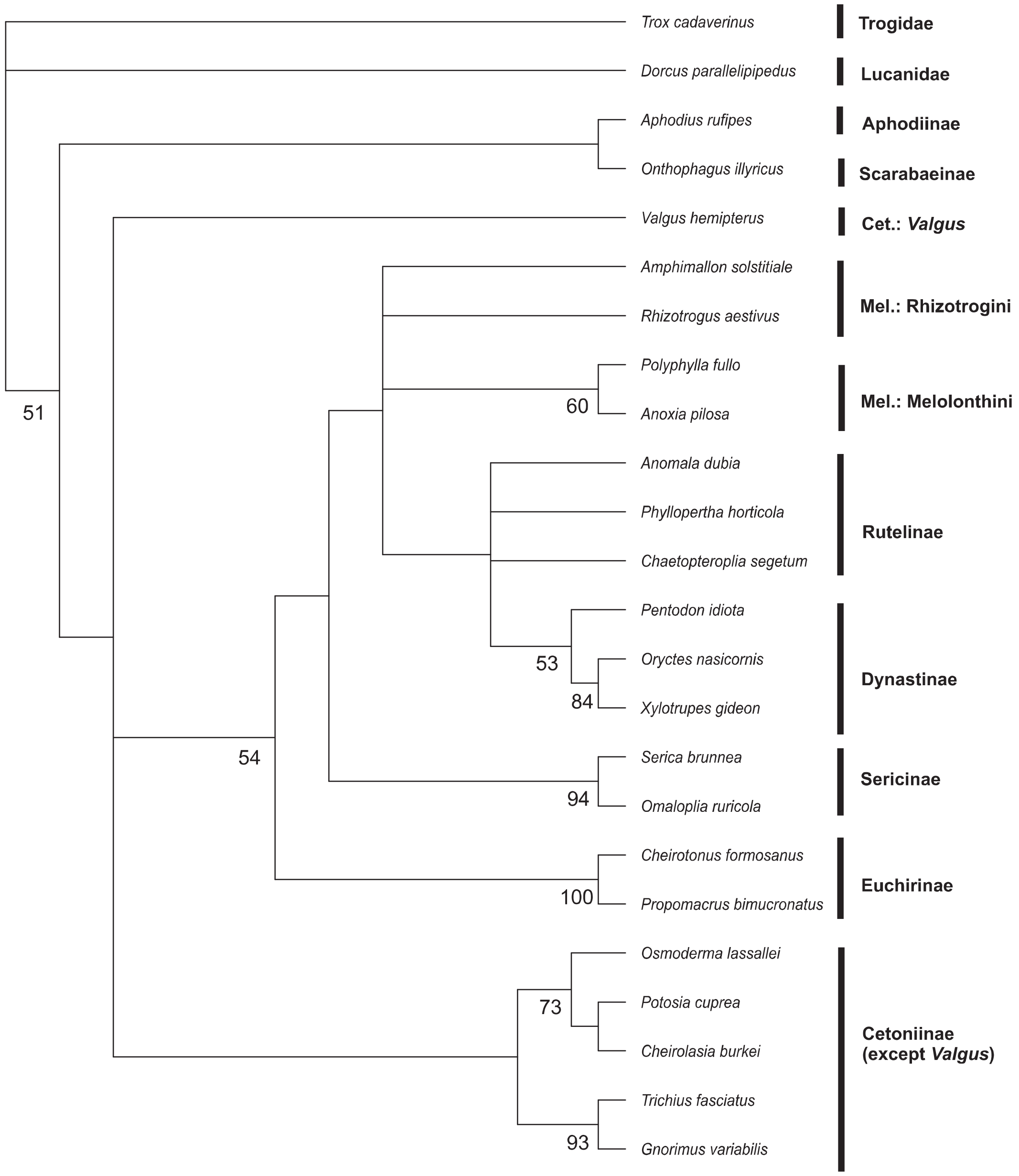


Fig. 9. Strict consensus tree of 32 most parsimonious trees obtained in the analysis of 55 larval morphological and ecological characters in 24 taxa of Scarabaeoidea (including *Xylotrupes gideon* and *Oryctes nasicornis*). Bootstrap values over 50% are given below branches.

allow us to hypothesise on the phylogenetic relationships of Euchirinae. The results of our analyses have corroborated the monophyly of Euchirinae, supported by two larval synapomorphies: acanthoparia with microsetae, except distal third with normally developed setae (21: 2); maxillary stridulatory teeth with desclerotised basal area (40: 1). On the other hand, we were not able to detect any synapomorphies for Euchirinae among the adult morphological characters. The lack of such adult synapomorphic characters was also demonstrated by previous authors, e.g. Young (1989) and Scholz and Grebennikov (2005).

Based on our results, we hypothesise Euchirinae to be a sister group of the remaining pleurostict scarabs (in our dataset) except Cetoniinae. This relationship was recovered in 8 out of the 12 analyses (RSV 63%, supported by the 'larval' and 'combined' datasets) and the clade was also present on the 50% majority rule consensus tree calculated from the strict consensus trees from analyses 1–12 (Table 1).

Since Arrow (1917), several authors have considered Euchirinae to be relatives to Melolonthinae. Lumaret and Tauzin (1992) hypothesised a close relationship between Melolonthinae (particularly Melolonthini) and Euchirinae, but quite illogically, still found enough distinctive characters to justify the separation of Melolonthinae and Euchirinae into separate subfamilies. On the other hand, Ahrens (2006) and Smith *et al*. (2006) have not found support for Euchirinae as a separate subfamily, considering them to be a part of the Melolonthinae (Smith *et al*. 2006) or of a clade composed of several representatives of Melolonthinae[1], Rutelinae, Dynastinae, as well as Cetoniinae (Ahrens 2006). With a single exception[2], the results of our current, as well as previous analyses (Šípek *et al*. 2009), do not corroborate a close relationship between Euchirinae and Melolonthinae representatives included in the analyses. Moreover, the previous Cetoniinae-focussed study (Šípek *et al*. 2009) has indicated a possible sister group relationship of Euchirinae to all other pleurostict scarab beetles. However, the recent molecular studies presented by Ahrens (Ahrens *et al*. 2007; Ahrens and Vogler 2008; Ahrens *et al*. 2011) have demonstrated the paraphyly of the Melolonthinae *per se*. Thus, the question is not whether or not the Euchirinae are members of the Melolonthinae, but what the sister group of Euchirinae is. To date, we have no reliable comprehensive study on the phylogeny of the megadiverse pleurostict or plant-feeding scarabs based on 'a total evidence' approach, which could elucidate the problem. The results presented here are based on a limited number of taxa (22 or 24), so a more densely sampled dataset is needed to test our results.

Relative contribution of larval versus adult morphology

Similarly to Micó *et al*. (2008) and Šípek *et al*. (2009), the availability of a separate larval and adult dataset enables us to compare the relative contribution of each 'partial' dataset to resolve the topology of the clades in a manner consistent with those obtained from the combined dataset. Our results indicate that larval characters (analyses 1–4) were relatively successful in resolving the clades, with RRV ranging between 60 and 90%, compared with adult characters (analyses 5–8) with RRV between 30 and 40%. Analysis number 1 (larval dataset, characters unordered, without successive weighting, Table 1) failed to recognise the genus *Valgus* Scriba, 1790 (or rather the species *V. hemipterus* (Linné, 1758)) among the Cetoniinae clade, which resulted in a relatively low RRV of 60%. This could be attributed to a significant number of derived characters possibly related to its preference of solid pieces of rotting wood as a substrate for development (e.g. shape of mandibles, cushion-like portion on dorsum of last abdominal segment) as well to its small size (reduction of various structures on hypopharynx, maxillae etc.). The effect of such characters was suppressed in subsequent analyses of larval dataset (analyses 2–4; Table 1). We consider the recovery of an alternative Cetoniinae (–) clade (e.g. all members of Cetoniinae except *Valgus*) found in the larvae-only analyses to be another result of the high number of derived characters of *Valgus* larvae.

The adult-only analyses consistently recovered only four out of the 10 clades highlighted in Table 1, namely the Euchirinae, Rutelinae, Sericini and Cetoniinae. They also failed to recover the Rutelinae-Dynastinae clade, attributing *Pentodon idiota* (Herbst, 1789) as a sister group of Cetoniinae or leaving its position unresolved among pleurostict scarabs, which resulted in several alternative groupings with low support (Table 1).

The combined dataset (analyses 9–12) yielded the most resolved topologies with RRV between 85 and 95% except analysis 9 (RRV 65%; characters unordered, no successive weighting), which again failed to detect the Rutelinae-Dynastinae clade.

Morphological features of larval Euchirinae

Lumaret and Tauzin (1992) gave a description of a third instar larva and pupa of *P. bimucronatus* and briefly discussed and compared its morphological characters with representatives of other Melolonthinae, eg. Diplotaxini, Plectrini and Melololonthini. They highlighted the unique pattern of the Euchirinae epipharynx, with the presence of proplegnatium and plegmatium, the absence of heli and epizygum; the presence and form of tarsal claws on all pairs of legs; absence of palia on raster and a 'massive' form of mandibles. Our results corroborate their findings with the exception of massive mandibles, as in all the studied specimens of three Euchirinae species we found mandibles with a narrow scissorial area bearing two large teeth resembling more or less the situation in larvae of the majority of Melolonthinae. This inconsistency might be due to the fact that Lumaret and Tauzin (1992) had only a single *Propomacrus* larva, which was apparently an old specimen with worn cuticular structures (demonstrated also by the absence of numerous setae on the epipharynx and maxillae etc. in their figures).

As mentioned above, we found two apomorphic characters of larval Euchirinae: the chaetotaxy of acanthoparia and maxillary stridulatory teeth with desclerotised basal area. Further important characters include the following: the shape of maxillar stridulation teeth (straight and conical, not bent, recurved or truncated; Figs 2*G*, 4*F*, 6*C, I*); the variable presence or absence of clithra, a low and flat sense cone with sensilla in proximal part (a possible fusion of sense cone with other structure, e.g. sclerotised plate; Fig. 6*F*); and finally the mandibular stridulation area with very fine microscuplture (Fig. 6*E, J*).

Direction of further research

The larvae of the nominotypic genus *Euchirus* Burmeister & Schaum, 1840 are as yet unknown. Knowledge of these larvae could confirm or refute the monophyly of Euchirinae (although the second option seems unlikely as there is a general congruence as concerns the monophyly of the group). On the other hand, as a clear adult morphological synapomorphy for Euchirinae has not been defined as yet, the verification of the larval synapomorphies proposed by us seems necessary. As indicated above, an analysis with more complete taxon sampling is needed to address the phylogeny of the pleurostict

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[1] Excluding Sericinae, Ablaberinae and representatives of fauna primarily confined to southern continents.

[2] In one out of the six equally parsimonous trees obtained from the first combined analysis (24 taxa, 105 characters), Euchirinae have been recovered as sister group of Sericinae, inside a melolonthinae clade.

scarabs on the whole. In particular, it is necessary to include as many Melolonthinae larvae as possible in the analysis, as this group represents the most diverse and lesser-known taxon in the pleurostict scarabs. As demonstrated here, the informative value of immature characters can be very high and thus there is a need to improve the sampling of immature data.

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Appendix 1. List of 105 morphological and ecological characters used in the analysis

Larvae

The abbreviation 'MMŠG' followed by a number indicates that the character has been used by Micó et. al. (2008). Abbreviation 'mod.' indicates that it was significantly re-worded compared with the original source.

(1) Stemmata: present, 0; absent or distinctly reduced, 1.

(2) Frontal suture: straight or slightly sinuate, 0; bisinuate (concave), 1; sinuate (convex), 2.

(3) Antenna: three segmented with the basal segment not subdivided, 0; three segmented with subdivided basal antennomere, the antenna appears to be four segmented, 1; antenna appears to be five segmented, 2.

(4) Ultimate antennomere: much smaller than other antennomeres, 0; comparably about the same size as other antennomeres, 1.

(5) Relative length of antennomeres (in antenna with four antennomeres): all antennomeres similar in length, first and fourth antennomere the longest, subequal or the first slightly longer, 0; antennomeres apparently differ in length, first antennomere longer than the others, 1; second antennomere longer than the others (first, third, fourth), 2; second and third antennomere subequal, and longer than first and fourth, 3.

(6) Setae on antennomeres: a few setae present at least at one antennomere (except minute setae in the apical sensory area of ultimate antennomere), 0; without setae, 1.

(7) Ultimate antennomere: with only apical sensoric field with several small setae, 0; with apical sensoric field and at least one dorsal or ventral field, 1.

(8) Number of dorsal sensory spots on the ultimate antennomere: one sensory spot, 0; two to four sensory spots, 1; more than four sensory spots, 2.

(9) Number of ventral sensory spots on the ultimate antennomere: less than three, 0; three or more, 1.

(10) Stridulatory area of mandible: absent or reduced to microridges, 0; present with several transverse ridges, 1.

(11) Number of scissorial teeth on right mandible: two, 0; three, 1; four, 2.

(12) Number of scissorial teeth on left mandible: two, 0; three, 1; four, 2; five, 3.

(13) First two scissorial teeth on right mandible (teeth before scissorial notch): separate well distinct, 0; fused into a blade like portion (second tooth can be indicated as a small process at the proximal end of the blade-like portion), 1.

(14) First two scissorial teeth on left mandible (teeth before scissorial notch): separate, well distinct, 0; fused, 1.

(15) Ventromolar setae of mandibles: present, 0; absent, 1.

(16) Dorsomolar setae on right mandible: present, 0; absent, 1.

(17) Basolateral region of mandibles: setae present, 0; setae absent, 1.

(18) Membranous lobe on molar part of left mandible – acia: present, without setae, 0; present with numerous setae, 1; absent, 2; present, but sclerotised, sometimes with a few setae, 3.

(19) Plegmata: present, 0; absent, 1.

(20) Proplegmata: present, 0; absent, 1.

(21) Acanthoparia: absent, 0; present, 1; setae of acanthoparia reduced to microsetae, only setae in apical part normally developed, 2.

(22) Haptolachus: with a more or less sclerotised and developed tubercle bearing a few pores (sense cone), 0; without pore-bearing tubercle or sense cone, 1.

(23) 'Sclerotised plate' of haptolachus: present, well sclerotised, 0; present, but desclerotised or faintly sclerotised, 1; absent, 2.

(24) Nesium (without pores) proximad to laetorma: present, 0; absent, 1.

(25) Distal margin of epipharynx: convex, 0; trilobed, 1; straight or slightly concave, 2; with several small lobes, 3.

(26) Epizygum: present, 0; absent, 1.

(27) Clithra: present, 0; absent, 1.

(28) Heli: present, 0; absent, 1.

(29) Chaetoparia: present, 0; absent, 1; reduced, 2.

(30) Phoba: present, 0; absent, 1; reduced, 2.

(31) Tormae: fused, 0; separated, 1.

(32) Anterior epitorma: present, 0; absent, 1; reduced, 2.

(33) Posterior epitorma: present, 0; absent, 1.

(34) Crepis: present, 0; reduced, 1; absent, 2.

(35) Galea and lacinia: separate, 0; separate or partially separate, but fitting tightly together, 1; fused, forming mala, dorsal galeolacinial suture distinct, 2; entirely fused forming mala, without any suture, or the suture only indicated, 3.

(36) Unci of galea and lacinia: both groups present, 0; only apical (galear) uncus present, 1.

(37) Number of lacinial unci: three, 0; two, 1; one, 2.

(38) Stridulatory apparatus on meso and metathoracic legs: absent, 0; present, 1.

(39) Maxillary stridulatory organs: present, 0; absent, 1; reduced to a single tubercle, 2.

(40) Maxillary stridulatory teeth: with fixed base, or with a sclerotised rim, 0; basal area of stridulatory teeth desclerotised, and paler than the rest of stipes, 1.

(41) Hypopharyngeal sclerome: consists of two separate sclerites (not fused), 0; fused, but the sclerites are narrow with medial anterior projections, 1; entirely fused forming a single very broad sclerite, 2.

(42) Dorsa of thoracic and abdominal segments: not divided into sub-lobes, 0; divided into sub-lobes, 1.

(43) Abdominal segments IX and X: separated, 0; fused dorsally, 1.

(44) Abdominal segments III–V: not distinctly thickened or forming a hump, 0; distinctly thicker and larger than thoracic and first two abdominal segments forming a dorsal hump, 1.

(45) Dorsum of last abdominal segments (excluding structures connected with anus): without any distinct structures, 0; with a semicircular or almost circular line or area, 1; with two paramedian cushion-like structures, 2.

(46) Shape of pretarsus: claw-like, 0; short, cylindrical with a distinct but small pointed tip, 1; pretarsus short conical, 2; pretarsus long cylindrical with or without a small tip, 3.

(47) Number of setae on pretarsus: two, 0; three, 1; more than three, 2.

(*continued next page*)

Appendix 1. (*continued*)

(48) Pretarsus: equal or sub-equal in all pairs of legs, 0; metapretarsus distinctly smaller, or without tip (if meso and propretarsus possess a tip), 1.
(49) Anal slit: Y-form, stem of anal slit much longer than the arms, 0; Y-form, stem of anal slit shorter or about the size of the arms, 1; transverse, 2.
(50) Hamate setae on the last abdominal sternite: absent, 0; present, 1.
(51) Palida: absent, 0; present, 1.
(52) Palida: monostichous, 0; polystichous, 1.
(53) Palida: transverse, 0; longitudinal, 1.
(54) Spiracles: biforat, 0; cribriform, 1.
(55) Larval feeding habits: ceratinofagous, 0; coprophagous, 1; phytophagous (roots of living plants), 2; decayed wood, other organic debris, 3; compact rotten wood, 4.

Adults
56. Surface of frons [MMŠG: 39]: convex, 0; concave, 1; with accessories, 2.
57. Clypeal surface [MMŠG: 40]: flattened or slightly convex, 0; slightly concave, 1; deeply concave or excavated, 2.
58. Anterior border of male clypeus [MMŠG: 41]: straight, slightly curved or sinuate, 0; clearly notched, 1; armed, 2.
(59) Ventral surface of labium [MMŠG: 42]: flattened or convex, 0; partially or slightly concave, 1; completely or deeply concave, 2.
(60) Anterior border of labrum [MMŠG: 43]: exposed, 0; hidden, 1. Weakly sclerotised, labrum is reduced or completely covered by clypeus and other mouthparts.
(61) Preoccular notch [MMŠG: 44]: absent, 0; present, 1.
(62) Antennal scapus [MMŠG: 45]: rounded, 0; widened and depressed, 1.
(63) Length of male antennal club [MMŠG: 46]: as long as or shorter than funicle, 0; clearly longer than funicle, 1.
(64) Sexual dimorphism on head [MMŠG: 47]: absent, 0; faint, 1; accentuated, 2.
(65) Apex of galea [MMŠG: 48]: toothed, 0; rounded, not toothed, 1.
(66) Central third of posterior border of pronotum [MMŠG: 49]: straight or curved, 0; clearly sinuate, 1; lobed, 2.
(67) Pronotal disc [MMŠG: 50, mod.]: simply convex, 0; with depressions or prominences, 1; with depression and prominences only in males, 2.
(68) Basal third of pronotum [MMŠG: 51]: reduced, 0; projected, 1.
(69) Anterolateral border of pronotum [MMŠG: 52]: with margin, 0; without margin, rounded, 1.
(70) Procoxae [MMŠG: 53]: transverse, slightly prominent, 0; nearly conical and clearly prominent, 1.
(71) Metacoxa [MMŠG: 54]: approximated, 0; widely separated, 1.
(72) Posterolateral corner of metacoxa [MMŠG: 55]: short, rounded, 0; prominent, acute, 1.
(73) External border of male protibia [MMŠG: 57, mod.]: with two, three teeth or more teeth, 0; without teeth or with apical tooth, 1.
(74) Inner border of male protibia [MMŠG: 58, mod.]: simple, 0; toothed or serrated, 1.
(75) Preapical ventral border of protibia [MMŠG: 59]: simple, flattened, 0; toothed, 1.
(76) Dorsal surface of mesotibia [MMŠG: 60]: with keels or spines, 0; without keels or spines, 1.
(77) Dorsal surface of male metatibia [MMŠG: 61]: with keels or spines, 0; without keels or spines, 1.
(78) Sexual dimorphism on protarsus [MMŠG: 62]: absent, 0; scarce, 1; accentuated, 2.
(79) Onychium [MMŠG: 63]: long, 0; short, 1; absent, 2. We take as a reference the dorsoventral basal width of one tarsal claw (as long as the dorsoventral basal width of tarsal claw or shorter than this).
(80) Preprosternum [MMŠG: 64]: without projection, 0; with erect tubercle or strong spine, 1.
(81) Postprosternum [MMŠG: 65]: without projection, 0; with erect tubercle or strong spine, 1.
(82) Mesometasternum [MMŠG: 66]: without projection, 0; with tubercle, 1.
(83) Proepimeron [MMŠG: 67]: nearly flattened or scarcely concave, 0; deeply concave, 1.
(84) Dorsal part of mesepimeron [MMŠG: 68]: completely covered or nearly so, 0; clearly exposed, 1.
(85) Proepisternal keel [MMŠG: 69]: absent or weakly defined, 0; clearly defined and outstanding, 1.
(86) Scutellum [MMŠG: 70]: completely exposed, 0; in most, partly covered or completely covered, 1.
(87) Posthumeral elytral emargination [MMŠG: 71]: weak or absent, 0; wide and deep, well defined, 1.
(88) Fifth abdominal sternite [MMŠG: 72]: nearly as long as fourth, 0; longer than fourth, 1.
(89) Fifth abdominal spiracle [MMŠG: 73]: annular, 0; tuberculiform, 1.
(90) Pygidium [MMŠG: 74]: wider than long, 0; as long as wide, or slightly longer than wide, 1.
(91) Propygidium [MMŠG: 75]: covered by elytra, 0; mostly exposed, 1.
(92) Dorsal vestiture [MMŠG: 76]: absent, 0; setiferous, 1; pruinose or cretaceous, 2. The vestiture of scarab beetles is usually a combination of microtrichia, cretaceous compounds and setae, but here we select the more extensive.
(93) Tarsal claw: without accesoric teeth on ventral margin, 0; with accesoric teeth on ventral margin, 1.
(94) Protarsal claw: symmetrical, 0; asymmetric, 1.
(95) Mandibles: almost entire mandible visible (from dorsal aspect), mandible not hidden by labrum, 0; only partially exposed, 1; hidden under labrum, 2.
(*96) Antenna*: 'Scarabeid type', 0; 'Lucanid type', 1.
(97) Mandibles: well sclerotised, with scissorial teeth, 0; parts or entire mandible desclerotised (but the degree of desclerotisation is even in entire mandible, except for acia), mandible flat, flexible usually with an inner membranous lobe, 1; lateral or basal margin well sclerotised, inner distal margin flat, desclerotised. Mandible triangular in cross-section, 2.
(98) Antennal club: three segmented, 0; seven segmented, 1; five segmented, 2.
(99) Mesocoxa: approximated, 0; separated, but the distance between the coxae not wider than the width of trochanter, 1; separated, the distance between coxae distinctly wider than the width of trochanter, 2.
(100) Metafemur: slender, 0; normally developed (slightly broadened, maximal width/length ratio below 0.4), 1; greatly enlarged (maximum width/length ratio above 0.4).

(*continued next page*)

Appendix 1. (*continued*)

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(101) Distal margin of pronotum: distinctly wider than proximal margin of elytrae, 0; as wide or almost as wide as proximal margin of elytrae, 1; distinctly narrower than proximal margin of elytrae, 2.

(102) Parameres: symmetric, 0; asymmetric, 1.

(*103) Number of metatibial spurs*: zero, 0; one, 1; two spurs, located below tarsal articulation, 2; two spurs located above and below tarsal articulation (spurs set apart), 3.

(104) Main flight activity: diurnal, 0; nocturnal and evening activity, 1; active whole day, 2.

(105) Food habits of adults: ceratinophagous, 0; coprophagous, 1; phytophagous (leaves), 2; phytophagous (fluids – pulp, sap), 3; phytophagous (unripe grass seeds), 4; phytophagous (pollen), 5.

Appendix 2. Matrix of 24 taxa and 105 larval and adult characters used in phylogenetic analysis

Taxa		Characters										
		0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	8888888889 1234567890	0000000001 9999999990 1234567890	11111 00000 12345
Trox cadaverinus	Trogidae	0000-10--0	0011011211	0100010120	011-000000	1100000000	0--0000000	00?0021000	0000000020	0000000000	0000100001	10200
Dorcus parallelipipedus	Lucanidae	1110200--0	1300111211	0000011112	001-00211-	2000001000	0--1401010	00-2100000	0000112020	00000001??	1000010-10	00213
Aphodius rufipes	Aphodiinae	0120-01000	0011001011	1021110110	001-000000	0100000021	1011100011	0010100000	0000000011	0000000000	000020?002	10301
Onthophagus illyricus	Onthophaginae	1110110--0	0100001211	1021110120	0102002000	00010---20	1011121010	0012100100	0000010020	00000100?1	0000202022	00101
Amphimallon solstitiale	Mel.: Rhizotrogini	1011211000	0011100100	1011001001	1110100000	2100000111	1011201010	0010000000	0110000110	0000000000	111020001?	10212
Rhizotrogus aestivus	Mel.: Rhizotrogini	1111301000	0000100100	1011001001	1110100000	2100010111	1111201010	0010000000	0100000?10	00000001?0	1110200011	10212
Polyphylla fullo	Mel.: Melolonthini	1111201000	0000100101	1011011001	1211100000	2110000121	1010201010	0010000000	0000002110	00000001?0	1210200101	10212
Anoxia pilosa	Mel.: Melolonthini	1111201000	0000100101	1011011001	1211100000	2100000121	0--1201010	0010000000	0110012120	0000000100	0110200201	10212
Serica brunnea	Mel.: Sericini	0111201000	0000100100	1101301002	1112100000	2100000100	1001201000	0010030000	0100001110	00000001?0	0010200011	11312
Omaloplia ruricola	Mel.: Sericini	1111201000	0000101101	1011101002	1112100000	2110000100	1001201000	0010000010	0000001010	00000001?0	0110200011	11302
Cheirotonus formosanuus	Euchirinae	1011201210	0000000200	2021111102	1111100001	2100010010	0--1402000	0111001010	0001000201	0000000100	0010202001	10313
Propomacrus bimucronatus	Euchirinae	1111201-10	0000100200	202111-102	1111100001	2100010010	0--1401000	0010000000	0000000111	0000000100	001010200?	10313
Anomala dubia	Rutelinae	1011201001	0000100101	1001001002	1211301000	2100100121	1111200000	0010000000	0100012110	0000000100	0001100012	10202
Phyllopertha horticola	Rutelinae	1011201001	0000100101	1001001002	1211301000	2100100021	1011201010	0010000000	0100001110	00000001?0	0101200011	10202
Chaetopteroplia segetum	Rutelinae	1011201001	0000100101	1001001000	1010301000	2100100021	1011201000	0010000000	0100012010	?000000100	010120000?	10204
Oryctes nasicornis	Dynastinae	0011211211	0111000011	1001001100	1211201001	2100100020	0--1320101	0002001000	0000001000	1000000100	1000100002	1021?
Xylotrupes gideon	Dynastinae	0011211211	1111000011	1001001102	1111200000	2100001020	0--1320101	0002032000	0000001100	0000000100	0000100002	10213
Pentodon idiota	Dynastinae	1111201001	0111000111	1001001002	1211200000	2100100021	0--1?01001	?000000000	0000001010	1000000100	0000100002	1021?
Potosia cuprea	Cetoniinae	1111111101	1200001311	1021110102	1112301000	2110032020	1011310001	1010110101	0100001001	0111101100	0000201012	20203
Osmoderma lassalei	Cetoniinae	11111111-1	1200001311	1021110102	1112301000	2110020020	0--1311001	1000001001	0000101010	0000100100	0000201001	20223
Cheirolasia burkei	Cetoniinae	0111111211	1200001311	1021110102	1112301000	2110032021	0--1321221	1012110101	0110001200	0111101000	0200201012	10203
Trichius fasciatus	Cetoniinae	0011011001	0100001311	1021011102	1112301000	2100000021	0--1400001	1000100101	0000002010	0000000100	0100201001	20205
Gnorimus variabilis	Cetoniinae	00110110-1	0100001311	1021011102	1112301000	2100000021	1111400101	1010100001	0000012010	1000000100	0200201001	20203
Valgus hemipterus	Cetoniinae	1211111000	1100111211	0021211102	111031-020	2100200020	0--?400001	1010001101	1000002020	0000100110	120020?021	20205