

The Internal Reproductive System of Panamanian *Aulacoscelis* sp. (Coleoptera: Chrysomelidae, Aulacoscelinae) and Comments on the Systematic Position of the Subfamily

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Abstract. We describe and illustrate the male internal reproductive system of *Aulacoscelis* sp., a species apparently related to *A. melanocera* Duponchel et Chevrolat, 1843. These are the first such data presented for the subfamily Aulacoscelinae, which has often been regarded as one of the most primitive groups within the family Chrysomelidae. The female spermathecal organ is additionally described and compared to that of other Chrysomelidae. The systematic position of the Aulacoscelinae is reviewed in the light of these and other morphological characters such as the hind wing venation and male external genitalia. That many of these characters are shared by both Aulacoscelinae and Orsodacninae leads us to propose that these are sister taxa allied closely to the cerambycid subfamily Lepturinae.

Key words: Chrysomelidae, Aulacoscelinae, *Aulacoscelis*, internal reproductive system, systematics.

Introduction

The chrysomelid subfamily Aulacoscelinae, established by F. Monrós in 1953, has been considered a phylogenetically important group because of its possible association with living descendants of the earliest seed plants, the Cycadales, and its many primitive (plesiomorphic) morphological characters. The 18 described species range from Florida and Central Mexico south through the Caribbean and Central America reaching several restricted localities in South America. The species are divided among two genera, *Aulacoscelis* Duponchel et Chevrolat, 1843 and *Janbechynea* Monrós, 1953. The latter is further subdivided into two subgenera, *Bothroscelis* Monrós, 1954 and *Janbechynea* s. str. Numerous workers including Crowson (1946), Monrós (1953, 1954), Jolivet (1957, 1959, 1988), Medvedev (1975), Suzuki (1994b, 1996), Reid (1995), and Schmitt (1996) have studied the systematic relationships of the Aulacoscelinae using data obtained largely from external morphology. Recently, Suzuki (1994b, 1996), Reid (1995), and Schmitt (1996) reviewed previous systematic and phylogenetic treatment of this subfamily. Based on the comparative morphology of the male external genitalia, hind wing venation, and female spermathecal

organ, Suzuki (1994b, 1996) tentatively placed the Aulacoscelinae between the subfamilies Megalopodinae and Sagrinae. According to this classificatory scheme, the Megalopodinae contain the tribes 'Zeugophorini', 'Palophagini', and 'Megalopodini', while the Sagrinae contain the 'Sagrini', 'Donaciini', and 'Criocerini' (Suzuki, 1996). The lack of useful characters has limited confidence in the systematic position of the Aulacoscelinae. While aspects of the life history and immature stages have remained unknown for a very long period, there are now signs that this is beginning to change. Adult *Aulacoscelis* have been collected from flowers (Asteraceae), possibly feeding on pollen (cf. Monrós, 1955), and Jolivet (1988) mentioned that possibly they feed on leaves of Cycadales (cf. Jolivet, 1988). A recent report by Windsor and Jolivet (1997) confirms that adult *Aulacoscelis* sp. actively feed on *Zamia fairchildiana* (Cycadales) leaves in Panama. The neonate larva of the species, which was obtained for the first time from eggs under laboratory condition, is currently being described (Cox & Windsor, in preparation).

In this paper we describe the male internal reproductive system and the female spermathecal organ. We then discuss the likely systematic position of the subfamily. The species examined in this study is referred to provisionally as "*Aulacoscelis* sp.", a spe-

cies apparently closely related to, but significantly different from *A. melanocera* Duponchel et Chevrolat, 1843 (M. Cox, personal communication). The description of this species will appear shortly in another communication (Cox & Windsor, in press).

Materials and Methods

In May 1997 the junior author collected greater than 50 adult *Aulacoscelis* sp. at La Fortuna (1,200 m), Chiriqui Province, Panama. These were maintained alive in the laboratory with little mortality within plastic containers provided three to four times per week with fresh mango slices. The senior author visited the Smithsonian Tropical Research Institute in Panama in July 1997 while several individuals were still alive. He dissected individuals and was able to observe and draw the delicate soft tissues of the internal reproductive systems of both sexes.

Dissection of the fresh insects was made following anesthesia with ethyl ether. Under a binocular microscope and while bathed in Ringer's solution prepared for drosophilid flies, the lateral membrane joining the abdominal segments was cut along one side and the sternites folded to one side as a single flap.

Description of the male and female internal reproductive systems

In the following description of the internal reproductive systems of both sexes the authors follow the terminology proposed by Suzuki (1988).

Male (Fig. 1): *Testis* (*Tes*) large, almost heart-shaped, covered with reddish-orange epithelial sheath; apparently two in number, each of which contains two large *Sperm tubes* (*ST*), short *Vas efferentia* (*Ve*) whose anterior length was about 2/3 of *Vas deferens* (*Vd*) (Type 3; see Suzuki, 1988). *Vd* almost uniform in width, length almost twice the long diameter of *Tes*, not forming a distinct *Seminal vesicle* (*Sv*). *Ejaculatory duct* (*Ed*) very long; anterior part branching into two *Lateral ejaculatory ducts* (*EdL*), apices (this part is sometimes called *Prostata*; cf. Suzuki, 1988) of each very swollen; *Common ejaculatory duct* (*EdC*) tapering, then thickening again forming a stout eversible duct (*Internal sac*; *IS*), a thick-walled muscular tube posteriorly, posterior part tapering again towards the base. A pair of small sac-like *Accessory glands* (*AG*) open into the anterior extremity (*Prostata*) of *EdL*.

Female (Fig. 2): Number of *Ovarioles* 70 (36–34) [total (left–right)]. *Spermathecal capsule* (*SptC*) simple, horseshoe-shaped, yellowish-brown; *Sperma-*

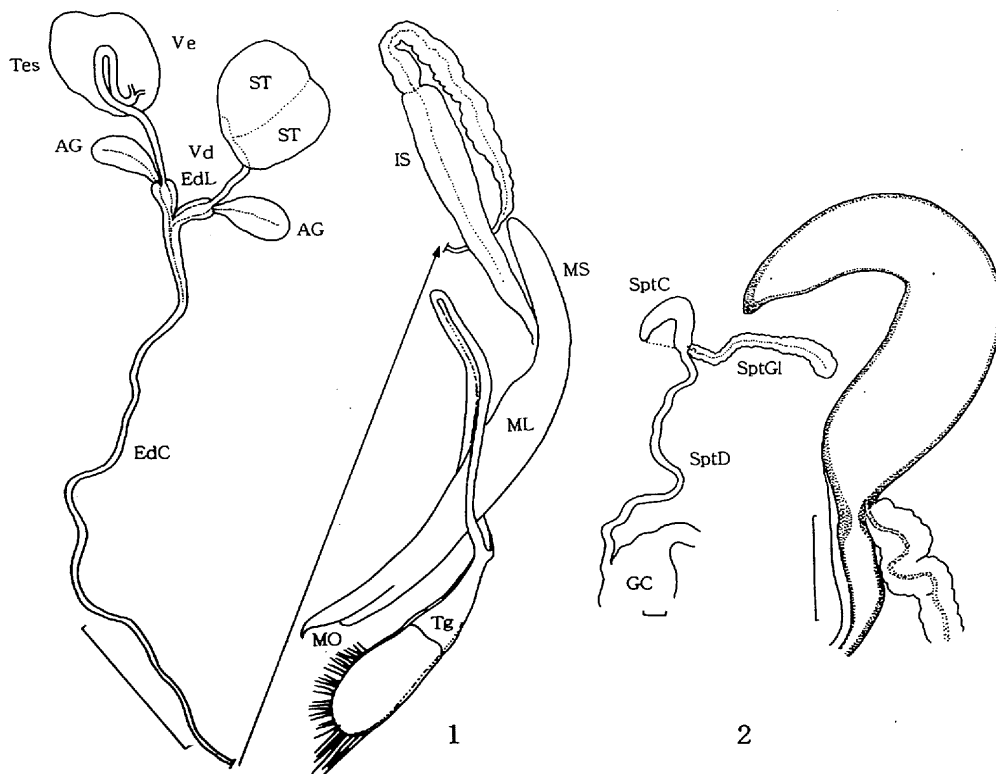


Fig. 1. Male reproductive system of *Aulacoscelis* sp. from Panama. AG: Accessory gland; EdC: common ejaculatory duct; EdL: lateral ejaculatory duct; IS: internal sac; ML: median lobe; MO: median orifice; MS: median strut; ST: sperm tube; Tg: tegmen; Tes: testis; Vd: vas deferens; Ve: vas efferens. Left testis: ventral view; right testis: dorsal view.

Fig. 2. Female spermathecal organ of *Aulacoscelis* sp. from Panama. GC: Genital chamber; SptC: spermathecal capsule; SptD: spermathecal duct; SptGl: spermathecal gland.

thecal wall (*SptW*) very thin, weakly sclerotized; Inner surface of spermathecal capsule (*SptSi*) and Outer surface of spermathecal capsule (*SptSo*) entirely smooth; Proximal part of spermathecal capsule (*SptCp*) less than half of Distal part of spermathecal capsule (*SptCd*) in length. Spermathecal duct (*SptD*) slender, long, unsclerotized, with its aperture opening into the subapical part of Genital chamber (*GC*). Spermathecal gland (*SptGl*) rather sac-like, somewhat swollen towards the apex, slightly shorter than *SptD*. *SptGl* opening into the base of *SptC*, which is situated near the opening of *SptC*.

Discussion

The male internal reproductive system of the subfamily Aulacoscelinae is described and illustrated for the first time in this paper. The basic structure of the internal male reproductive system is nearly identical to that reported by Suzuki (1988) for *Orsodacne arakii* Chûjô, 1942 (Orsodacninae). Although some parts of the male internal reproductive system show varying degrees of similarity to those of other chrysomelid subfamilies, it should be noted that the particular combination of characteristics occurs only in the subfamilies Orsodacninae and Aulacoscelinae.

An earlier paper (Suzuki, 1994b) described the principal female reproductive organs of seven species of the Aulacoscelinae: *Aulacoscelis melanocephala* Jacoby, 1877; *A. confusa* Monrós, 1954; *A. costaricensis* Bechyně, 1950; *A. tibialis* Jacoby, 1888; *A. variabilis variabilis* Jacoby, 1888; *A. candezei* Chapuis, 1874; and *Janbechynea (Janbechynea) elongata* (Jacoby, 1888). Only minimal differences were noted among species in the structure of the spermathecal organ. The spermathecae were characterized by a simple *SptC*, a long but non-coiled *SptD*, and the direct opening of the *SptGl* into the basal part of *SptC*. The position of the *SptD* and *SptGl* openings varied slightly among species: being completely united in *Aulacoscelis melanocephala*, *A. confusa*, *A. costaricensis*, *A. tibialis*, and *Janbechynea (Janbechynea) elongata*; closely spaced but opening independently into the base of *SptC* in *A. variabilis variabilis* and *A. candezei*. Although the spermathecal organs bear many similarities in the subfamilies Orsodacninae, Sagrinae, Megascelinae, and Eumolpinae (cf. Suzuki, 1988, 1994b), the structure of this organ in the subfamilies Aulacoscelinae and Orsodacninae are essentially identical.

Suzuki (1994b) described and illustrated the male external genitalia of the following four Aulacosceline species: *Aulacoscelis melanocera*; *A. candezei*; *Jan-*

bechynea (Bothroscelis) fulvipes (Jacoby, 1888); and *J. (Janbechynea) elongata*. From the viewpoint of external male genital morphology the subfamily is characterized by having a median strut whose apex is deeply bifurcated (lateral lobes) and a ring-like tegmen. The former characteristics occur prominently in the subfamilies Orsodacninae, Zeugophorinae, Palophaginae, Megalopodinae, and Megascelinae, while the latter characteristics occur in these five subfamilies and the subfamilies Sagrinae, Donaciinae and the genus *Timarcha* Latreille, 1829 (Chrysomelinae). The male external genitalia of the Aulacoscelinae also closely resembles that of the Orsodacninae.

Hind wing venation has been considered a rich source of systematic characters in the Chrysomelidae (cf. Jolivet, 1957, 1959; Suzuki, 1969, 1994a, b). The hind wing venation of *Aulacoscelis melanocera* is well known (Jolivet, 1959). Recently, Suzuki (1994b) described and illustrated the hind wing venation of an additional 13 species of the Aulacoscelinae: *Aulacoscelis candezei*; *A. confusa*; *A. melanocera*; *A. costaricensis*; *A. sanguinea* Jacoby, 1888; *A. melanocephala*; *A. variabilis variabilis*; *A. tibialis*; *A. grandis* Jacoby, 1888; *Janbechynea (Bothroscelis) fulvipes*; *J. (B.) melyroides* (Crowson, 1946); *J. (B.) femorata* (Jacoby, 1888); and *J. (Janbechynea) elongata*. The hind wing venation of *Aulacoscelis* sp. examined in the present study is nearly identical to that of *A. melanocera*.

Hind wing venation in the Chrysomelidae can be classified into two major groups; one with the 2nd Cubital cell (*2Cuc*) and the other without it. The subfamily Aulacoscelinae belongs to the group without the 2nd Cubital cell (*2Cuc*), along with the following nine subfamilies (Suzuki, 1994a): Orsodacninae, Zeugophorinae, Megalopodinae, Donaciinae, Criorcerinae, Synetinae, Chrysomelinae, Galerucinae, and Alticinae. The 10 *Aulacoscelis* species (including the present *A. sp.*) show stable hind wing venation. The combination of the following characteristics in hind wing venation is peculiar to this genus: a well-developed *Postcubitus* (*Pcu*); a well-developed long *Cubitus*_{1a} (*Cu*_{1a}) and an almost always well-developed *cu*_{1a}-*cu*_{1b} crossvein (*cu*_{1a}-*cu*_{1b}). On the other hand, the four *Janbechynea* species also display a stable hind wing venation differing from the former genus in having a subdivision of *Cu*_{1a} into two subbranches of which the basal part of the upper always disappears. These characteristics are stable within the genera, *Aulacoscelis* and *Janbechynea*, and show only slight difference from those of the subfamily Orsodacninae (for the hind wing venation of *Orsodacne cerasi* Linnaeus, 1758 and *O. arakii* see Chûjô, 1952 and Suzuki,

1994a, respectively) in which the Cu_{1a} forks into two subbranches, the lower of which combined with the longer $cu_{1a}-cu_{1b}$ crossvein to form a peculiar Y-shaped venational area between the lower subbranches of Cu_{1a} and Cu_{1b} . No interspecific variation has been found in this Y-shaped venational area (Suzuki, 1969, 1994a).

Systematic position of the subfamily Aulacoscelinae

The history of taxonomic and/or systematic treatment of the subfamilies Aulacoscelinae and Orsodacninae was reviewed and compiled by Suzuki (1996) and Schmitt (1996). While these works underline the similarities between these two subfamilies, opinions still differ regarding their proper placement among other chrysomelid subfamilies. Before Monrós (1953) established the subfamily Aulacoscelinae, the genus *Aulacoscelis* was often treated as a member of the subfamily Sagrinae (e.g., Jacoby, 1880, 1888–1892; Leng, 1920), though Chapuis (1874, 1875) treated the genus *Aulacoscelis* as a monotypic taxon constituting an independent subfamily 'Aulacoscelites'. Crowson (1946) recognized the independence of the genus *Aulacoscelis* from any other chrysomelid group. He treated it as an independent tribe 'Aulacoscelini' within the subfamily, 'Sagrinae', which included many heterogeneous genera [*Hornibius* Fairmaire, 1888 ('Hornibiini'), *Cucujopsis* Crowson, 1946, *Syneta* Dejean, 1835, *Zeugophora* Kunze, 1818, *Hemydacne* Bechyně, 1951 ('Orsodacnini'), *Duboulaia* Baly, 1871, *Coologardica* Blackburn, 1899, *Megamerus* MacLeay, 1827, *Polyoptilus* Germer, 1848, *Neodiaphanops* Blackburn, 1899, *Rhagiosoma* Chapuis, 1878, *Diaphanops* Schönherr, 1845, *Carpophagus* MacLeay, 1827, *Mecynodera* Hope, 1840, *Ametalloides* Crowson, 1946, *Ametalla* Hope, 1840, *Atalasis* Lacordaire, 1845, and *Sagra* Fabricius, 1792 ('Sagrini')]—although this lumping of diverse taxa within the 'Sagrinae' was later to change. After Monrós (1953) established the subfamily Aulacoscelinae, the following hypotheses on the systematic position of this subfamily were proposed by many workers [for details see Suzuki (1996) and Schmitt (1996)]:

1. Crowson (1955) treated the Aulacoscelinae as a subfamily within the Chrysomelidae along with the following 13 subfamilies: Orsodacninae, Donaciinae, Criocerinae, Chlamisinae, Clytrinae, Cryptocephalinae, Lamprosomatinae, Eumolpinae, Chrysomelinae, Galerucinae, Halticinae (= Alticinae), Cassidinae, and Hispinae. Here, it should be noted that he classified the superfamily Chrysomeloidea into five families and that the subfamilies Megalopodinae and Zeugophorinae were separated from other chrysomelid

groups as an independent family 'Megalopodidae'. Moreover, this subfamily 'Sagrinae' was treated as a member of his family 'Bruchidae' along with all of other genuine Bruchidae.

2. Jolivet (1959; 1988, slightly modified) treated the subfamily Aulacoscelinae as a group close to the subfamily Chrysomelinae and put it between the subfamily Criocerinae and the subfamilies Chrysomelinae + Galerucinae + Halticinae (= Alticinae) (he treated all of these subfamilies as families). His system was followed by Medvedev (1971). Jolivet and Petitpierre (1981) and Jolivet (1988) classified the family Chrysomelidae into five 'Section's. They treated the subfamily Aulacoscelinae as a member of the first Section 'Eupoda' along with the following seven subfamilies: Sagrinae, Orsodacninae, Zeugophorinae, Donaciinae, Megalopodinae, Criocerinae, and Synetinae.

3. Monrós (1959) classified the superfamily Chrysomeloidea into two large groups, 'Chrysomelae' (consisting of three subgroups including seven subfamilies and the 'Bruchidae') and 'Alticae' (consisting of two subgroups including 11 subfamilies). He treated the subfamily Aulacoscelinae as a member of the subgroup 'Chrysomeliformes' of the 'Chrysomelae' along with the subfamily Chrysomelinae. His systematic treatment of the subfamily Aulacoscelinae has been basically followed by Mann and Crowson (1981, 1983a, 1983b, 1996) who classified the superfamily Chrysomeloidea into three families Disteniidae, Cerambycidae, and Chrysomelidae (including 18 subfamilies and the 'Bruchidae'). Suzuki (1988) also followed Monrós's opinion.

4. Reid (1995) classified the superfamily Chrysomeloidea into seven families. In his system the subfamily Aulacoscelinae (his 'Aulacoscelidinae') is treated as a member of the family Orsodacnidae along with the subfamily Orsodacninae. The subfamilies Megalopodinae, Palophaginae, and Zeugophorinae constitute an independent family 'Megalopodidae' and separated from the above 'Orsodacnidae' and 'Chrysomelidae' including all other chrysomelid subfamilies and the 'Bruchidae'. His recognition of the close relationship among the Aulacoscelinae and Orsodacninae agrees with treatments by Schmitt (1966) and Samuelson (1996).

The systematic position of the subfamily Aulacoscelinae should be discussed in relation to the subfamily Orsodacninae. The systematic position of the Orsodacninae has been addressed by many workers including Sharp and Muir (1912) who noted "the two struts of the median lobe and the long sac place this (*Orsodacne nigriceps* Latreille, 1807 = *O. lineola* Panzer,

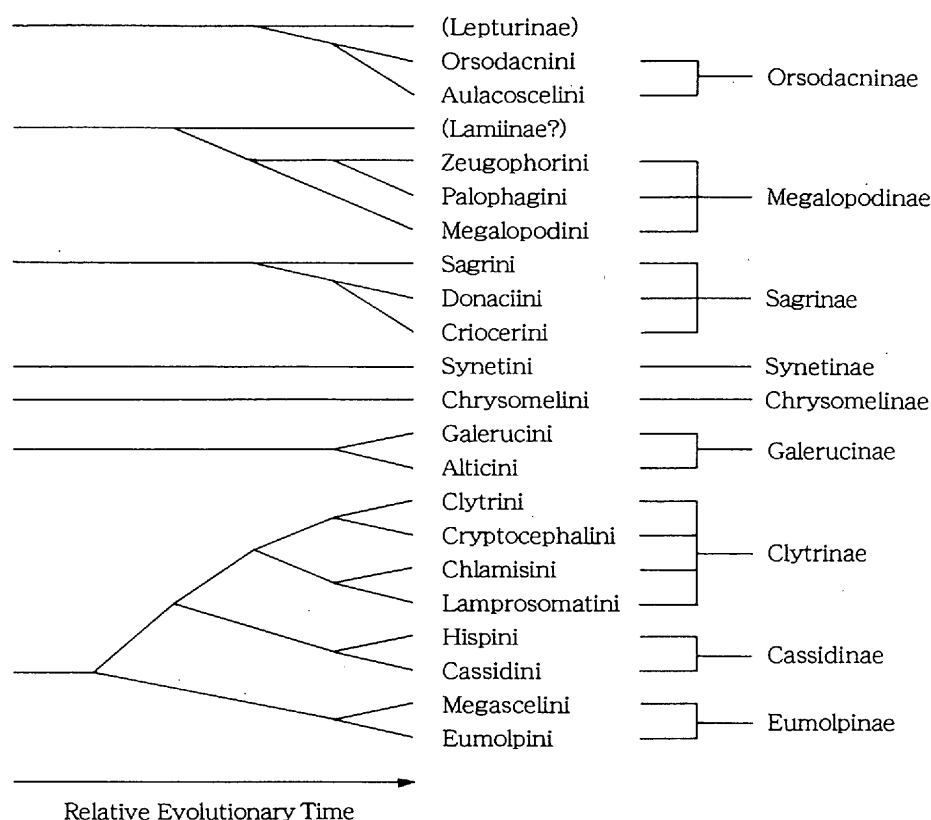


Fig. 3. Phylogenetic relationships among the subfamilies of the family Chrysomelidae. (After Suzuki, 1994a, 1996; revised)

1795) nearer to the Longicorn type than to other Chrysomelidae". They considered *Orsodacne* a transitional group from which all other members of the Chrysomelidae and Bruchidae (superfamily Chrysomeloidea) had originated. Other hypotheses have been proposed concerning the phylogenetic relationships between the Orsodacninae and other chrysomelid taxa. A list of these hypotheses is as follows:

1. The Orsodacninae are closely related to other members of the so-called 'Eupoda', the subfamilies Sagrinae, Donaciinae and Criocerinae (Jacoby, 1908; Gressitt, 1942).

2. They constitute a monophyletic group along with the subfamilies Donaciinae and Criocerinae (Reitter, 1912).

3. They constitute a monophyletic group 'Orsodacnidae' along with the subfamily Zeugophorinae (Böving & Craighead, 1931).

4. They are a sister group along with the subfamily Sagrinae (Chen, 1940; Medvedev, 1971).

5. They have no direct relationship to other chrysomelid groups nor is it the most primitive group from which other chrysomelid subfamilies have diverged (Chûjô, 1953).

6. They have a close relationship to the subfamily

Megalopodinae (Crowson, 1955; Lee, 1993).

7. They are a paraphyletic group within the subfamilies of the "Alticiformes" (Monrós, 1959).

8. They are a closely related to the subfamily Synetinae (Jolivet, 1959).

9. They constitute a monophyletic group with Megalopodinae, Zeugophorinae, and Synetinae (Chen, 1964).

10. They have a common ancestor with a certain ancestral form of the subfamilies Synetinae, Eumolpinae, Galerucinae, and Alticinae (Crowson, 1981).

11. They constitute a monophyletic group with the subfamilies Synetinae and Zeugophorinae (Jolivet, 1988).

12. They have a close relationship to cerambycid subfamily Lepturinae (Suzuki, 1988).

13. They have a close relationship to the subfamily Aulacoscelinae (= 'Aulacoscelidinae') (Reid, 1995; Schmitt, 1996; Samuelson, 1996).

14. They have no direct relationship to any chrysomelid subfamilies (Suzuki, 1996).

Aulacoscelis sp. and *Orsodacne arakii* share numerous characteristics of male internal reproductive anatomy. While these shared male internal reproductive systems of these two subfamilies are similar, no other

subfamily of the Chrysomelidae shares this combination of characters. This suggests that the subfamily Aulacoscelinae constitutes a sister group of the subfamily Orsodacninae.

The authors would like to conclude that the subfamilies Orsodacninae and Aulacoscelinae share a closer common ancestor among themselves than either does with any other chrysomelid subfamily. We think it is likely that the Orsodacninae might have diversified in the Palearctic and Nearctic Regions after diverging from the ancestral stock, whereas the Aulacoscelinae might have specialized in the Neotropical Region. Recently, Reid (1994), based on a cladistic analysis using a large number of defined characters concluded that these two subfamilies are sister taxa. Schmitt (1996) supported this basic conclusion. The present study of the internal reproductive systems of both sexes, additionally supports Reid's conclusion.

Suzuki (1988, 1994a, etc.) has long emphasized that the subfamily Orsodacninae is closely related to certain genera (e.g., *Dinoptera*, *Lemula*, etc.) of the cerambycid subfamily Lepturinae. This means that the family Chrysomelidae is a polyphyletic group at the subfamily level in relation to the Cerambycidae auct. Various morphological characteristics which can be recognized in both male and female reproductive systems of the subfamilies Orsodacninae and Aulacoscelinae are not only similar to each other but also differ widely from any other chrysomelid subfamilies. The senior author retains his belief that the Chrysomelidae are polyphyletic. The present authors would like to revise the senior author's higher classification system of the family Chrysomelidae and phylogenetic relationships among the subfamilies (Suzuki, 1996) as shown in the following Table and Fig. 3. The descending taxonomic treatment of the ranks of all the accepted subfamilies is based on the idea that the number of higher taxa should be decreased because of a basic requirement in the current Linnaean hierarchic classification. In this revised system, the subfamily 'Aulacoscelinae' is put in the subfamily 'Orsodacninae' as a sister tribe 'Aulacoscelini' of 'Orsodacnini'.

Higher classification system of the family Chrysomelidae

- Superfamily Chrysomeloidea
 - (Family Cerambycidae)
 - (Family Bruchidae)
 - Family Chrysomelidae
 - Subfamily I. Orsodacninae
 - Tribe 1. Orsodacnini

- Tribe 2. Aulacoscelini
- Subfamily II. Megalopodinae
 - Tribe 3. Zeugophorini
 - Tribe 4. Palophagini
 - Tribe 5. Megalopodini
- Subfamily III. Sagrinae
 - Tribe 6. Sagrini
 - Tribe 7. Donaciini
 - Tribe 8. Criocerini
- Subfamily IV. Synetinae
 - Tribe 9. Synetini
- Subfamily V. Chrysomelinae
 - Tribe 10. Chrysomelini
- Subfamily VI. Galerucinae
 - Tribe 11. Galerucini
 - Tribe 12. Alticini
- Subfamily VII. Clytrinae
 - Tribe 13. Clytrini
 - Tribe 14. Cryptocephalini
 - Tribe 15. Chlamisini
 - Tribe 16. Lamprosomatini
- Subfamily VIII. Cassidinae
 - Tribe 17. Hispini
 - Tribe 18. Cassidini
- Subfamily IX. Eumolpinae
 - Tribe 19. Megascelini
 - Tribe 20. Eumolpini.

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