

The first instar larva of *Aulacoscelis appendiculata* n. sp. (Coleoptera: Chrysomelidae: Aulacoscelinae) and its value in the placement of the Aulacoscelinae

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Of all of the chrysomelid subfamilies, only the larvae of the Aulacoscelinae remain undescribed. The adults and first instar larva of *Aulacoscelis appendiculata* sp. n., from Panama are described, as well as the eggs. Larval characters, eggs, and oviposition behaviour are used to relate the Aulacoscelinae with other chrysomelid subfamilies, in support of what is known to date concerning adult morphology.

KEYWORDS: Coleoptera, Chrysomelidae, Aulacoscelinae, *Aulacoscelis*, morphology, new species, eggs, larvae, relationships, subfamilies.

Introduction

Taxonomic History

The name *Aulacoscelis* is probably derived from the Greek meaning furrowed leg (Duponchel and Chevrolat, 1842).

The Aulacoscelinae was only established as a separate chrysomelid subfamily by Monrós (1953). It is a small, New World group comprising only 18 described species to date (Suzuki, 1994a). Thirteen of these are presently placed in *Aulacoscelis* Duponchel and Chevrolat, 1842, and five in *Janbechynea* Monrós, 1953. Monrós (1954) divided *Janbechynea* into *Janbechynea sensu stricto* and *Bothroscelis*. According to Arnett (1973) two *Aulacoscelis* species occur in New Mexico, Arizona and California in southwestern USA. However, according to Suzuki (1994a), who reviewed the Aulacoscelinae, only *A. candezei* Chapuis occurs there, but he did not include California in the area of distribution of this genus. In addition, *Janbechynea (Bothroscelis) fulvipes* (Jacoby) occurs in Arizona (Arnett, 1973; Suzuki, 1994a). *A. candezei* and *J.(B.) fulvipes* also occur further south in Central America. In addition, twelve other *Aulacoscelis* spp., plus one other *Janbechynea (Bothroscelis)* sp. occur in Central America. Although Suzuki (1994a: 46) stated that the subgenus

Janbechynea sensu stricto seems to be limited to South America, he shows in figure 1, p. 49 that *J. (J.) elongata* (Jacoby) occurs in Central America. In fact it was described from Playa Vicente in Mexico. However, the other two species in *Janbechynea s.s.* only occur in South America as far south as Bolivia, Peru and Brazil.

Apparently, there are undescribed species. J. A. Santiago-Blay is to describe two new species belonging to the subgenus *Bothroscelis* from Mexico and Suzuki (1994a) mentioned that he has also seen undescribed *Aulacoscelis* species in the Pic Collection, Muséum National d'Histoire Naturelle, Paris.

In 1842 Duponchel and Chevrolat briefly described the genus *Aulacoscelis* and the species *melanocera* which they considered close to *Phyllocharya* of the Chrysomelinae. In Dejean's catalogue (1837), the genus and species were credited to Chevrolat, but these are nomen nuda and thus the reference is invalid. Stål (1865) described *Aulacoscelis melanocera* without referring to Duponchel and Chevrolat and placed it in the Chrysomelinae. In 1874, Chapuis created the tribe Aulacoscelini (as Aulacoscérites) and transferred *Aulacoscelis* from the Chrysomelinae to the Sagraeae. He also described a second species from Guatemala. Gemminger and Harold (1874) listed the known *Aulacoscelis* species as Sagraeae. Jacoby (1877, 1880, 1888) described and illustrated several *Aulacoscelis* species and listed those species known from Central America. He placed the genus in the Sagraidae. In 1903, in the revision of the genera of Sagraidae for Wytzman's *Genera Insectorum*, Jacoby excluded *Aulacoscelis* which he referred to the Chrysomelinae. Clavareau (1913) listed the 12 known *Aulacoscelis* species and placed the genus in the tribe Aulacoscelini at the end of the Sagraeae. In the catalogues of Leng (1920) and Blackwelder (1946), *Aulacoscelis* was included in the Aulacoscelini of the Sagraeae. Maulik (1941) briefly stated that *Aulacoscelis* cannot be considered as belonging to the Sagraeae.

In 1946 Crowson revised the genus which he placed in the Aulacoscelini, one of the three Sagraeae tribes. Sagraeae sensu lato was used and included *Orsodacne* and related genera which are now placed in the Orsodacninae, Zeugophorinae and Syntetinae; as well as the Hornibiini which are now considered primitive Eumolpinae. Crowson stated that *Aulacoscelis*, though included in the Sagraeae is evidently not nearly related to any of the genera of Sagraeae, nor can it easily be included in Orsodacnini, so that he thought that it must constitute a separate tribe. However, he considered *Aulacoscelis* as one of the most anomalous of the entire Chrysomelidae, and from a purely theoretical point of view might even be regarded as meriting a subfamily of its own.

Monrós (1949) excluded the Aulacoscelini from the Sagraeae and suggested a position among the primitive Eumolpinae. Later, in 1953, he established the new subfamily Aulacoscelinae when he described the new genus *Janbechynea* from Bolivia. He made a comprehensive revisional study of the Aulacoscelinae in 1954, but did not elaborate on its phylogenetic or systematic position, merely suggesting that it was among the most ancient of the living Chrysomelidae. Jolivet (1959, 1988), Crowson (1955), Monrós (1955, 1959a, b), Iablokoff-Khnzorian (1966, 1967), Medvedev (1971), Arnett (1973), Jolivet and Petitpierre (1981), Mann and Crowson (1981, 1983a, b, c), Seeno and Wilcox (1982), Petitpierre *et al.* (1988), Suzuki (1994a, 1994b, 1996) all recognized the subfamily Aulacoscelinae. However, Suzuki (1974a, 1980, 1985, 1988) placed the two tribes Aulacoscelini, plus the Chrysomelini in the subfamily Chrysomelinae. Reid (1995) divided the Chrysomeloidea into seven families, one of which, the Orsodacnidae comprised the subfamilies Aulacoscelidinae (= Aulacoscelinae) and the Orsodacninae.

Medvedev (1975) described three new *Aulacoscelis* species and a new subspecies of *A. variabilis* Jacoby.

Distribution

The Aulacoscelinae are restricted to the Western Hemisphere and are principally Neotropical in distribution. However, two species occur in the southwestern states of the USA. Apparently, *Aulacoscelis hogeii* Jacoby, described from Vancouver Island in western Canada is probably a labelling error (Monrós, 1954). The Central American mainland has most *Aulacoscelis* species. The subfamily is absent from the Caribbean Islands, as are the Megascelinae, although it occurs at equivalent latitudes on the Central American mainland. Some species have wide distributional ranges (see Monrós, 1954: figure 3, p. 354), although *A. melanocera*, one of the most widespread, may be a species complex.

Adult feeding habits

The adults are known as Cycadophyta leaf feeders and as flower visitors. The following information is available regarding the food plants of adult aulacoscelines.

According to Monrós (1954), *Aulacoscelis costaricensis* Bechyné occurred on the leaves of *Cycas revoluta* in Costa Rica. A series of specimens in the BMNH were collected feeding on *Zamia fairchildiana* in Costa Rica. In Mexico and El Salvador, *A. melanocera* occurred on the sago palm, *Cycas revoluta*, Cycadaceae in Honduras. The adults of *A. candezei* Chapuis are known from the flowers of Asteraceae in New Mexico (Monrós, 1954). A heavy infestation of *Janbechynea (J.) elongata* (Jacoby) occurred on cycads in Mexico (Monrós, 1954).

Apparently, according to Monrós (1959b) adults of *Aulacoscelis vogti* Monrós were taken on the flowers of *Hechtea texensis* (Bromeliaceae) from the Rio Grande area of southern Texas.

Aulacoscelis species are probably not host specific, since *A. costaricensis* and *A. melanocera* are reported feeding on the introduced *Cycas revoluta*.

It is noteworthy that the Aulacoscelinae are not represented in Florida or the West Indies, although *Zamia* and other cycads are known in these areas.

Ecology

Aulacoscelis seem to prefer semi-arid conditions, although *A. costaricensis* and *A. melanocera* are found in tropical rain forest. However, the latter species can occur in a variety of habitats, from the high plateaus of central Mexico, to the limestone country of north Yucatan and the tropical rain forest of the Canal Zone (Monrós, 1954). However, those specimens from the Canal Zone, may well turn out to belong to *A. appendiculata* n. sp. Monrós (1954) reported taking *A. candezei* from a dry, highly irrigated and cultivated area in New Mexico, not far from Albuquerque. The only specimen collected was found on the flowers of an indet. Asteraceae, and its behaviour was similar to that of *Orsodacne* adults. It was collected at about 11.00 am on 14 June, 1953, and it was not very active, but tried to fly away. It is possible that adults are also active at night since those of *A. hogeii* occurred at light. Data from museum specimens suggests that the adults of some species can occur between 100–1415 m altitude in Mexico and Panama, for example *A. costaricensis*, at 1200 m in Costa Rica; *A. hogeii*, 1415 m in Mexico; *A. appendiculata* sp. n., 100–1230 m in Panama; *A. sanguinea* Jacoby, 1415 m in Mexico and *J.(B.) melyroides* (Crowson), 1415 m in Mexico.

Apparently, nothing is published concerning the adults dates of occurrence. From museum specimens *C. costaricensis* occurs during May; *C. hoguei* and *J.(B.) melyroides* during June; and *C. sanguinea* and *J.(J.) paradoxa* Monrós during July. The adults are probably relatively short-lived but adults of *C. appendiculata* sp. n. occur from late April into May but some survived during 1997 from May for two months when enclosed within a terrarium with soil and cycad material.

Of the Chrysomelidae, only the larvae of the Aulacoscelinae remain undescribed and nothing is known concerning the larval feeding habits. Crowson (1946: 85) stated 'it would be desirable to obtain larvae of some species of *Aulacoscelis*, as the larval habits and structure should be of great assistance in determining its systematic position'. The aim of this paper is to describe the adults and first instar larva of *Aulacoscelis appendiculata* sp. n. The first instar larva is the most useful from a phylogenetic standpoint, since it often carries egg bursters which are lost at the first moult and the chaetotaxy is simplified comprising only primary setae which in later instars sometimes becomes obscured by the addition of secondary setae. Its morphological characters are used to relate the Aulacoscelinae to other chrysomelid subfamilies, especially the Orsodacninae.

The systematic position of the Aulacoscelinae is still much confused which is surprising considering that the adult morphology in this small group is relatively consistent and well studied. The adult morphology will be reviewed and the larval characters discussed against what is known concerning the adult characters of mandibles, maxillary digiform sensilla, metendosternite, wing venation, male and female genitalia, tarsal adhesive setae and claws.

Materials and methods

On 7 May 1993, numerous adults of *Aulacoscelis appendiculata* sp. n. were collected from low vegetation at the 1,100 m pass, La Fortuna catchment, 3 km north of Hornitos, Chiriqui, Panama. On 12 May 1997, numerous adults were again collected at this pass as they settled on the vegetation from a migratory swarm. Adults of the same species were observed flying from damaged *Zamia fairchildiana* foliage on 5 May 1991, at Cerro Azul (850 m), 300 km east of the Chiriqui site and 20 km northeast of Panama City. On 25 April 1997, a single adult of the species was observed actively feeding on a *Z. fairchildiana* leaf at the same location. *A. appendiculata* sp. n. fed on *Z. fairchildiana* plants throughout the month of May 1997 at this and a second location, Madden Forest (300 m), 20 km north of Panama City. A single oviposition was obtained from one of thirty adults collected from the migratory swarm in Chiriqui, enclosed within a terrarium with soil, cycad and fresh strips of mango for two months. Approximately 40 eggs were clumped without any order, attached to the underside of a piece of cycad stem lying upon the soil. Oviposition occurred on 24 June, eclosion on 6 July, incubation thus requiring about 12 days.

Most of the eggs were fatally attacked by fungi, nematodes and Acari, but six larvae successfully eclosed.

Key to adults of the *Aulacophora melanocera* species group

- 1 Females with a basal elytral tubercle between scutellum and humerus; females with final ventrite with median lobe apically (figure 37) *tuberculata* Medvedev
- Females without a basal elytral tubercle between scutellum and humerus; females with final ventrite evenly curved apically (figures 27, 31, 34) 2

- 2 Antennae entirely dark brown or black; legs black, except coxae yellowish; segments of maxillary palpi entirely dark brown; Costa Rica; on cycads, *Cycas revoluta*, *Zamia fairchildiana* *costaricensis* Bechyné
- Antennae not entirely dark brown or black, basal segment reddish brown; legs reddish orange with apical quarter of femora, tibiae, tarsi black or dark brown; maxillary palpi with only apical segment dark brown 3
- 3 Elytra with apical sutural tooth in female (figures 58, 59); males with median lobe of aedeagus 2.75–3.13 mm in length, apically entire, tegmen 2.65–3.05 mm in length with large lateral lobe (figures 2, 4); Panama; on *Zamia* spp. including *fairchildiana* *appendiculata* sp. n.
- Elytra usually without apical sutural tooth in female; males with median lobe of aedeagus shorter, 2.54–2.70 mm in length, apically very narrowly split, tegmen shorter, 2.10–2.43 mm in length, with smaller lateral lobe (figures 10, 13); Mexico; on *Cycas revoluta*. *melanocera* Duponchel and Chevrolat

Aulacoscelis appendiculata sp. n.

(figures 1–9, 24–27, 48, 51, 54–69, 70, 71)

Material

HOLOTYPE♂, **Panama**: Chiriqui Province, 3 km N. of Hornitos, 7.v.1993, swarming on *Zamia* sp. (*Stockwell and Gillogly*) (BM(NH)). **PARATYPES** (same data as Holotype), 6 ♂♂, 10 ♀♀ (BM(NH)); also ♂, Volcan de Chiriqui, 800–1066m (*Champion*, BCA coll. VII as *melanocera*); 2 ♂♂, 4 ♀♀, Chiriqui Province, La Fortuna, 1200 m., 8°45'N, 82°15'W, 15.v.1991 (*Windsor*); 1 ♂, Chiriqui Province, Reserva La Fortuna, 15.v.1993 (*Gillogly*); 1 ♀, Chiriqui Province, La Fortuna Pass, 12.v.1997 (*Windsor*); 2 ♂♂, 1 ♀, Pmá Province, Cerro Azul, 800 m, 9°13'N, 79°24'W, 5.v.1991 (*Windsor, Stockwell*); 1 ♂, Colon Province, Madden Dam, 100 m, 9°12'N, 79°37'W, 14.v.1997 (*Windsor*); 2 ♀♀, Volcan de Chiriqui, 530–800m (*Champion*, BCA coll. VI. I as *melanocera*).

Distribution

A. appendiculata is widespread in Panama, occurring from Chiriqui Province in the west to Colón Province north of Panama City, east to Panamá Province. Apparently, it does not occur in Costa Rica and Colombia, countries bordering Panama.

Description Body length (mm): ♂♂ 6.21–7.73, \bar{x} = 6.95 (n = 12); ♀♀ 6.49–8.23, \bar{x} = 7.62 (n = 17). Dorsally entirely reddish orange, except parts of palpi, mandibles, antennae and legs black.

Head slightly narrower than anterior margin of pronotum; sparsely, moderately finely punctured, also indistinctly reticulately microsculptured; antennae similar in both sexes, black, except basal segment reddish brown; maxillary palpi with apical segment black, segment one yellowish, segment two slightly darker; labial palpi with apical segment brownish, segments one and two yellowish; mandibles apically unidentate in both sexes, apex black.

Pronotum slightly wider than long, ratio width: length, ♂♂, 1.35–1.50, \bar{x} = 1.41 (n = 7); ♀♀, 1.37–1.44, \bar{x} = 1.40 (n = 12); broadest just before middle; anteriorly unmarginated, anterior corners rounded; laterally with fine margin, sinuous, with fine inner sulcus; basally slightly sinuous, with distinct margin with furrow anteriorly, sublaterally on each side with obtuse tooth arising from margin, anterior to this a larger, backwardly-directed, apically rounded process; posterior angles distinct;

very slightly obtuse; punctuation sparse, moderately fine, shallow, fine reticulate microsculpturation throughout; bearing very few, scattered, erect golden setae.

Scutellum tongue-shaped, gradually narrowing to broadly rounded apex, punctuation moderately fine, sparse, usually in pre-apical transverse band; finely reticulately microsculptured; bearing few sparse silvery setae basally.

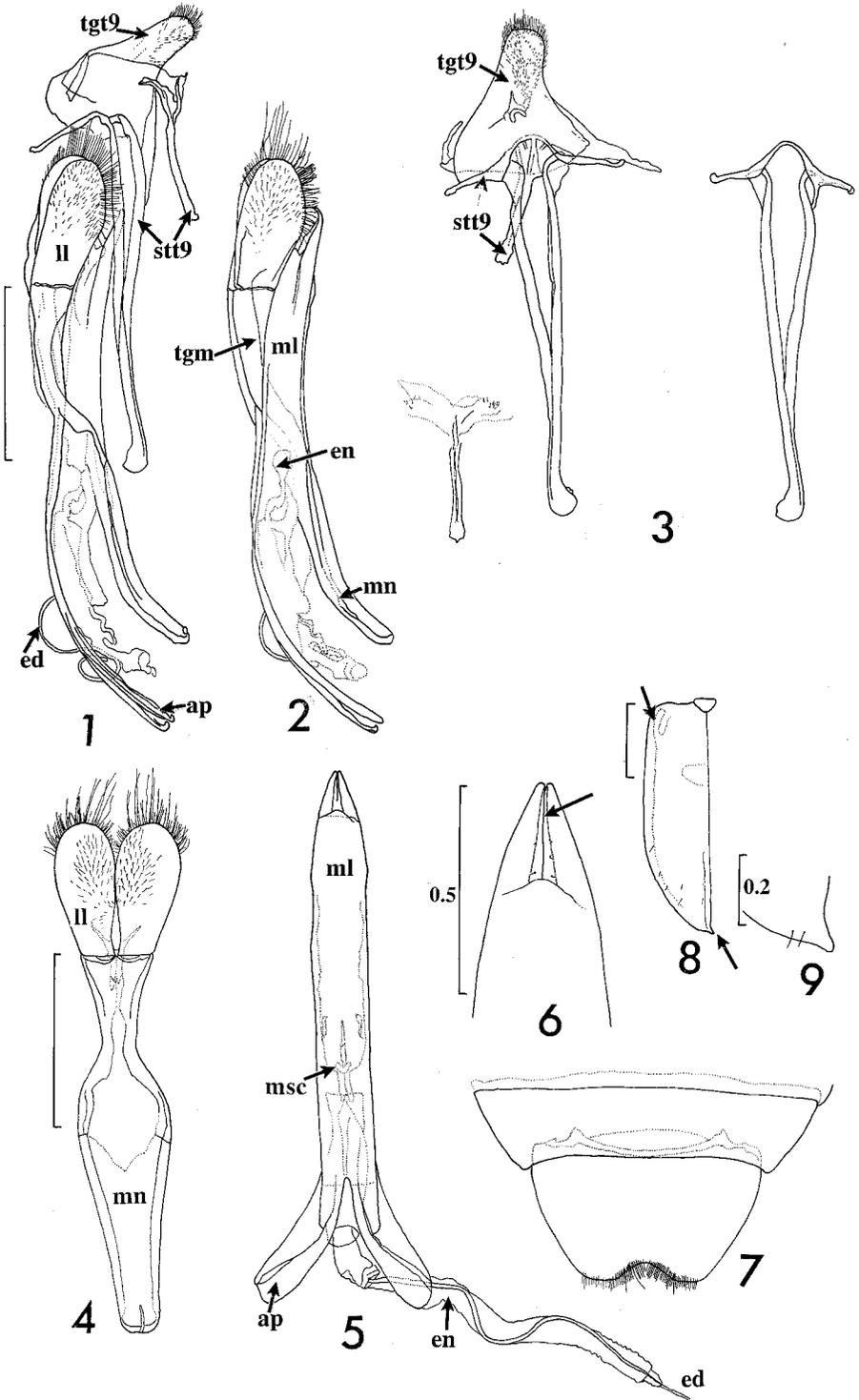
Elytra with length about three times width, ratio length: width, ♂♂, 2.91–3.34, \bar{x} = 3.15 (n = 8), ♀♀, 3.05–3.23, \bar{x} = 3.14 (n = 11); humeri distinct, in females continuing as distinct humeral costa for about one quarter elytra length, then becoming an indistinct, broad, sublateral costa almost to apex; elytra in females with transverse depression about one third length from base; males with elytra shiny, reticulate microsculpturation indistinct as is green/purple metallic lustre, apically simple, without tooth at sutural angle; females with elytra dull, reticulate microsculpturation distinct as is green/purple metallic lustre, apical sutural angle with moderately long, slightly curved tooth (figures 58, 59); suture convex with lateral sulcus running about one third elytral length from apex; punctuation moderately fine, confused; bearing 6, usually incomplete rows of sparse, semierect, long golden setae, one along suture, 4 on disc, one sublaterally; epipleura widest at humeri, gradually narrowing posteriorly, terminating just before apex, slightly inclined basally, subhorizontal towards apex, bearing short, sparse golden setae, also along inner margin.

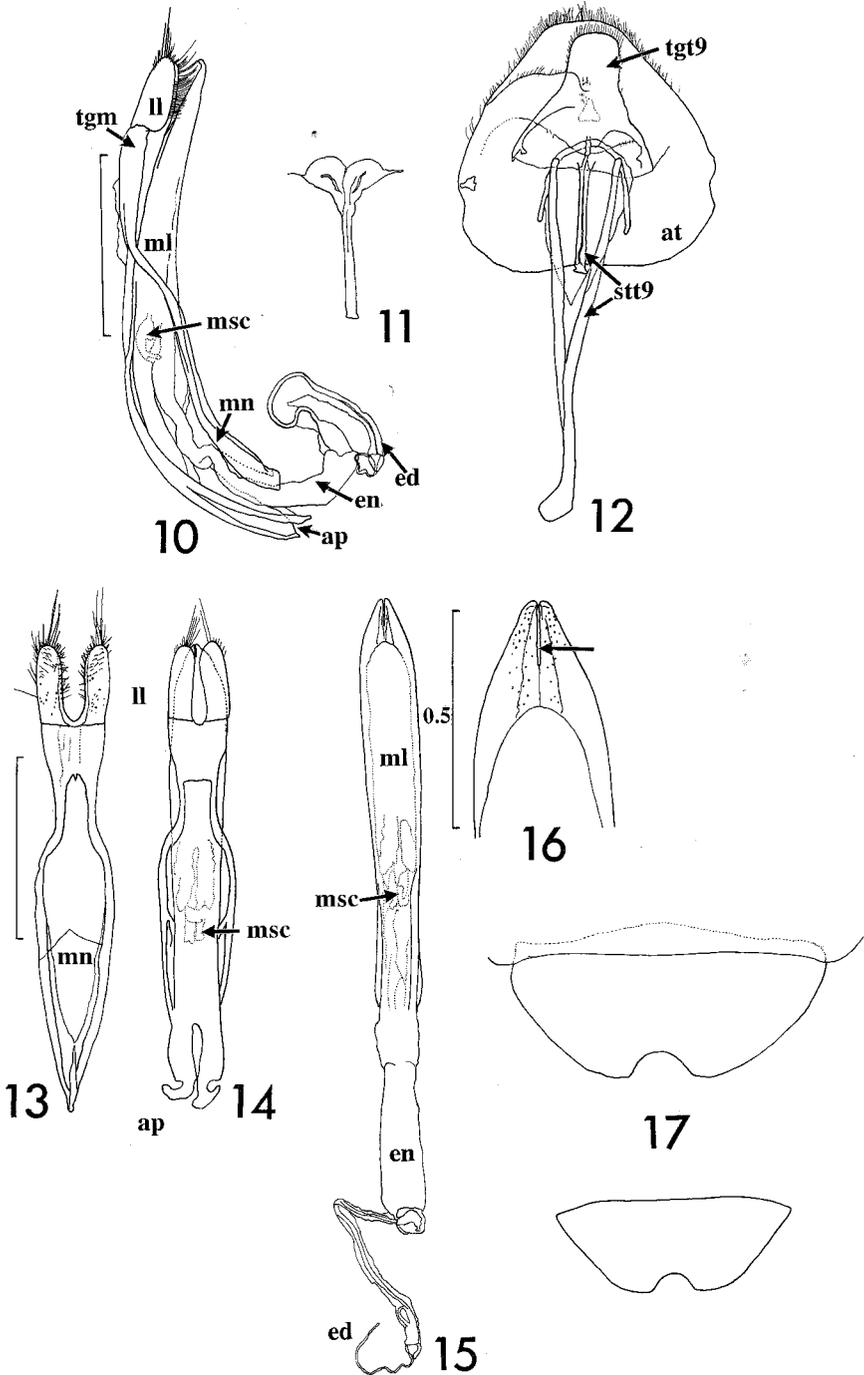
Ventrally entirely reddish orange; legs black, except coxae, trochanters, basal three quarters femora reddish orange; sometimes tibiae and tarsi brownish; claws yellowish, with tips pale brown; males pro-, mesotarsal segments one broadened, slightly broader than tibial apices; females pro-, mesotarsal segments one, not broadened, narrower than tibial apices; males last abdominal sternite with median apical emargination (figure 7); females last abdominal ventrite (figure 27) sub-circular, with apex very gradually evenly rounded.

Male genitalia (figures 1–7) with median lobe uniformly sclerotized, apex acuminate, with deep median furrow, not longitudinally split into two parts, proximally divided into pair of long, rod-like apodemes (median struts); endophallus (internal sac) long, extending well beyond the ends of the median struts, with distinct median sclerites; tegmen ring-like, united dorsally, forming lateral lobe (distal lobe, styli, or tegmental cap) over apical portion of median lobe; lateral lobe broad, densely setose dorsally and apically, deeply bilobed apically; manubrium (basal piece) formed by arms of ring piece of tegmen fusing lies ventrally to apodemes; sternite 9 (spiculum gastrale) large, consisting of two parts, a larger, Y-shaped part more than half length of median lobe, with a fused basal half, each arm apically with recurved, short dorsal arms about one sixth length of sternite 9 and about 45° to this, in addition, there is another approximately T-shaped piece about one quarter length of median lobe, with symmetrical, short, diverging arms, with apodeme moderately long; tergite 9 spatulate; apical tergite gradually narrows to evenly rounded apex.

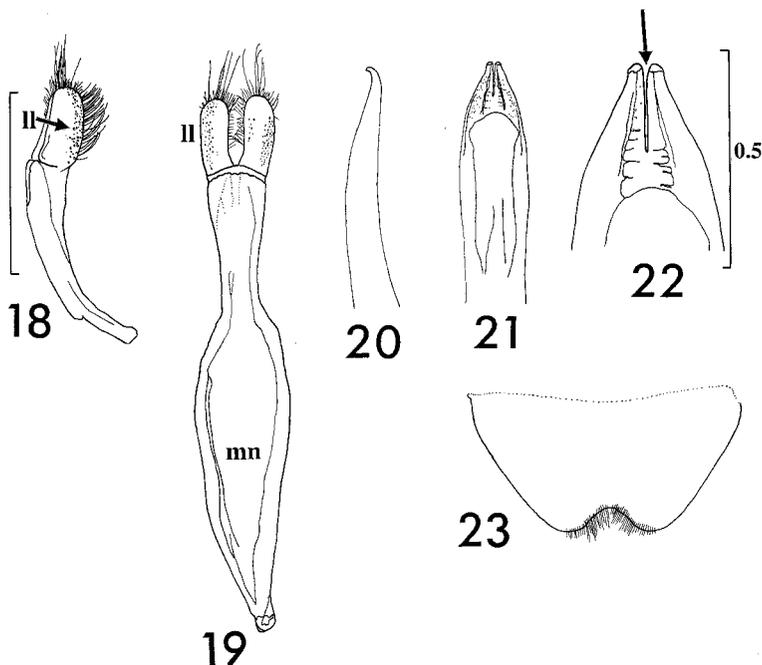
Female genitalia (figures 24–27) with ovipositor rather strongly sclerotized and

FIGS. 1–9. Parts of male genitalia, *Aulacoscelis appendiculata* sp. n.: (1) lateral view male genitalia complete; (2) lateral view aedeagus complete; (3) dorsal views parts of sternite 9; (4) dorsal view tegmen; (5) dorsal view median lobe; (6) apex median lobe enlarged; (7) apical ventrites 4 and 5; (8) dorsal view left elytron♀; (9) apex of elytron enlarged. Abbreviations: ap, apodeme; ed, ejaculatory duct; en, endophallus; ll, lateral lobe; ml, median lobe; mn, manubrium; msc, median sclerites; stt9, sternite 9; tgm, tegmen; tgt9, tergite 9. Scale line in mm and equal to 1 mm, unless otherwise stated.





FIGS. 10–17. Parts of male genitalia, *Aulacoscelis melanocera*: (10) lateral view aedeagus complete; (11) dorsal view part of sternite 9; (12) dorsal view sternite 9 complete, *in situ*; (13) dorsal view tegmen; (14) dorsal view tegmen and median lobe; (15) dorsal view median lobe; (16) apex median lobe enlarged; (17) apical ventrites. Abbreviations: ap, apodeme; at, apical tergite; ed, ejaculatory duct; en, endophallus; ll, lateral lobe; ml, median lobe; mn, manubrium; msc, median sclerites; stt9, sternite 9; tgm, tegmen; tgt9, tergite 9. Scale line in mm and equal to 1 mm, unless otherwise stated.



FIGS. 18–23. Parts of male genitalia, *Aulacoscelis costaricensis*: (18) lateral view tegmen; (19) dorsal view tegmen; (20) lateral views apex median lobe; (21) dorsal view apex of median lobe; (22) apex median lobe enlarged; (23) apical ventrite. Abbreviations: ll, lateral lobe; mn, manubrium. Scale line in mm and equal to 1 mm, unless otherwise stated.

pigmented, elongate valves subparallel-sided, cylindrical, elongate, supported by two somewhat sinuous, sclerotized rods running entire length; valves (coxites/hemisternites) with apices rounded, bearing about 6 or 7 very long setae, plus long, finger-like styli with apically one long seta, plus usually one or two much shorter setae, rarely three such setae; bursa copulatrix moderately short, sac-like, median oviduct joining below (posterior to) junction of spermathecal duct; spermatheca U-shaped, basal nodulus only slightly dilated, cornu much shorter than nodulus, slender, upturned, apically pointed; collum short; moderately long, non-coiled spermathecal duct and short spermathecal gland opening into base of collum; spiculum ventrale sternite 8 (spiculum ventrale) elongate, narrow, about as long as ovipositor, with basal short hook, apically divided into three short processes; apical tergite gradually narrowing to evenly rounded apex.

Differences from closely related species

A. melanocera is probably the closest relative of *A. appendiculata*. The males have very similar morphology. However, the male genitalia differ in that the median lobe is apically bilobed and deeply split in dorsal view in *melanocera* (figure 16), but apparently entire in *appendiculata* (figure 6). The lateral lobe is much larger in the latter (figures 1, 5) than in the former (figures 10, 13, 14). The relative lengths of the median lobe, tegmen and sternite 9 in these two species are shown in the table below.

	<i>A. appendiculata</i>			<i>A. melanocera</i>		
	range	x	n	range	x	n
median lobe length (mm)	2.75–3.13	3.00	10	2.54–2.70	2.59	5
tegmen length (mm)	2.65–3.05	2.88	12	2.10–2.43	2.25	8
sternite 9 length (mm)	2.05–2.38	2.17	12	1.62–2.00	1.77	8

The females of the two species are usually readily separated externally by the presence of the posthumeral costa, apical sutural tooth and distinct reticulate microsculpturation of the elytra in *appendiculata*.

A. costaricensis is also similar to *appendiculata* but the former has the antennae entirely dark brown or black, including the basal segment, whereas this is reddish brown in *appendiculata*. Moreover, the maxillary palpi are entirely dark brown or black in *costaricensis* but with only the apical segment dark in *appendiculata*. In addition, in *costaricensis*, the legs are almost entirely black, apart from the coxae which are yellowish. The male genitalia also differ as for *melanocera*. The females of *costaricensis* differ since they lack the elytral apical sutural tooth.

A. tuberculata Medvedev is similar to *appendiculata*, but also *melanocera* and *hogeii* Jacoby. Female specimens misidentified as *hogeii* (2 from BCA Col. VI. I Supplement) and three misidentified as *melanocera* are in the BM(NH) collection. Females of *tuberculata* differ from *appendiculata* and *melanocera* since the basal antennal segment is dark, concolorous with the remaining segments and the elytra basally have a blunt elongate tubercle between the humerus and the scutellum, whilst in *appendiculata* and *melanocera* the basal antennal segment is reddish, paler than the remaining segments and the elytra basally lack a tubercle. Moreover, females of *tuberculata* have the final ventrite with a median lobe apically (figure 37), whereas those of the other species have the final ventrite evenly curved apically (figures 27, 31, 34). The styli in females of *A. tuberculata* have a single long apical seta (figure 36), whilst in the other species in addition there are usually one or two shorter setae (figures 26, 28, 29, 33). *A. hogeii* differs from *appendiculata* and *melanocera* since the pronotum has a distinct anterior margin.

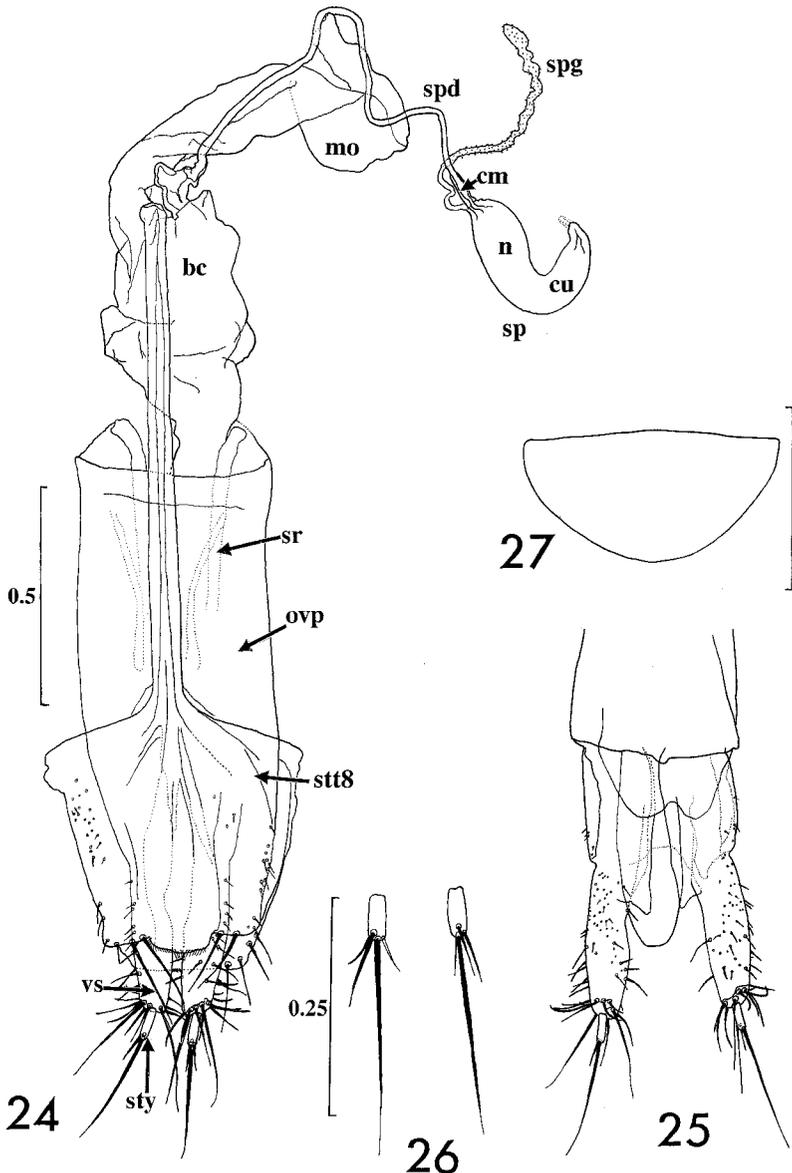
Description of immature stages of *Aulacoscelis appendiculata*

Eggs.

The following description is of eggs laid in the Panama laboratory, 24 June 1997. Approximately 40 eggs were deposited irregularly and attached to the underside of a piece of cycad stem laying upon the soil. The egg mass apparently consisted of packets comprising two, four, six, seven, and nine eggs. The ovariole number of an individual dissected female was 70 (36 left, 34 right) (D. Windsor personal observation). The eggs are white, very elongate, usually straight, or sometimes slightly curved and blunt, evenly rounded at both ends, with neither end more pointed than the other. They vary in length from 1.29 to 1.52 mm, with a mean of 1.43 mm, whilst their width varies from 0.27 to 0.35 mm with a mean of 0.29 mm ($n=20$). The chorion is transparent, without evident microsculpturation. Apparently, they are not covered with a colourless spumaline secretion.

Larvae (figures 54–69)

First instar larva Head width: 0.21–0.23 mm, $x=0.22$ mm ($n=5$);
 Body length: 1.38–1.86 mm, $x=1.70$ mm ($n=5$);
 Body width: 0.20–0.31 mm, $x=0.26$ mm ($n=5$).



FIGS. 24–27. Parts of female genitalia, *Aulacoscelis appendiculata* sp. n., (24) dorsal view entire; (25) dorsal view genital valves; (26) genital styli enlarged; (27) apical ventrite. Abbreviations: bc, bursa copulatrix; cm, collum; cu, cornu; n, nodulus; mo, median oviduct; ovp, ovipositor; sp, spermatheca; spd, spermathecal duct; spg, spermathecal gland; sr, sclerotized rod; stt8, sternite 8; sty, styli; vs, valves. Scale line in mm.

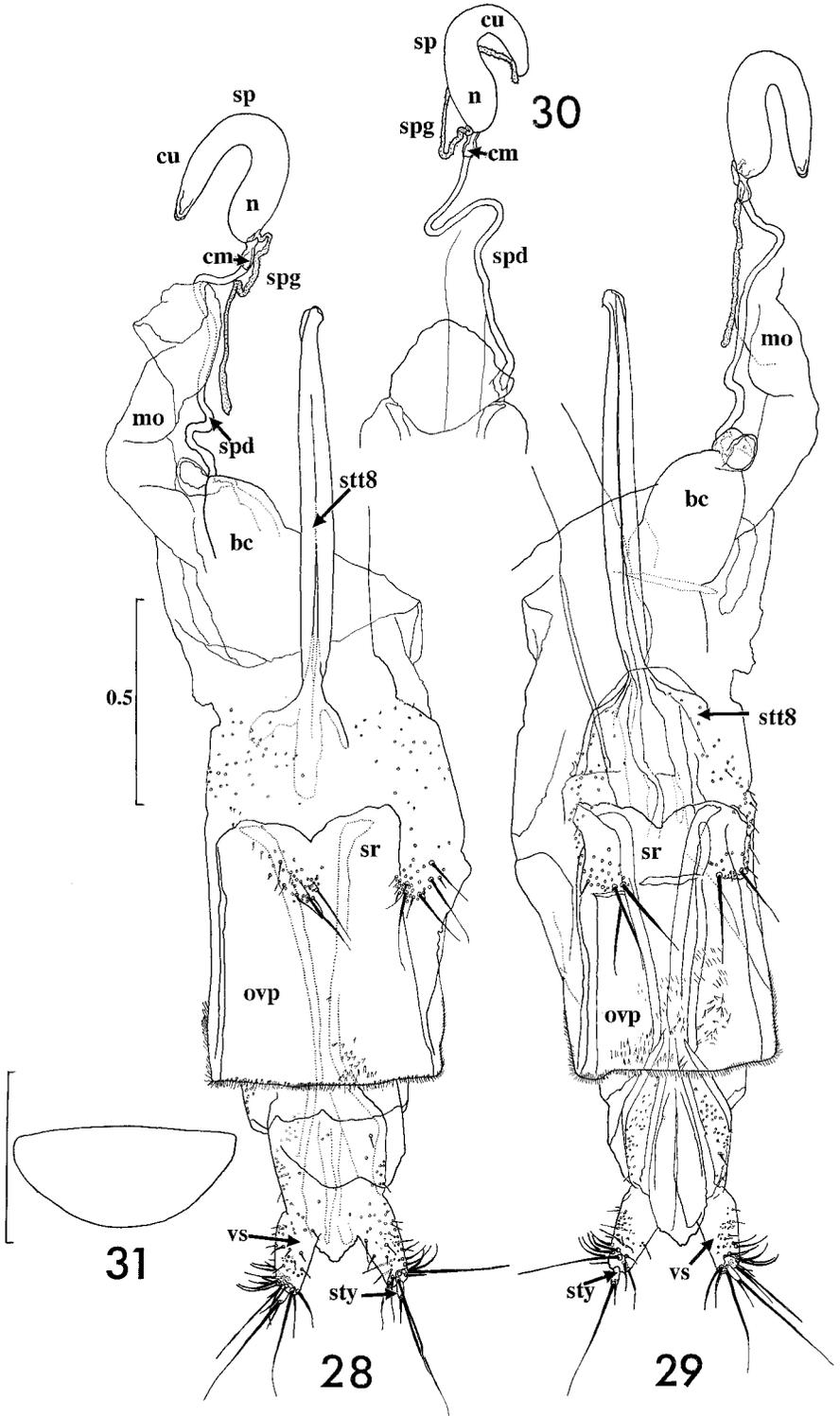
General habitus (figures 61, 62). White; head, anal plate pale yellow. Elongate, narrow, approximately same width along entire length; greatest width at about abdominal segments two to three; length approximately six times greater than width. Tubercles pale yellow, small, indistinct, somewhat darker, more distinct ventrally. intertubercular plates indistinct, multidentate posteriorly (figure 65). Setae well developed, longest on head, anal plate apically, ventrally on abdominal segment 9;

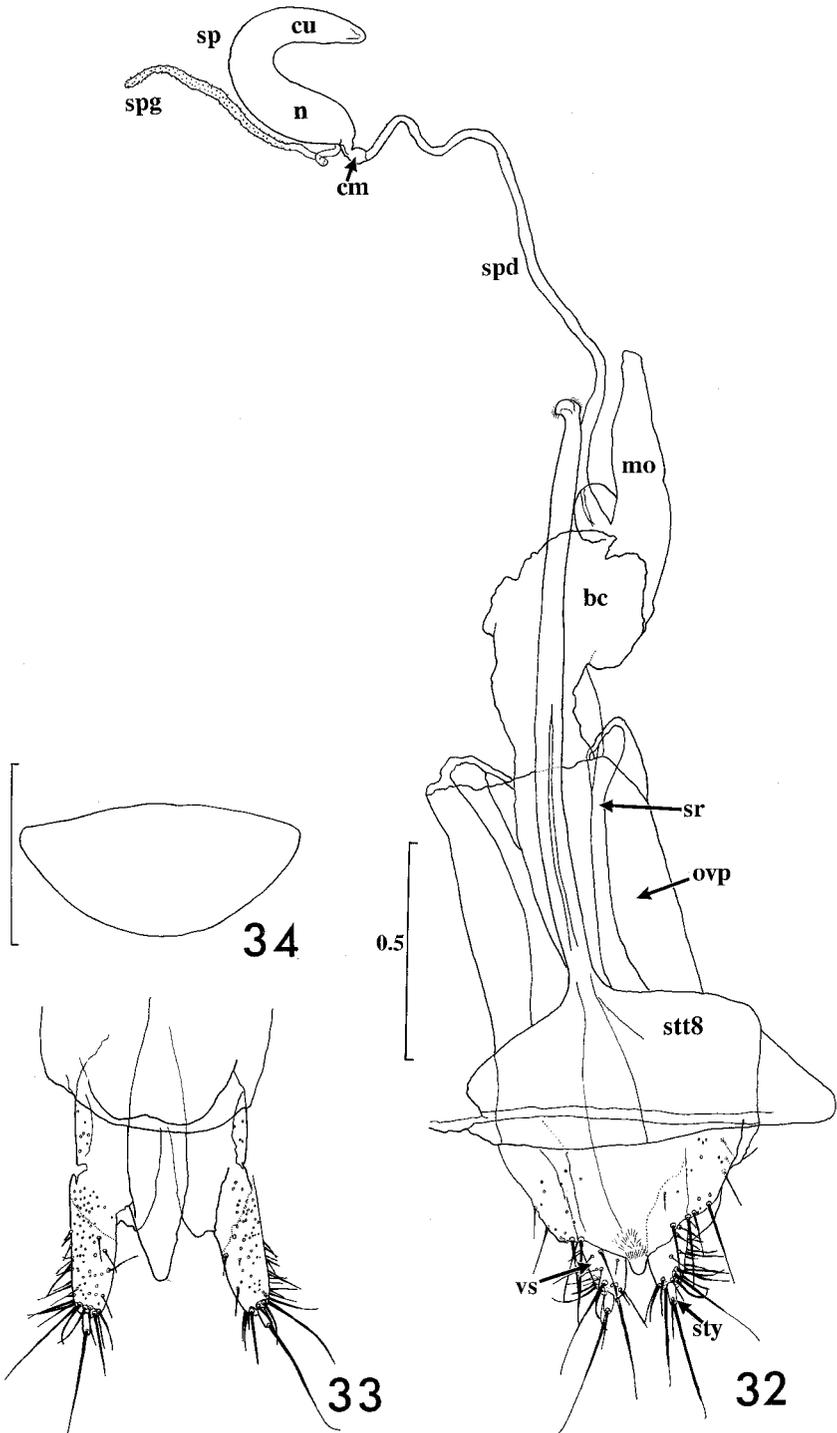
ventral body setae generally longer than dorsal setae. Thoracic legs moderately long, prothoracic legs slightly shorter than others.

Head (figures 54–60). pale yellow, pro- to hypognathous, exserted, slightly elongate-oval; epicranial suture with stem short; frontal sutures narrow, reaching antennae; endocarina (median suture) entire, reaching to indistinct, incomplete, fronto-clypeal suture; frons bearing three large setae (f_2, f_4, f_5), 4 campaniform sensilla, f_3, f_6 represented by one sensilla each; vertex bearing no large setae, v_2, v_3, v_4, v_6 , represented by sensilla, four other sensilla forming triangle dorsal to v_2 , gena bearing two large, one very small seta; ocelli, very small, indistinct, one posterior to antennae; clypeal area bearing four small setae, plus two sensilla; clypeo-labral suture indistinct; labrum (figure 55) with anterior margin evenly curved, not incised medially, bearing two long, two short, plus two sensilla dorsally, six setae antero-dorsally, 10 or 11 mostly flattened, curved setae along anterior margin on each side, antero-medially bearing numerous elongate spicules; mandibles (figures 56, 57) pale, apical part brown, sub-triangular, apically four dentate, dorsally bearing one long, one shorter seta, plus three campaniform sensilla, penicillus well developed, consisting of 12 or 13 densely-packed setae of varying lengths inserted on ventral surface about mid-way along inner margin; antennae short, apparently two segmented, anteriorly-directed, attached to head by broad basal articulating membrane, first segment at least two times broader than long, bearing campaniform sensilla laterally, dorsally bearing four short setae, segment two, plus an accessory conical process, about two times longer than segment 2, segment two pill-box-shaped, apically bearing four short setae, a peg-like seta, plus cigar-shaped process, about half length of segment two; labium (figure 58) with submentum bearing two long setae, mentum bearing two long setae, plus two campaniform sensilla anteriorly, labial palpi two segmented, apical segment slightly longer, narrower than basal segment, palpiger bearing basally one short seta, plus one sensilla, segment one bearing sensilla interolaterally, segment two with extero-lateral sensilla, apically bearing about five very short setae, plus cigar-shaped process, ligula bearing two setae, four campaniform sensilla, plus numerous, short, curved setae anteriorly; maxillae (figure 58) moderately long, cardo bearing very short seta, stipes bearing one very long seta basally, with sensilla lateral to it, also shorter seta apically, palpi three segmented, basal two segments subequal in length, apical segment two times longer than two basal segments, with about 11 short setae forming ring apically, also cigar-shaped process, palpifer bearing one long seta laterally, lacinia not differentiated, apparently fused with galea, galea bearing dorsally one sensilla, three setae plus pedunculate seta, ventro-laterally bearing fringe of about 13 variable setae, extending ventrally onto apical margin; stipes and basal part of galea ventrally bearing scattered elongate spicules, in places grouped two, three, four or five together in line; hypopharynx densely setose, with subparallel rods or bracon extending backwards from long mentum setae.

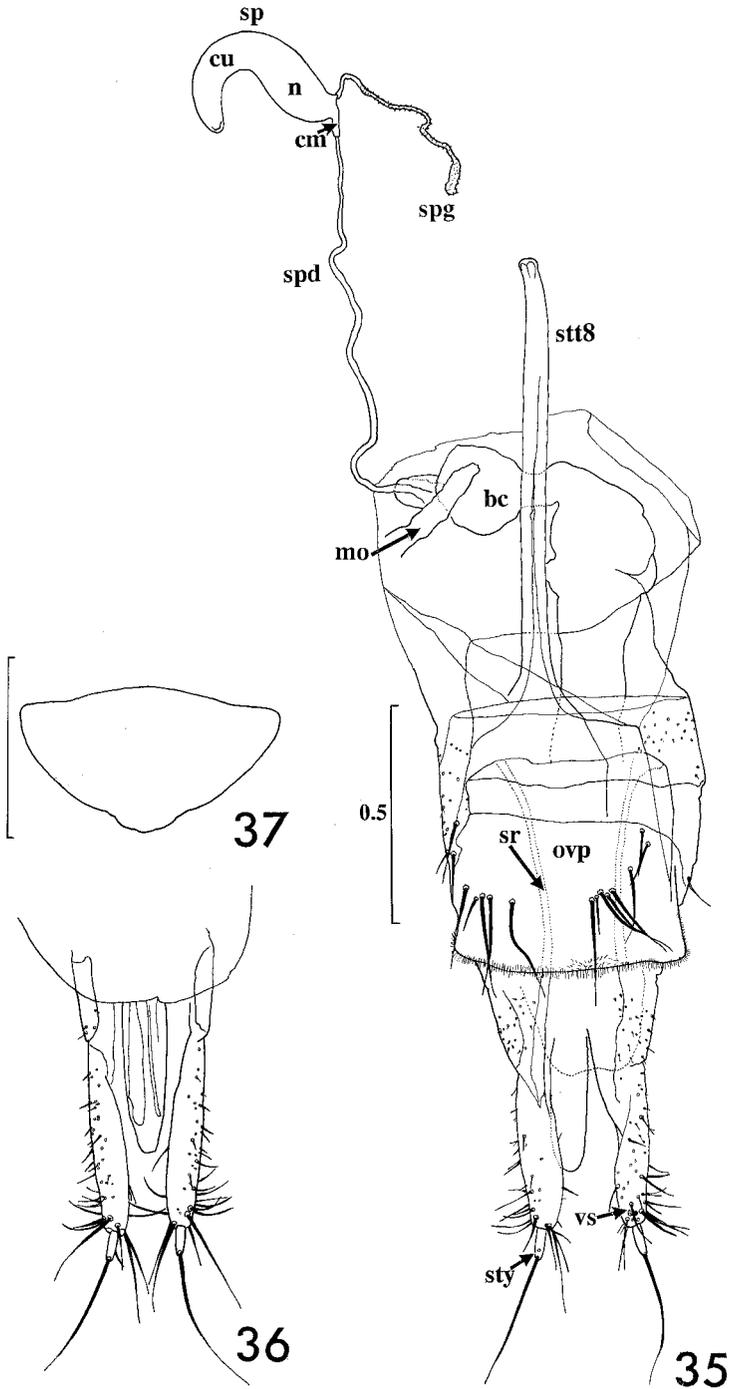
Body (figures 63–69). Whitish, elongate, subparallel-sided, tubercles indistinct, except for pronotum, tubercles DLae–DLpe on meso- and metathorax, anal plate;

FIGS. 28–31. Parts of female genitalia, *Aulacoscelis melanocera*: (28) ventral view entire; (29) dorsal view entire; (30) spermatheca; (31) apical ventrite. Abbreviations: bc, bursa copulatrix; cm, collum; cu, cornu; n, nodulus; mo, median oviduct; ovp, ovipositor; sp, spermatheca; spd, spermathecal duct; spg, spermathecal gland; sr, sclerotized rod; stt8, sternite 8; sty, styli; vs, valves. Scale line in mm.

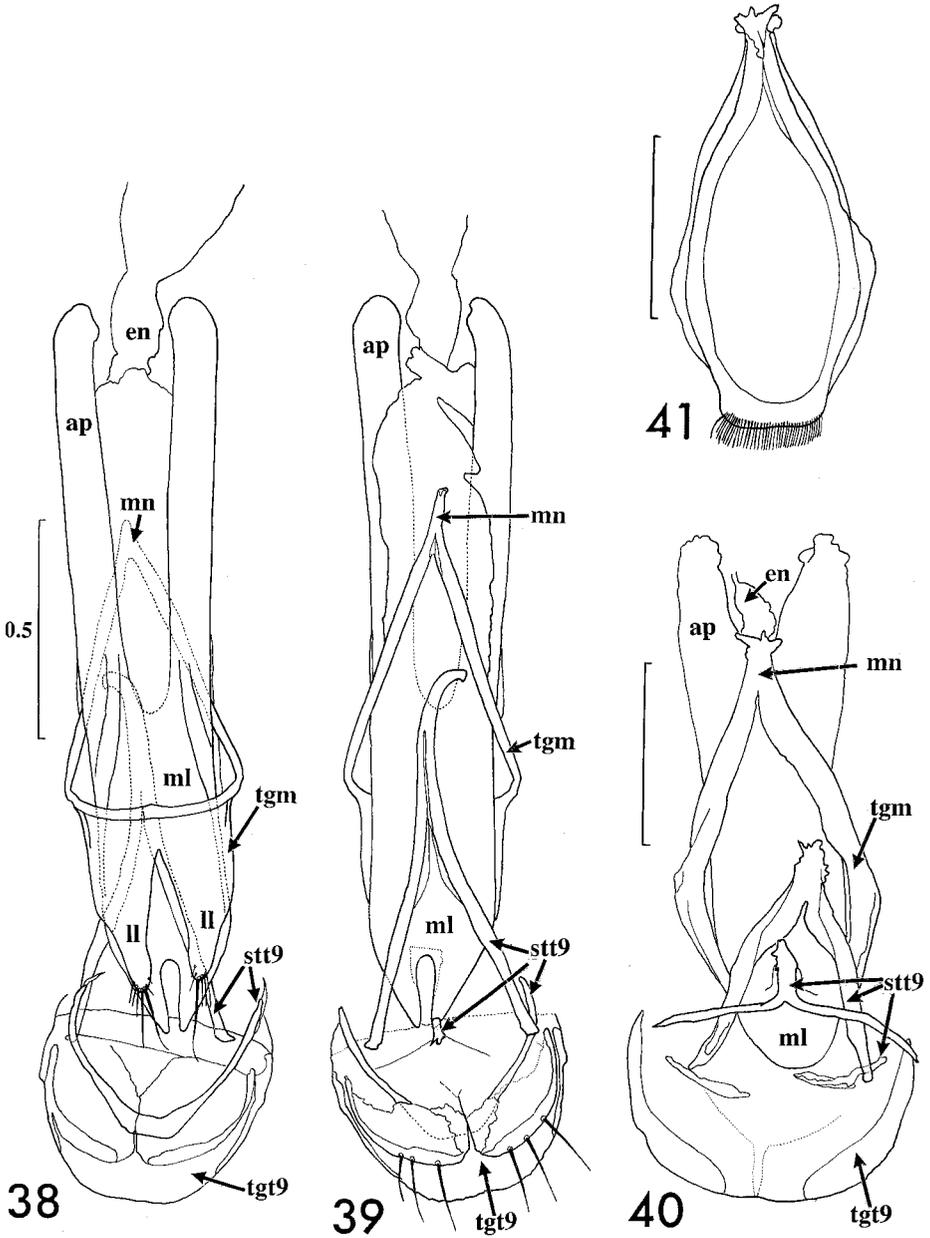




Figs. 32–34. Parts of female genitalia, *Aulacoscelis costaricensis*: (32) dorsal view entire; (33) dorsal view genital valves and styli; (34) apical ventrite. Abbreviations: bc, bursa copulatrix; cm, collum; cu, cornu; n, nodulus; mo, median oviduct; ovp, ovipositor; sp, spermatheca; spd, spermathecal duct; spg, spermathecal gland; sr, sclerotized rod; stt8, sternite 8; sty, styli; vs, valves. Scale line in mm.



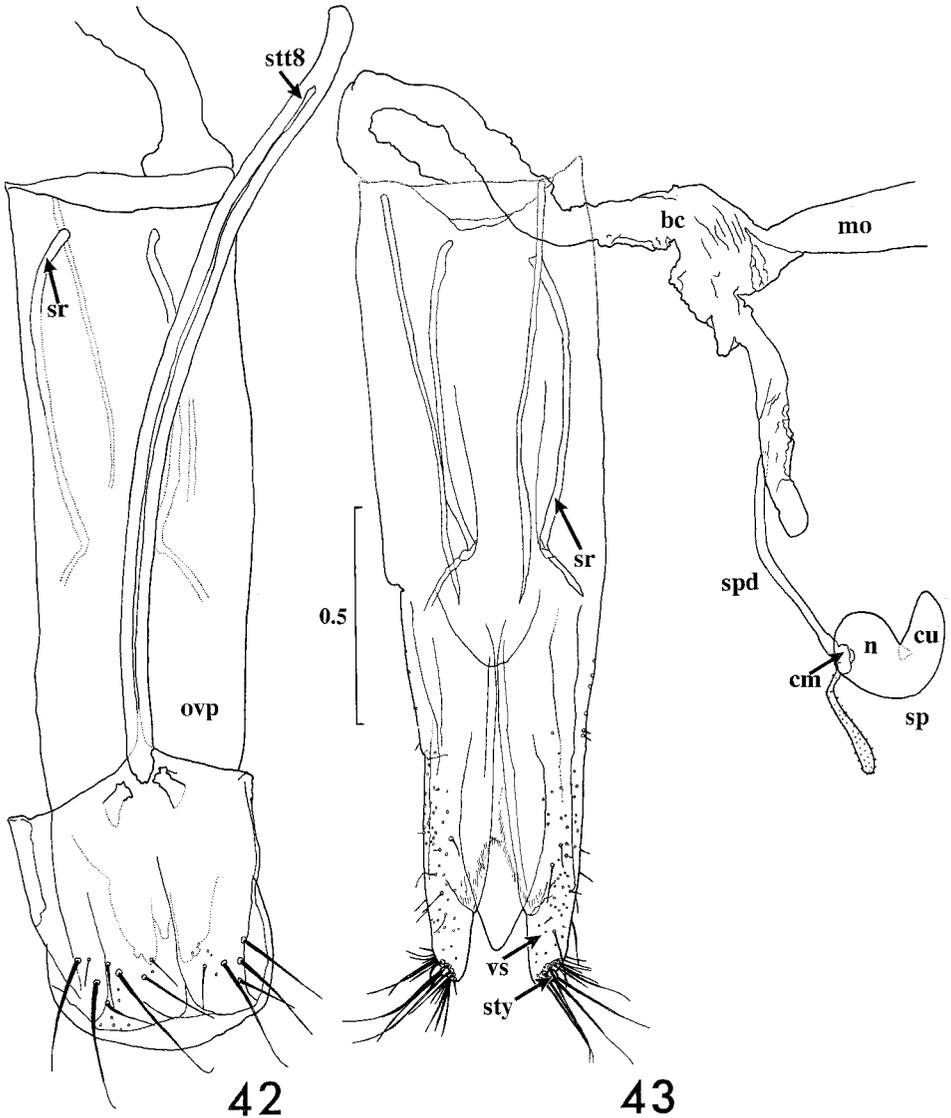
FIGS. 35–37. Parts of female genitalia, *Aulacoscelis tuberculata*: (35) dorsal view entire; (36) dorsal view genital valves and styli; (37) apical ventrite. Abbreviations: bc, bursa copulatrix; cm, collum; cu, cornu; n, nodulus; mo, median oviduct; ovp, ovipositor; sp, spermatheca; spd, spermathecal duct; spg, spermathecal gland; sr, sclerotized rod; stt8, sternite 8; sty, styli; vs, valvae. Scale line in mm.



FIGS. 38–41. Parts of male genitalia Orsodacninae and Chrysomelinae; (38, 39) *Orsodacne cerasi*; (38) dorsal view entire; (39) ventral view entire; (40, 41) *Timarcha goettingensis*, (40) ventral view entire; (41) tegmen dorsal view. Abbreviations: ap, apodeme; en, endophallus; ll, lateral lobe; ml, median lobe; mn, manubrium; stt9, sternite 9; tgm, tegmen; tgt9, tergite 9. Scale in mm.

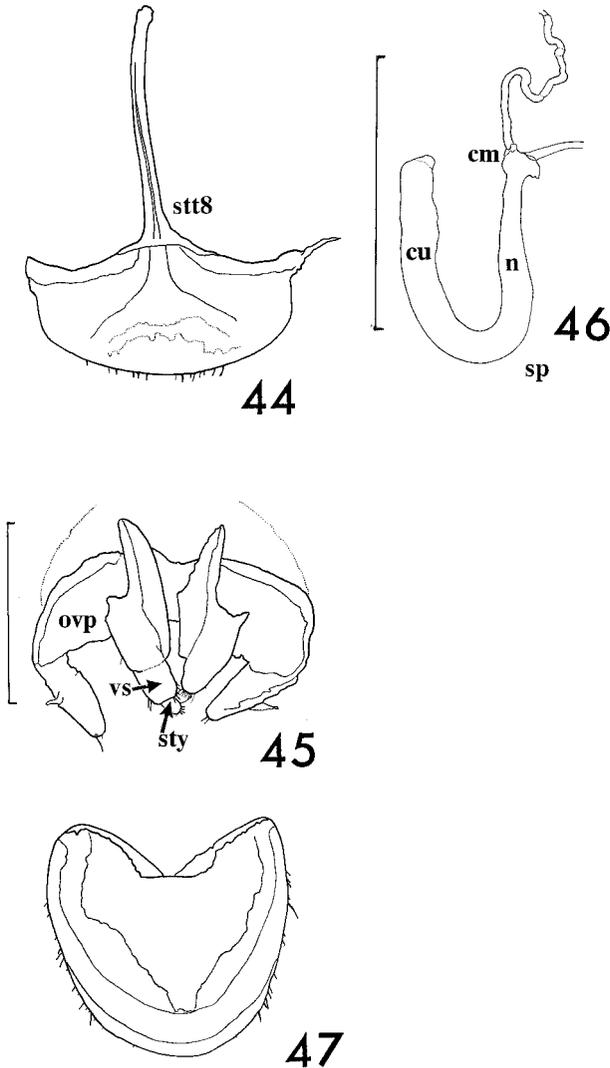
small, conical egg bursting spine on pronotum, meso- and metathorax, anterior to seta IV.

Thorax (figures 64, 65, 67). Prothorax with pronotal plate large, bearing nine or ten short setae, plus one very long antero-lateral seta, setae I–VIII present, setal



FIGS. 42–43. Parts of female genitalia, *Orsodacne cerasi*; (42) dorsal view ovipositor; (43) ventral view entire. Abbreviations: bc, bursa copulatrix; cm, collum; cu, cornu; n, nodulus; mo, median oviduct; ovp, ovipositor; sp, spermatheca; spd, spermathecal duct; spg, spermathecal gland; sr, sclerotized rod; stt8, sternite 8; sty, styli; vs, valves. Scale line in mm.

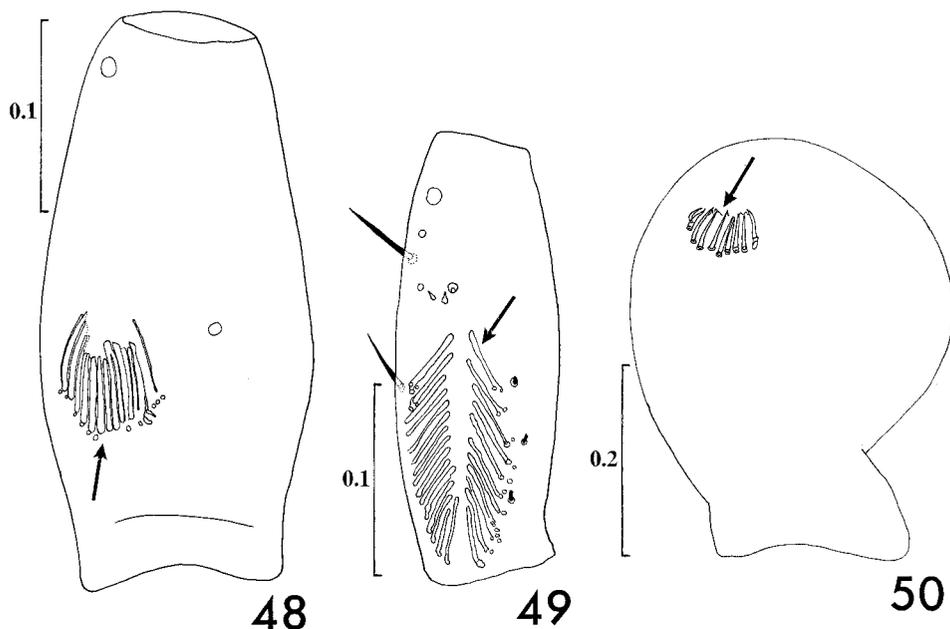
groups I, III and IV probably bisetate, a conical hatching spine anterior to seta IV, five or six small campaniform sensilla; tubercles EPa, EPp bearing setae IX, X, respectively; T present, bearing seta XI, plus two minute setae anteriorly; P indistinct, seta XII present; As, Ps absent; Es and Ss fused (not fused across mid-ventral line) bearing two large setae, XV and XVI. Meso- and metathorax with tubercles Dai, Dpi, Dae, Dpe probably fused, bearing four setae, I, II, III, and IV, a small conical egg burster anterior to seta IV; tubercles DLai, DLpi, DLae, DLpe probably fused, bearing four setae, V, VI, VII, and VIII, plus one or two minute setae, and



FIGS. 44–47. Parts of female genitalia, *Timarcha goettingensis*; (44) sternite 8; (45) ovipositor, valves and styli; (46) spermatheca; (47) apical ventrite. Abbreviations: cm, collum; cu, cornu; n, nodulus; ovp, ovipositor; sp, spermatheca; stt8, sternite 8; sty, styli; vs, valves. Scale line in mm.

one or two minute sensilla; annular spiracles present on mesothorax, lateral to DLai–DLpi–DLae–DLpe; EPa, EPp unisetate, bearing seta IX and X, respectively; T bearing two minute setae, seta XI missing; tubercles As, Ps absent; Es, Ss unisetate on each side.

Legs (figure 66). Three pairs well developed, moderately long thoracic legs all essentially similar as regards chaetotaxy, prothoracic legs very slightly shorter than others; coxa bearing four or five long setae, plus about 10 short setae, and several sensilla; trochanters bearing one long seta, two or three short setae, four campaniform sensilla; femora with three long setae, three short setae; tibiotarsi subequal in length to femora, usually bearing three long, two slightly shorter setae; tarsunguli



FIGS. 48–50. Apical segment of maxillary palpi, outer face showing digitiform sensilla; (48) *Aulacoscelis appendiculata* sp. n.; (49) *Orsodacne cerasi*; (50) *Timarcha goettingensis*. Abbreviations: ds, digitiform sensilla. Scale line in mm.

elongate, very slightly curved, slightly shorter than tibiotarsi, bearing long seta on inner margin.

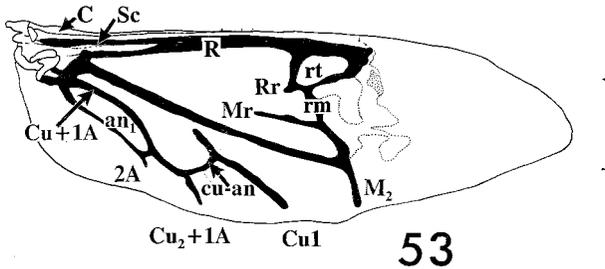
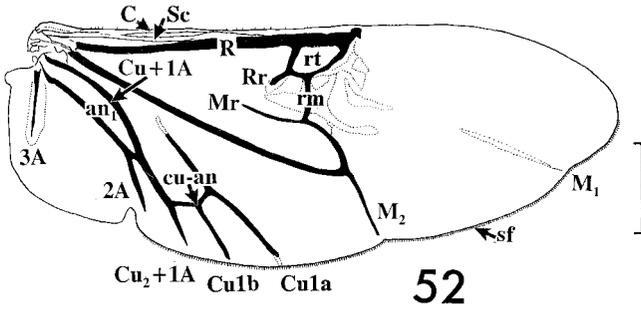
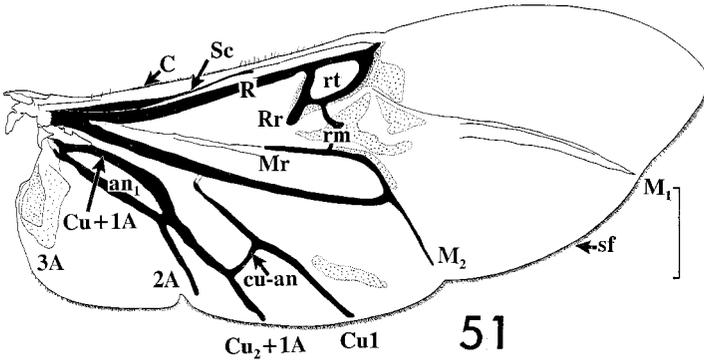
Abdomen (figures 64, 69). Abdominal segments 1–8 with setae I–XVI present, sometimes borne on indistinct tubercles, setae V, VII, VIII on tubercle DLai–DLae–DLpe, EPa–EPp fused, indistinct tubercle bearing two setae, IX, X; tubercles T, P, As, Ps, Es, Ss indistinct, apparently unisetate, except for Ps which is bisetate, bearing seta XIV, also apparently a much reduced seta XI; annular spiracles on tubercles DLai–DLae–DLpe. Abdominal segment 9 dorsally bearing large anal shield, fused across mid-dorsal line, bearing numerous small, variably-shaped pores, probably bearing setae IV–XIV, setae IV, VIII, IX shortest, setae XI, XII, XIII, and XIV long, apically situated; ventrally bearing two setae, XV short, XVI long. Abdominal segment 10, ventrally situated, bearing two moderately long setae, plus six short setae and an anal proleg.

Discussion

Adults

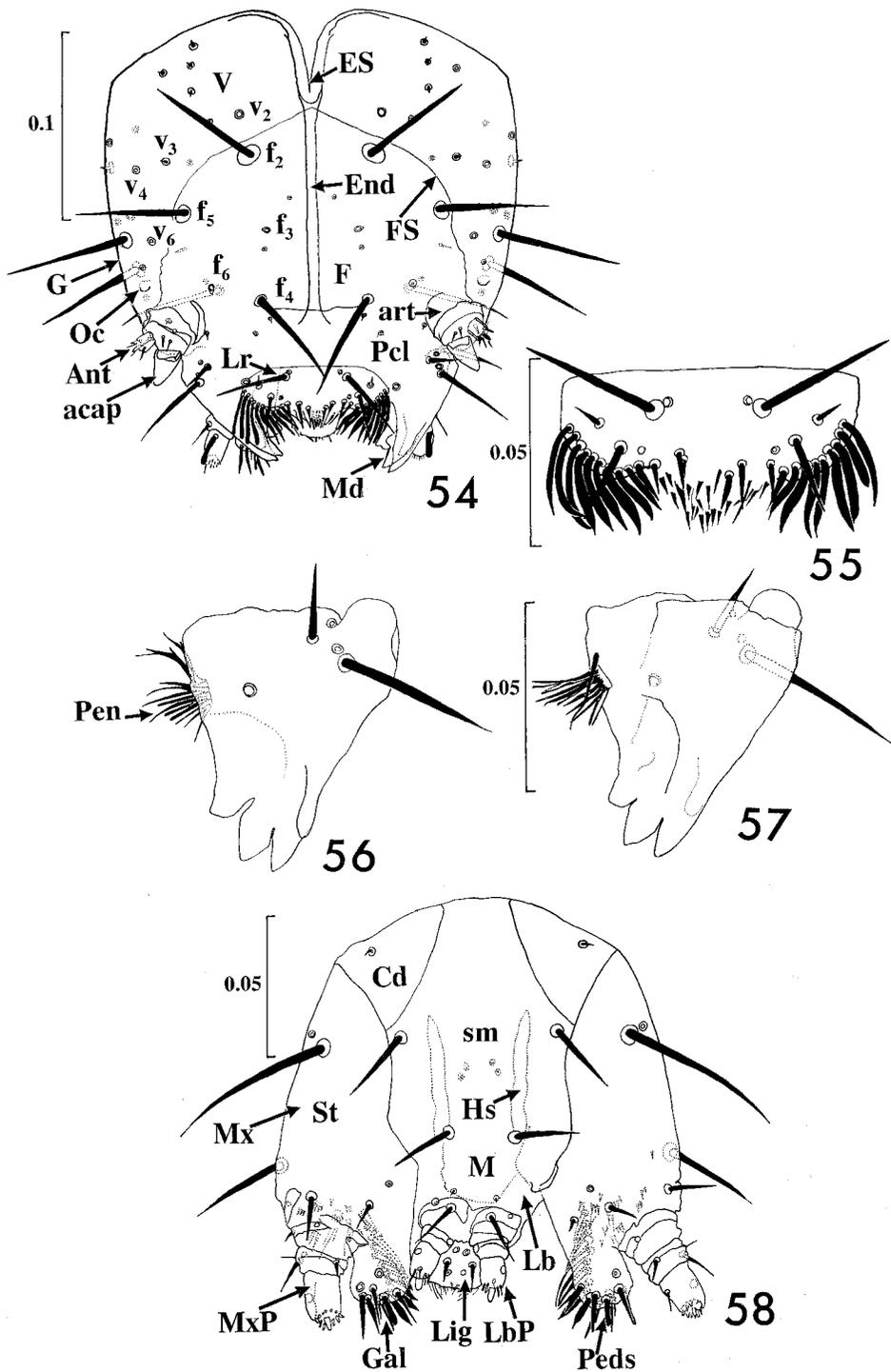
Mouthparts: mandibles

Mann and Crowson (1981) described the mouthparts of *A. melanocera*. The mandibles are long and stout with a sharp, incurved two-toothed apex and an uneven setose cutting edge. They have a membranous prostheca with a setose fringe, as in *Orsodacne*. In addition, a basal prosthecal lobe is present. A well developed asperated mola is characteristic of *Aulacoscelis* and also *Orsodacne* in which pollen-eating habits are well known (Crowson and Crowson, 1996:115). In adult Chrysomeloidea, there is an apparent correlation between the presence of an



FIGS 51–53. Right Metathoracic wings: (51) *Aulacoscelis appendiculata* sp. n.; (52) *Orso-daene cerasi*; (53) *Goniocтена olivacea*. Abbreviation: sf, setal fringe. Scale line in mm.

FIGS 54–58. Head parts first instar larva, *Aulacoscelis appendiculata* sp. n.: (54) frontal view of head; (55) labrum; (56) left mandible dorsal view; (57) right mandible ventral view; (58) labium and maxillae. Abbreviations: acap, accessory conical antennal process; Ant, antenna; art, basal antennal segment; Cd, cardo; End, endocarina; ES, epicranial suture; F, frons; f_2 , f_3 , f_4 , f_5 , f_6 , frontal setae 2–6; Gal, galea; Hs, hypopharyngeal sclerite; Lb, labium; LbP, labial palpus; Lig, ligula; Lr, labrum; M, mentum; Md, mandible; Mx, maxilla; MxP, maxillary palpus; Oc, ocellus; Pcl, postclypeus; Peds, pedunculate seta; Pen, penicillus; sm, submentum; St, stipes; V, vertex; v_2 , v_3 , v_4 , v_6 , vertex setae 2, 3, 4 and 6 (represented by sensilla only). Scale line in mm.

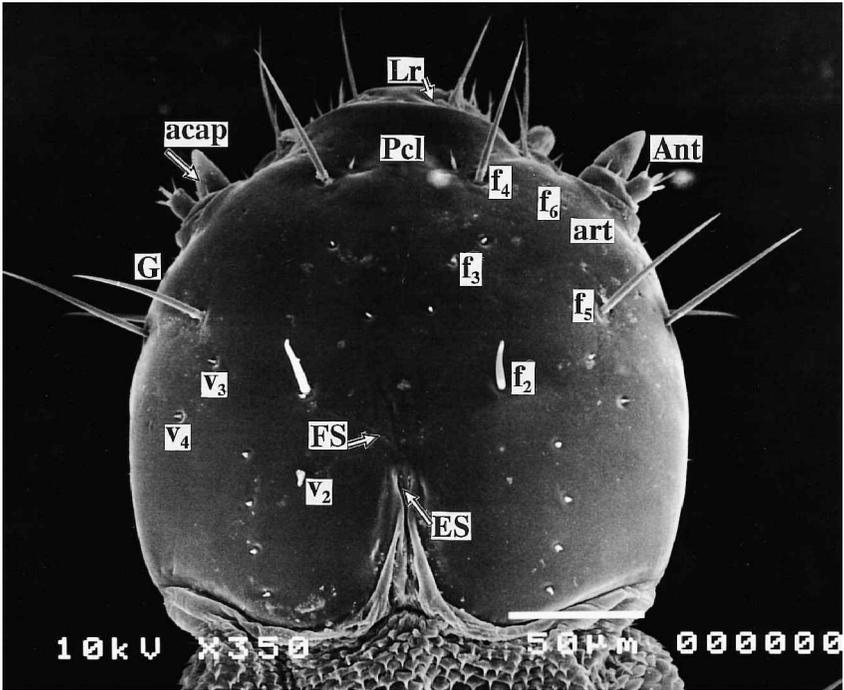


asperated or tuberculated mola and the habit of frequenting flowers and ingesting pollen. Mann and Crowson (1981) examined the gut contents of wild caught adults and the only species in which the gut-contents of at least some individuals were mainly pollen grains were species of Lepturinae, Bruchidae, Orsodacninae and Aulacoscelinae (*A. melanocera*), all of which had a definitely asperated molar part. This part probably holds and cracks individual pollen grains to release the nutrients from the impermeable grains. As will be shown later, the adults of *A. appendiculata* apparently feed upon sap exuding from foliar trenches. Kuschel and May (1990) showed the presence of a molar part on the mandibles of larval *Palophagus* which probably serves to grind Araucarian pollen grains against the epipharyngeal lining which provides a crushing surface. The systematic distribution of this specialized mola in the Chrysomeloidea strongly suggests that it was an ancestral character implying originally pollen-eating habits.

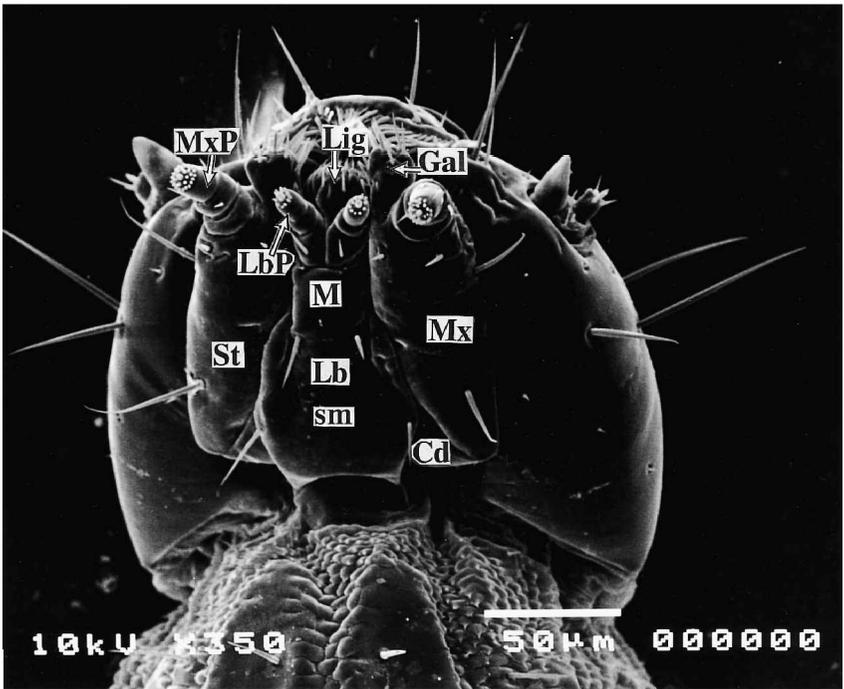
Mouthparts: maxillae and labium. Fuchs (1974) pointed out that pollen-eating beetles tended to have different types of apical vestiture on the galea from that of related leaf-eating types. Both *Aulacoscelis* and *Orsodacne* have rather long apically incurved setae on the galea, rather like those figured by Fuchs for the floricolous cerambycid, *Rhagium bifasciatum* F. The labium has a densely setose, flap-like, deeply bilobed membranous ligula, characteristic of primitive Chrysomelidae, including the Orsodacninae. The three-segmented labial palpi have the third segment longest, without digitiform pegs, but with a special sensillum preapically on its outer face. The maxillae resemble those of *Orsodacne*, but the setae of the galea and lacinia are relatively longer, the apical ones of the galea having short, incurved apices and the lacinia is slightly less pointed.

The form of the digitiform sensilla, sets of grooves, each with an elongate sensillum on the outer face of the apical, fourth segment of the maxillary palpi was described as U-shaped, as in *Orsodacne* (Mann and Crowson, 1981) but as somewhat different by Mann and Crowson (1994). In *A. melanocera*, the sensilla are situated near the base of the segment and are arranged in a shallow transverse curve. They lie in shallow grooves with their tips directed towards the apex of the segment. In *A. appendiculata*, the sensilla lie in about 15 grooves forming a U-shape, some way from the base of the apical segment of the maxillary palp (figure 48). In *Orsodacne cerasi* (figure 49) the sensilla number about 26 and are set in a narrow U-shaped pattern in the basal half of the segment. They are deeply sunk in the grooves with their tips pointing towards the median axis of the U. Apparently, this U-shaped form is characteristic of actively flying and floricolous species (Mann and Crowson, 1994). It is possible that this U-shaped configuration is derived by extension of an originally simple transverse row, as in *Aulacoscelis melanocera*, as a method of increasing the number of pegs in a narrow palpus, since it is not found in any species with the last palpal segment strongly broadened or securiform. In *Timarcha tenebricosa* (figure 50), there are about 10 preapical sensilla arranged in an arc. The shape

Figs. 59–60. Head first instar larva, *Aulacoscelis appendiculata* sp. n.: (59) dorsal view; (60) ventral view. Abbreviations: acap, accessory conical appendage; Ant, antenna; art, basal antennal segment; Cd, cardo; End, endocarina; ES, epicranial suture; F, frons; f_2, f_3, f_4, f_5, f_6 , frontal setae 2–6; Gal, galea; Lb, labium; LbP, labial palpus; Lig, ligula; Lr, labrum; M, mentum; Mx, maxilla; MxP, maxillary palpus; Pcl, postclypeus; sm, submentum; St, stipes; V, vertex; v_2, v_3, v_4 , vertex setae 2, 3 and 4, seta v_6 , not visible, represented by sensilla. Scale line represents 50 μm .



59



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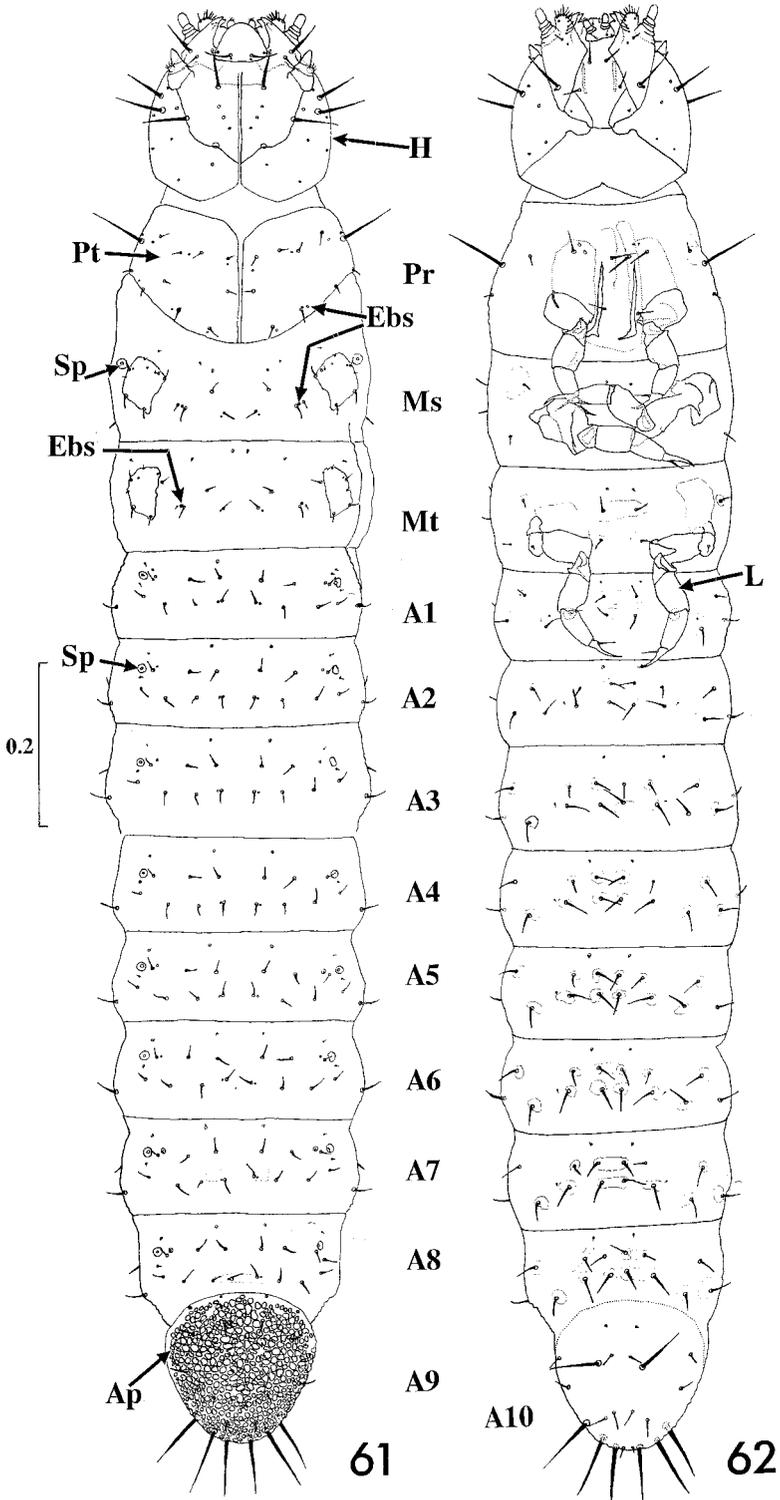
of the apical palpal segment is elongate and truncate in *Aulacoscelis* and *Orsodacne* and globular in *Timarcha* of the Chrysomelinae.

Thorax. Defensive glands in the pronotal and elytral cuticle are apparently absent in Aulacoscelinae, Orsodacninae and other primitive groups (Reid, 1995). The pronotum is laterally margined in *Aulacoscelis* and chrysomelines, but unmargined in Orsodacninae.

Hind wing venation. The hindwing venation of *Aulacoscelis* spp. has been studied by Jolivet (1959) and Suzuki (1994a,b). Jolivet described and figured the venation in *A. melanocera* and this is similar to that of *A. appendiculata* sp. n. (figure 51). The costal, subcostal and radial veins join a little before the radial triangle and *rm* is indistinct. The radials and M1 of the distal sector are distinct. The medians are normal, unmodified. The cubito-anal system is of the chrysomelid type in which Cu_1 is simple, with at its middle *cu-an*. The veins 1A and 2A rejoin at their middle to delimit the first anal cell. Vein 3A is well developed, but fine and not enlarged basally. The wing venation of *A. hogeii* Jacoby is essentially identical. In *A. melanocephala* Jacoby, the venation is generally similar, but Cu_1 rejoins M_2 in the left wing and is interrupted before the reunion in the right wing. Jolivet considered the venation to be of the chrysomelid type, but equally similar to that of *Orsodacne* (figure 52). Suzuki (1994a,b) studied the venation of nine *Aulacoscelis* spp. including *melanocera*, *Janbechynea* (*Janbechynea*) *elongata* (Jacoby) and three *Janbechynea* (*Bothrosclis*) spp. The Aulacoscelinae belongs to the chrysomelid group without a second cubital cell (2Cuc), along with the Orsodacninae, Zeugophorinae, Megalopodinae, Donaciinae, Criocerinae, Synetinae, Chrysomelinae, Galerucinae and Alticinae. All of the *Aulacoscelis* species examined have a very constant venation with a well developed postcubitus (Pcu), an almost always well developed Cu_1a-Cu_1b crossvein and a long Cu_1a which does not fork into two subbranches. In contrast, all of the *Janbechynea* species studied differ from *Aulacoscelis* since Cu_1a forks into two subbranches and the proximal (basal) half of the upper subbranches is usually missing and cross vein Cu_1a-Cu_1b is often incomplete.

In this study, the hind wings of *A. appendiculata* sp. n. were examined. A fringe of short setae is present along the entire posterior margin to the apex (figure 51). This was not illustrated or mentioned in the description of the wings by Jolivet (1959), and Suzuki (1994a,b). A similar fringe is present in *Orsodacne cerasi* (figure 52) running from vein 2A to the apex (Cox, 1976). It is interesting that this fringe is absent in all of the hindwings of the Chrysomelinae, examined by Cox (1976) (*Leptinotarsa*, *Chrysolina*, *Gonioctena* (figure 53), *Gastrophysa*, *Plagioderia*, *Hydrothassa*, *Prasocuris*, *Phratora*, *Phaedon*, *Chrysomela*, *Linaeidea*) and is not present in the photographs of the chrysomelines, *Agasta*, *Corystea* etc. published by Jolivet (1959).

Elytron to body meshing structures. Samuelson (1996) performed a scanning electron microscope study of the binding sites, the elytron to body meshing structures, involving discrete sites of extremely small and closely arranged spicules that interdigitate when the elytra and body are properly fitted together. The conformation of



the basal elytral patch and second patch, when present, offer characters that may potentially diagnose supragenetic clades, certainly some tribes, and perhaps subfamilies within Chrysomeloidea. In Orsodacninae and Aulacoscelinae, the basal elytral patch is single, well developed and fairly narrow and elongate in the former, but elongate-ovate in *Janbechynea* (*Janbechynea*) *paradoxa* Monrós of the latter subfamily. In both subfamilies, the second patch is absent. In contrast, the arrangement in the Chrysomelinae is usually complex, with double patches (basal plus second patch); the second sometimes associated with a bar; or rarely single and simple. *Chrysomela* has only the basal patch and has neither a trace of the second patch nor a foundation for it in the two species seen. Well developed double patches occur in *Timarcha*, which has a strongly reduced metathorax and completely apterous condition.

Metendosternite

The metendosternite in *Aulacoscelis hogeii* Jacoby is of the Eupodan type (Crowson, 1946) with a broad lamellar plate at the base of the arms (Reid, 1995), as in the Orsodacninae etc. *Orsodacne lineola* (Panzer) has a metendosternite with the lamina well developed, the tendons separated, and the arms are moderately free, though somewhat short (Crowson, 1938). The primitive chrysomelid furca would be a Eupodan type resembling that of *Orsodacne*, but with rather closer anterior tendons as in *Carpophagus* (Crowson, 1944). The Cyclica, including the Chrysomelinae form a uniform group whose furcae have reached the 'pair of arms' condition (leaving little trace of the ancestral form). The tendons are widely separated on the arms as in *Timarcha tenebricosa* F., *Phratora*, *Phaedon*, *Gonioctena*, etc. (Crowson, 1938).

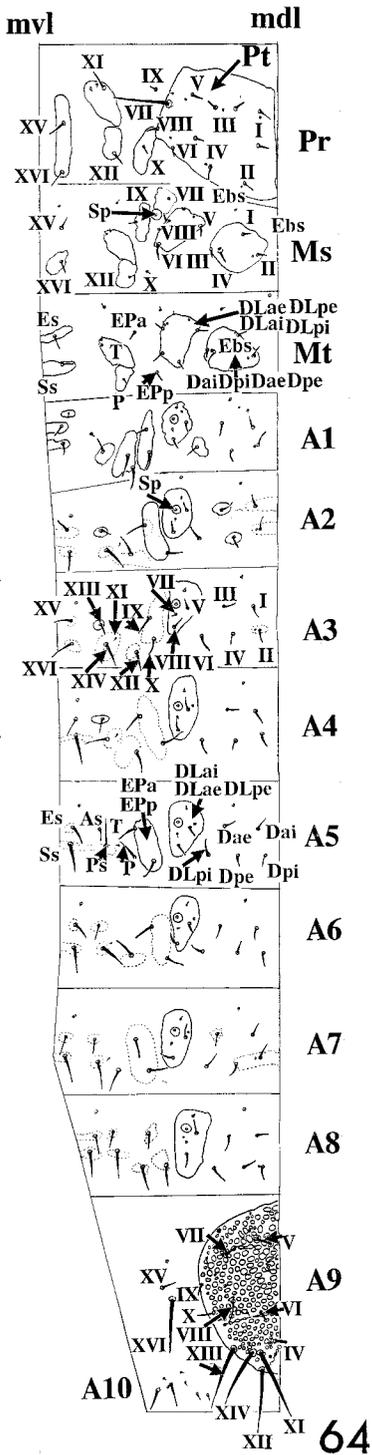
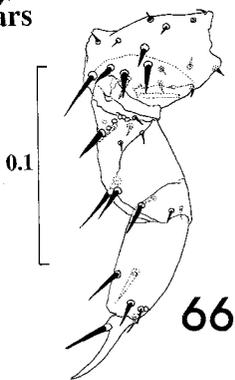
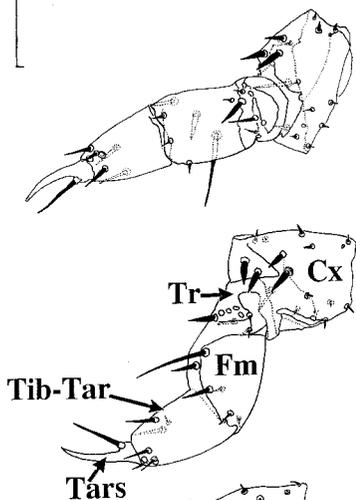
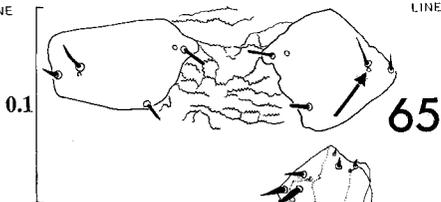
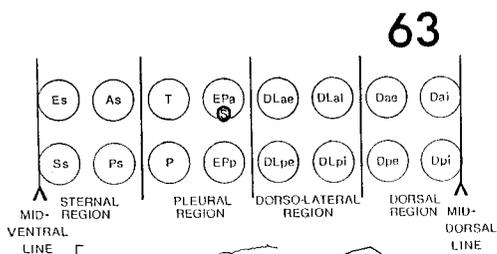
Tarsal setae

Mann and Crowson (1981) found simple spatulate adhesive tarsal setae on tarsal segment 3 in *Aulacoscelis*, *Orsodacne*, as well as many other subfamilies, including the Chrysomelinae.

Abdomen

Male genitalia. Monrós (1954) illustrated the simple, tubular, invaginated internal sac with the ejaculatory duct opening at its tip in *Aulacoscelis variabilis* Jacoby, which according to Mann and Crowson (1996) appears very similar to the one observed in the Orsodacninae-Megalopodinae-Zeugophorinae line. The simple tubular sac in *A. variabilis* appears to have developed into the large membranous sac terminating in the long stout flagellum of present day Timarchinae and Chrysomelinae (Mann and Crowson, 1996). Jolivet (1959) illustrated the median lobe and tegmen of the male genitalia of *A. melanocera*. In his dorsal view it can be

FIGS. 63–66. Body and legs first instar larva, *Aulacoscelis appendiculata* sp. n.: (63) tubercle nomenclature for typical body segment of generalised chrysomelid (After Cox 1976, modified after Kimoto 1962); (64) left half of the body showing tubercle arrangement and arrangement of setae I–XVI; (65) detail of cuticle between tubercles Dai-Dpi-Dae-Dpe on mesothorax; (66) left, pro-, meso-, metathoracic legs, respectively, outer view. Abbreviations: A1–10, abdominal segments 1–10; Cx, coxa; Ebs, egg bursting spine; Fm, femur; mdl, middorsal line; Ms, mesothorax; Mt, metathorax; mvl, midventral line; Pt, pronotum; Tars, tarsungulus; Tib-Tar, tibiotarsus; Tr, trochanter. Scale line in mm.



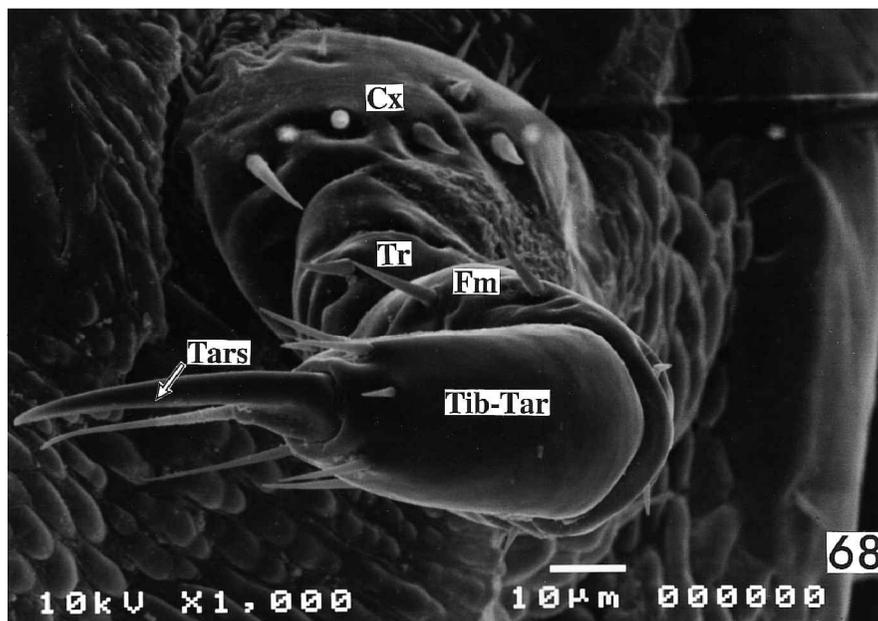
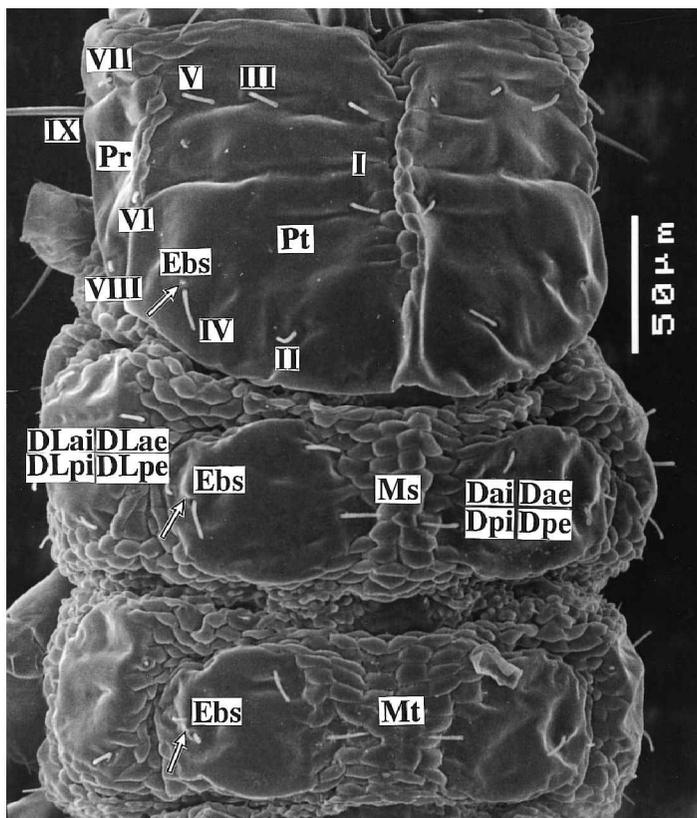
clearly seen that the apex of the median lobe is bilobed and it is described as deeply split when seen from above. However, I have examined the median lobe of *A. appendiculata* sp. n. and although with a deep median furrow it is apparently not split into two parts. Suzuki (1994a) figured the male genitalia of *A. melanocera*, *A. candezei* Chapuis, *Janbechynea (Bothroscelis) fulvipes* (Jacoby) and *Janbechynea (J.) elongata* (Jacoby). The proximal part of the median lobe is divided into a pair of long rod-like median struts. The median lobe is uniformly sclerotized and the apex is acuminate (sometimes bilobed as in *Orsodacne*). The apodemes are present in the Orsodacninae (figures 38, 39), Zeugophorinae, Megalopodinae, Megascelinae and Palophaginae and the ring-like tegmen with lateral lobe and manubrium is present in these 5 subfamilies, plus the Sagrinae, Donaciinae and the genus *Timarcha* of the Chrysomelinae (Suzuki, 1994a). Sternite 9 is similar in Orsodacninae (figures 38, 39) and Aulacoscelinae, except that the smaller T-shaped piece of the latter is greatly reduced in the former. *Timarcha* differs from the Aulacoscelinae, since this T-shaped piece is much larger, with long lateral arms; also the lower arms of the larger Y-shaped part are widely separated, not fused into a semicircular sclerite. Moreover, the tegmen in *Timarcha* lacks the lateral lobe (figure 41).

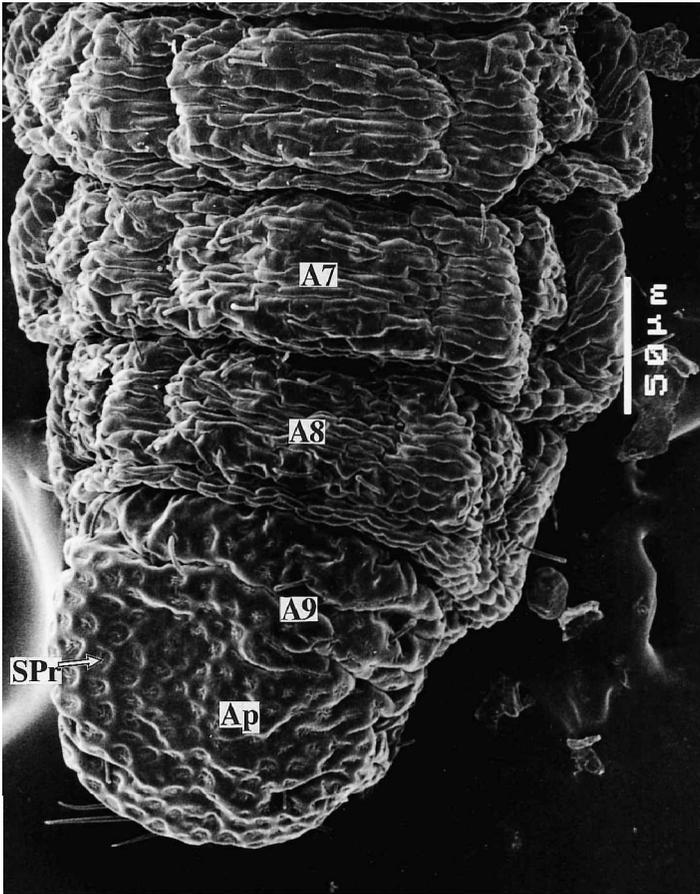
Female genitalia The female genitalia of *A. appendiculata* were examined in this study. Until Suzuki (1994a) figured the spermatheca of six *Aulacoscelis* species and *Janbechynea (J.) elongata* (Jacoby) no accurate information was available for the Aulacoscelinae. He showed that the form of the spermatheca is uniform in this subfamily and is characterized by the simple, U-shaped spermathecal capsule, consisting of the basal, at the most only slightly dilated nodulus, a slender, upturned, apically pointed cornu; a collum of variable length and form; the long, non-coiled spermathecal duct, and the spermathecal gland opening directly into the basal part of the nodulus, or apparently at the base of the collum. A similar spermatheca is found in the Sagrinae, Megascelinae and Eumolpinae (Suzuki, 1988), but also according to Cox (1976) in the Orsodacninae and Donaciinae.

Mann and Crowson (1983a) found one sac-like vaginal pouch on either side of the vagina close to the base of the bursa copulatrix in *Aulacoscelis melanocera*. However, such structures were not observed in well preserved specimens of *A. appendiculata* sp. n. The pouches are broad and round basally and taper towards the upper end. The presence of what appear to be vaginal pouches in *Aulacoscelis* as well as in the Sagrinae favours the theory that such structures, and presumably symbionts of some kind, were present in ancestral Chrysomelidae.

The ovariole number of 70 (36 left ovary, 34 right ovary) for *A. appendiculata* sp. n. is much greater than that of *Orsodacne arakii* Chûjô (17–19 per ovary), *Zeugophora annulata* (Baly), *Z. nigricollis* (Jacoby) (14 per ovary), *Temnaspis japonicus* Baly (7 per ovary) and *Plateumaris* sp. (20–22 per ovary), this compares with 5–44 per ovary for various chrysomelines (Suzuki, 1974b). In this study the ovariole number of *Orsodacne cerasi* varied in total between 24 to 30 with a mean of 26.8 (n = 10). This is somewhat fewer than in *O. arakii*.

FIGS. 67–68. Body parts first instar larva, *Aulacoscelis appendiculata* sp. n.: (67) thorax, dorsal view; (68) left prothoracic leg; (17) ninth tergite, dorsal view. Abbreviations: I–IX, setae 1–9; Cx, coxa; Ebs, egg bursting spine; Fm, femur; Ms, mesothorax; Mt, metathorax; Pt, pronotum; Tars, tarsungulus; Tib-Tar, tibio-tarsus; Tr, trochanter. Scale line represents 10 μ m (figure 16).





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FIG. 69. Apex of abdomen, dorsal view, first instar larva, *Aulacoscelis appendiculata* sp. n. Abbreviations: A7, A8, A9, abdominal segments 7–9; Ap, anal plate; SPr, sensory pore. Scale line represents 50 μm .

Fossil evidence for cycad-feeding

The earliest fossils of reliably identified Chrysomeloidea, the Protoscelinae were described by Medvedev (1968) from the late Jurassic or very early Cretaceous Kara Tau deposits of Central Asia. The protoscelines show a close resemblance to the present-day Aulacoscelinae and Sagrinae. They presumably fed on some kind of Gymnospermae, since the first Angiospermae did not appear until much later.

The Cycadaceae, a very old group of the Gymnospermae are well represented by fossils in the same deposits as Medvedev's Protoscelinae (Mann and Crowson, 1983a). The food selection of several *Aulacoscelis* species is probably a remnant of the fact that the primitive protoscelines fed on cycads and that they co-evolved.

Definite links between *Carpophagus*, a relict Australian sagrine, and cycads are still to be demonstrated. Early records of *C. banksiae* MacLeay adults on the foliage of the cycads *Macrozamia* and *Banksia* are probably accidental occurrences, but the adults have been observed to feed on pollen of *Angophora* (Myrtaceae) (Reid, 1995).

Reid also recorded adults of other sagrine genera feeding on the pollen of *Melaleuca* (Myrtaceae) and *Acacia* (Mimosaceae) in Australia.

Apparently, *Lilioceris* species are cycad-feeders. *L. nigripes* (Fabricius) feeds in the adult and larval stages on the young expanding foliage of cycads, including *Cycas* species (Cycadaceae), *Bowenia spectabilis* (Stangeriaceae) and *Macrozamia* species (Zamiaceae) in Queensland and New South Wales, Australia, whilst in Papua New Guinea, *L. clarki* (Baly) feeds on a *Cycas* sp. (Hawkeswood, 1992; Forster and Machin, 1994). In addition, an indet. *Lilioceris* sp. was found feeding on the leaflets of *Cycas siamensis* in northeastern Thailand. Many cycads were significantly damaged (Shepard, 1997).

According to Schmitt (1985b) the Cycadaceae were the probable food plants of the earliest members of the 'Crioceriformes' that are known as fossils from the Jurassic, and recorded as fossils within the same rock stratum. It also seems probable that in the upper Jurassic, the 'Proto-Crioceriformes' lived on the Cycadaceae and later the Criocerinae evolved when the terrestrial monocotyledons arose in the mid-Cretaceous (Schmitt, 1988).

Cytogenetics

Virkki (1964) was the first to work out the chromosome number and meioformula for *Aulacoscelis melanocera*. It has a chromosome number of 23 and a formula of $11+x$. According to Petitpierre (1988), the Segrinae and Aulacoscelinae are archaic beetles, but neither of the two species checked, including *A. melanocera*, share the primitive formula of Polyphagan Coleopterans, $9+x_{y_p}$. That of *A. melanocera*, $11+x$, is also shared by quite a large number of Chrysomelinae species, an allied and possibly derived subfamily (Crowson, 1955), though it is not the ancestral formula of the latter. Despite the derived nature of the xo system of *A. melanocera*, the x chromosome at metaphase 1 still has nucleolar substance attached to it, suggesting a recent disappearance of the y_p .

Biology

Eggs and oviposition. The eggs of *A. appendiculata* sp. n. are the most elongate of any chrysomelid so far examined, with a length: width ratio of about 4.8: 1.0. They are very similar to those of *Orsodacne cerasi* described by Cox (1981).

Host plants

According to Jolivet (1988), adult aulacoscelines seem to feed on Cycadales, but there is also mention of Asteraceae and Bromeliaceae flowers.

In Panama, the adults of *Aulacoscelis appendiculata* sp. n. are associated with *Eumaeus* caterpillars and adults of *Nomotus* (Languriidae). In Australia, larvae of *Lilioceris nigripes* and the lycaenid butterfly, *Theclinessthes onycha* (Hewitson) feed together on the young fronds of *Macrozamia* and *Cycas*, cycads, as well as the languriid, *Xenocryptus tenebrioides* Arrow (P. Jolivet pers. comm.). The cucujid, *Planismus* also feeds on *Zamia* in Florida where there are no *Aulacoscelis* (P. Jolivet pers. comm.).

Feeding damage. On 5 May 1992 a group of 8–10 adult *Aulacoscelis appendiculata* on a new, fully expanded leaf of *Zamia fairchildiana* (Cycadales) near the beginning of the 'Camino Cantar' nature trail in Cerro Azul, Panama, at 700 m altitude apparently caused a brownish discoloration and chafing of the apical third of the leaflet. In addition, during the last week of April 1997, following the first



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FIGS. 70–71. *Aulacoscelis appendiculata* sp. n. feeding on *Zamia fairchildiana* leaf June 1997, at Madden Forest, Panama.

soaking rain of the new rainy season, a single *Aulacoscelis* adult was again observed on the foliage of one of the plants at Cerro Azul. The beetle which had just landed, continued lengthening a shallow feeding trench 2 mm in width another 15 mm toward the tip of the leaflet (figures 70, 71). The damage resembled that observed five years before, in that the upper surface was only lightly scored. Feeding appeared to consist of lapping juices from the perforated epidermis, rather than wholesale ingestion of parenchyma. The feeding area darkened noticeably over time (Windsor and Jolivet, 1997). Trenching of the upper leaf epidermis is known in the Donaciinae, Criocerinae, Galerucinae, but the habit of sap ingestion is apparently only recorded in the Megalopodinae. In the megalopodine, *Sphondylia tomentosa* (Lacordaire), the females cut off the terminal leaf of a twig of *Rhus zeiheri*, eat the pith and suck the exuding sap (Schulze, 1996).

Larva

The larva of *Aulacoscelis appendiculata* sp. n. keys to Orsodacninae at couplet 10 in the key to families and subfamilies of larval Chrysomeloidea by Mann and



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Crowson (1981). However, it differs from Orsodacninae in the absence of paired urogomphi on abdominal tergite 9.

For a comparison of the first instar larval characters of Aulacoscelinae, Orsodacninae and Chrysomelinae, see table 1. Characters of relevance and those differing between these subfamilies are as follows.

Apparently, the antennae are two-segmented in Aulacoscelinae and Orsodacninae (incorrectly given as three-segmented by Cox, 1981) (synapomorphy), whilst in the Chrysomelinae, they are distinctly three-segmented. In the first two subfamilies, the second antennal segment is much shorter than the accessory conical process, whilst it is usually much longer in the Chrysomelinae. In the Orsodacninae, the second segment is flat, bearing several long setae, whilst in the Aulacoscelinae, this segment is about half the length of the accessory conical process and bearing only short setae.

In the larva of Aulacoscelinae and Orsodacninae, a small ocellus lacking pigmentation is present posterior to the antennae on each side (synapomorphy). The reduction in the number of ocelli probably suggests subterranean or internal feeding habits for these groups. In contrast, all of the Chrysomelinae including representatives from all of the recognised tribes, have the plesiomorphy of six ocelli on each side of the head. All of these are external foliage feeders.

Table 1. Comparison of first instar larval characters of Aulacoscelinae, Orsodacninae and Chrysomelinae.

Character	Aulacoscelinae	State	Orsodacninae	State	Chrysomelinae	State
Head shape	normal, oval	0	normal, oval	0	normal, oval	0
Head position	protracted	1	protracted	1	protracted	1
Epicranial suture	present	0	present	0	present	0
Frontal suture	present	0	present	0	present	0
Endocarina	present	0	present	0	present	0
Frontal setae	3+ pairs	0	3+ pairs	0	3+ pairs	0
Frontal papillate setae	absent	0	absent	0	absent	0
Fronto-clypeal suture	present	0	present	0	present	0
Antennal segments	2	1	2	1	3	0
Ocelli	1	5	1	5	6	0
Occipital foramen	single	0	single	0	single	0
Hypopharyngeal sclerite	present	0	present	0	present	0
Anterior labral margin	not incised	0	not incised	0	incised	1
Labral setae	more than 8	0	more than 8	0	more than 8	0
Mandibles shape/teeth	triangular/4	0	triangular/6	0	palmate/5,6	1
Penicillus	present	1	present	1	absent (+ rare)	0(1)
Mandibular setae	2	0	2	0	2	0
Cardo	present	0	present	0	present	0
Maxillary palpi	3-segmented	0	3-segmented	0	3-segmented	0
Galea/Lacinia	fused	0	fused	0	fused	0
Postmental setae	4	0	4	0	6	1
Labial palpi	2-segmented	0	2-segmented	0	1 or 2-segmented	0,1
Pronotal type	D-DL	1	D-DL	1	D-DL, D-DL-Ep	1,0
Thoracic egg bursters	Pr, Ms, Mt	0	Pr, Ms, Mt	0	Ms, Mt	1
Abdominal egg bursters	absent	4	absent	4	absent I-V, I-II, I	2,0,2,3
Spiracles	annular	0	annular biforous	1	annular	4,0
Dorsal body setae	pointed	0	pointed	0	pointed, capitate	0,1
Dorsal ampullae	absent	0	absent	0	absent	0
Anal plate with numerous pores	present	1	present	1	absent	0
Paired urogomphi	absent	1	present	0	absent	1
Venter of abdomen + long setae	present	1	present	1	absent	0
Tibio-tarsal paronychial appendix	absent	0	absent	0	present	1
claw (pretarsus)	very elongate	0	very elongate	0	short	1
claw seta	present	1	present	1	present	1
pulvillus	absent	0	absent	0	absent	0

0, Plesiomorphic state

1, 2, 3, 4, 5, Apomorphic state

The mandibles are approximately triangular in the Aulacoscelinae and Orsodacninae with four and six teeth respectively. They lack a distinct mola in both of these subfamilies, as do the majority of chrysomelid larvae, except those of *Palophagus* which feeds on pollen of *Araucaria* (Kuschel and May, 1990). It is unlikely, therefore, that the larva of *Aulacoscelis* feeds on the pollen in cycad cones. *Aulacoscelis* and *Orsodacne* larvae bear a penicillus consisting of a dense tuft of about 12 or 13 or 10 closely packed setae, respectively (synapomorphy). In the majority of Chrysomelinae, the penicillus is absent, but according to Reid (1995) it is present in *Geomela*. Crowson (1946) defined the larvae of Sagraeinae as having mandibles with a single apical tooth and considered that if the larva of *Aulacoscelis* were to have a two- or three-toothed mandibular apex, that character alone would warrant the removal of the genus from the Sagraeinae, probably to constitute a separate subfamily. The four-dentate mandibles of *A. appendiculata* support this removal.

In the pronotum of *Aulacoscelis appendiculata* apparently tubercle EPP is present, so that the pronotum is of the D-DL type as it is in Orsodacninae (synapomorphy). In the larvae of Chrysomelinae, both the D-DL and D-DL-EP types are both commonly represented.

The egg bursters on the larva of *A. appendiculata* occur in similar positions on the pronotum, meso- and metathorax to those in the Orsodacninae (Cox, 1981, 1994). They are not situated on strictly homologous tubercles since those of *A. appendiculata* are on tubercle Dai-Dpi-Dae-Dpe, whilst in Orsodacninae, they occur on tubercle Dae-Dpe. However, they are absent from the abdomen in both groups which is a synapomorphy. In the Chrysomelinae they are rarely absent, they are never on the pronotum, but they may be on the mesothorax; on both the meso- and metathorax; on meso-, metathorax, and abdominal segment 1, sometimes also on abdominal segment 2, rarely also on abdominal segments 2-5. They are usually on the small to large, well sclerotized tubercle DLpi (Cox, 1994).

The spiracles in *A. appendiculata* are annular, since they are ring-shaped and lack lateral openings or pouches of the atrium. In contrast, those of the Orsodacninae are annular biforous, since they are ring-like, but have two lateral openings or pouches of the atrium. Those of all the Chrysomelinae examined are of the annular type as in the Aulacoscelinae.

In *A. appendiculata* the ninth abdominal segment bears a well sclerotized dorsal tubercle, the anal plate, apparently with numerous pores, which are probably gland openings, which are also present in the Orsodacninae (Cox, 1981). This is considered a synapomorphy. The position of feeding of the larvae of these two groups is not known with certainty, although Cox (1981) suggested that those of *Orsodacne* may be subterranean root-feeders since the larvae of the Galerucinae, *Luperus* and *Aulacophora* have similar anal plates with similar gland openings and feed at the roots of grasses and Cucurbitaceae, respectively. According to Crowson and Crowson (1996) although the anal plate is well developed, the gland openings are apparently absent in the internal-monocot-bulb-feeding *Exosoma*. The anal plate in Chrysomelinae larvae is usually present, but lacks the numerous pore-like openings.

Crowson (1946) included *Aulacoscelis* in the Sagraeinae sensu lato on account of the bilobed ligula and the essentially Eupodan form of the head, metendosternite and coxal cavities. However, he considered that it also has significant resemblances to the Chrysomelinae in the shallowly bilobed third tarsal segment, the hind wing venation, and the aedeagus, which much resembles that of *Timarcha*.

Kuschel and May (1990) favoured the transfer of Aulacoscelidinae from the Chrysomelidae and an association of this subfamily with the Orsodacninae, under a separate family Orsodacnidae. This was based upon similarities in the detailed structure of the male and female genitalia. In the male genitalia, the aedeagal apodemes are either entirely free, or free to a large extent, and the apodemal bridge is large, occupying at least the basal third of the apodemes. The endophallus is usually long, extending well beyond the ends of the aedeagal apodemes and with basal and/or median sclerites. In the female, the ninth sternite (proximal hemisternites) are long, with sclerotization and pigmentation confined to distinct struts or bars (paraprocts), and the styli are usually large. Moreover, the valves (distal hemisternites or coxites) are not constricted, and not distinctly curved outward at the apex. The present study supports these findings.

In this study, the larva of *Aulacoscelis* shares eight synapomorphies with that of Orsodacninae, but only four with that of Chrysomelinae, two of which are only rarely expressed as apomorphies. The adults of *Orsodacne* and *Aulacoscelis* share similarities of the maxillary palpal shape, the shape of the digitiform sensilla, wing venation with posterior setal fringe, mandible morphology, male and female genitalia and elytron to body meshing structures.

The feeding position of *Aulacoscelis* larvae is still unresolved and this must be one of the priorities of future work and to determine if they are cycad-associated.

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