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Systematic Position of the Subfamilies Megalopodinae and Megascelinae (Chrysomelidae) Based on the Comparative Morphology of Internal Reproductive System

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ABSTRACT

The internal reproductive systems (IRS; the whole system for male and the spermathecal organ for female) are reported for three Panamanian genera (*Megalopus*, *Mastosthetus*, and *Agathomerus*) of Megalopodinae for the first time. They show fundamentally the same characteristics as those of Japanese *Colobaspis japonica* (Baly) studied by Suzuki (1988). Several common stable characters could be found for these four megalopodine genera and *Zeugophora* (Zeugophorinae). This strongly indicates that Megalopodinae and Zeugophorinae, as well as the Australasian Palophaginae studied by Kuschel and May (1990), must constitute sister groups derived from one monophyletic stock as suggested by Suzuki (1988, 1994a, 1996), Reid (1995) and Suzuki and Windsor (1999). The IRSs of two (one Panamanian and one Mexican) *Megascelis* species of Megascelinae clearly indicate a close relationship to those of Eumolpinae. The male IRS of Megascelinae is reported for the first time. As several workers have pointed out Megascelinae and Eumolpinae are sister groups of a single monophyletic group. Based mainly on the results of the comparative morphology of the IRS and several other morphological characters (hind wing venation, male external genitalia, etc.), that have been considered phylogenetically important, the systematic position of Megalopodinae and Megascelinae is discussed.

KEY WORDS: systematic position, Chrysomelidae, Megalopodinae, Megascelinae, internal reproductive system (IRS)

INTRODUCTION

I visited the Smithsonian Tropical Research Institute (STRI), Panama, in July 1997 and, therefore, had a fortunate opportunity to dissect fresh material of several species of three phylogenetically important subfamilies Aulacoscelinae, Megascelinae, and Megalopodinae with the aid of Donald M. Windsor (STRI). The geographical distribution of the first and second groups is restricted in Central and South America. Several workers have proposed hypotheses about the systematic position of these three subfamilies within the superfamily Chrysomeloidea and/or the family Chrysomelidae (cf. Reid, 1995; Suzuki, 1996). I have also occasionally given a review of higher classification of the

family Chrysomelidae since 1980 (cf. Suzuki, 1996). But until today no reliable system covering the whole of this family has been established.

Suzuki and Windsor (1999) already published the results of comparative morphological studies on *Aulacoscelis* sp., a species closely related to *Aulacoscelis melanocera* Duponchel and later described as a new species *A. appendiculata* (Cox and Windsor, 1999). It was clearly established that the subfamilies Aulacoscelinae and Orsodacninae are sister groups of single monophyletic stock (Suzuki and Windsor, 1999). This conclusion also supports the proposal by Reid (1995).

In this paper, I would like to report the results of the comparative morphology of both male and female internal reproductive systems (IRS) of other two subfamilies Megalopodinae and Megascelinae and to give some comments on their systematic position.

Subfamily Megalopodinae

The subfamily Megalopodinae auct. should be classified into the three sister groups. Suzuki (1996) treated all of them as 'tribes'; that is, Megalopodini, Zeugophorini and Palophagini. Table 1 shows the previous and current studies that have been made for the IRS of the subfamily Megalopodinae *s. str.* (Suzuki's 'tribe Megalopodini')

Table 1. IRS studies of Megalopodinae *s. str.*
Colobaspis japonica (Baly) ♂ and ♀ Suzuki (1974, 1988)
Colobaspis sp. ♀: Present study
Agathomerus sp. ♂ and ♀: Present study
Mastostethus sp. ♀: Present study
Megalopus sp. ♂ and ♀: Present study

The male and female IRSs of the subfamily Megalopodinae *s. str.* have been reported so far for only one Japanese species *Colobaspis japonica* (Baly) (Suzuki, 1988). The IRSs of three genera, *Megalopus*, *Mastosthetus*, and *Agathomerus*, of this subfamily *s. str.* are reported here for the first time. Fig. 1 shows both male and female IRSs of *Colobaspis japonica* from Japan cited in Suzuki (1988). The male IRS of *C. japonica* is characteristic in having a fused *testis*, long *lateral ejaculatory ducts*, a well-developed *ejaculatory sac*, and very long *posterior ejaculatory duct*. Fig. 2 shows the female spermathecal organ (SptO) of *Colobaspis* sp. whose locality is unknown. The female SptOs of the two *Colobaspis* species examined are quite similar to each other and have very specialized *spermathecal capsules*, long *spermathecal ducts*, and a very long *spermathecal gland*. Fig. 3 shows the male IRS and female SptO of *Megalopus* sp. In the male IRS an apparently fused *testis*, long *vas efferens*, and long *common* and *posterior ejaculatory ducts* with a well-developed *ejaculatory sac* are characteristic. Other than the subfamily Megalopodinae *s. str.*, fused *testes* can be seen only in the species of the subfamilies Galerucinae and Alticinae. In the female SptO, a strongly specialized *spermathecal capsule*, a long *spermathecal duct*, and a very long *spermathecal gland* are characteristic of Megalopodinae. Fig. 4 shows the SptO of *Mastostethus* sp. It is very similar to those of *Colobaspis* species and *Megalopus* sp. I could not observe the male IRS of this *Mastostethus* species. Fig. 5 shows the male IRS and female SptO of *Agathomerus* sp. Both male and female systems are identical with those of previous four species of the three genera. Table 2 shows the main characteristics in both male and female IRSs of the subfamily Megalopodinae *s. str.*

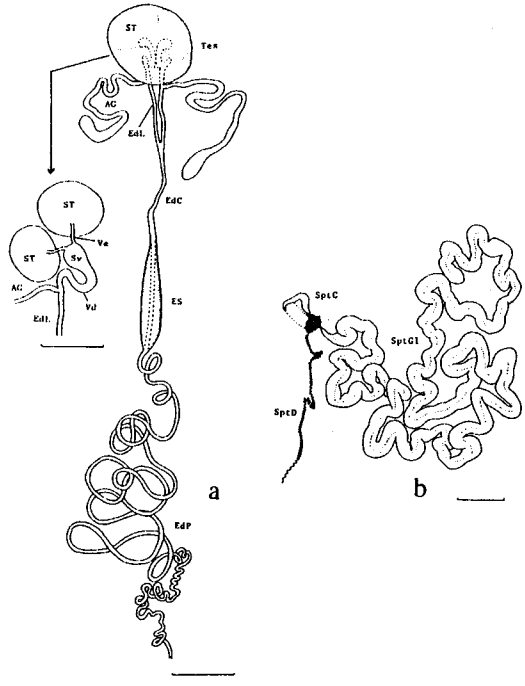

Fig. 1. The male IRS (a) and female SptO (b) of *Colobaspis japonica* (Baly) (Megalopodinae, 'Megalopodini') from Japan. Scale bar 1.0 mm. (after Suzuki 1988).

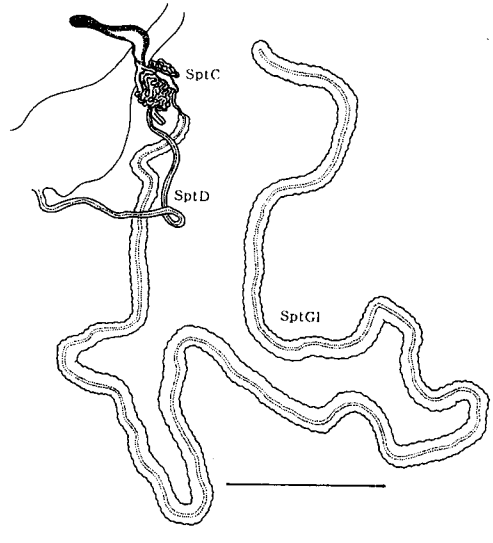

Fig. 2. The female SptO of *Colobaspis* sp. (locality unknown; Museum of Comparative Zoology Coll.). (Megalopodinae, 'Megalopodini'). Scale bar 1.0 mm.

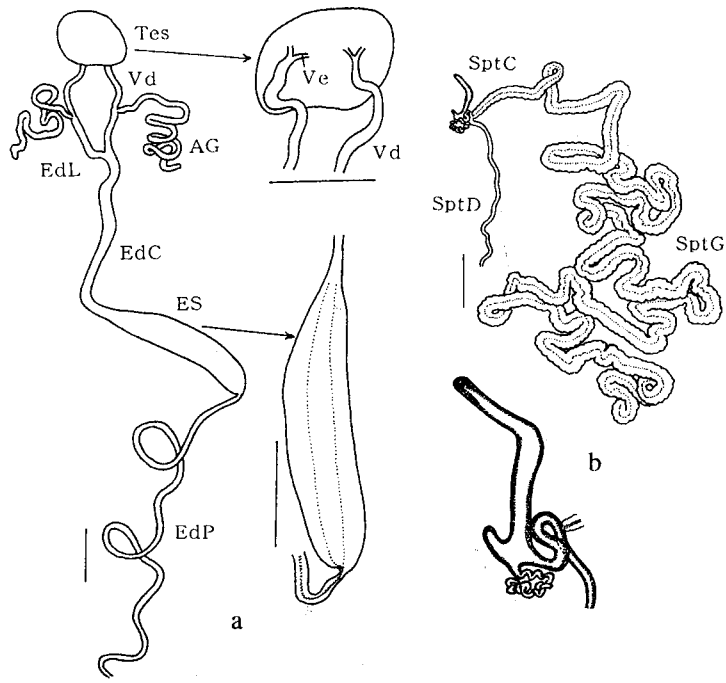

Fig. 3. The male IRS (a) and female SptO (b) of *Megalopus* sp. (Megalopodinae, 'Megalopodini') from Panama (Chiriqui Prov., 1300 m alt., 4-VII-1997, J. Wappes leg.). Scale bar 1.0 mm.

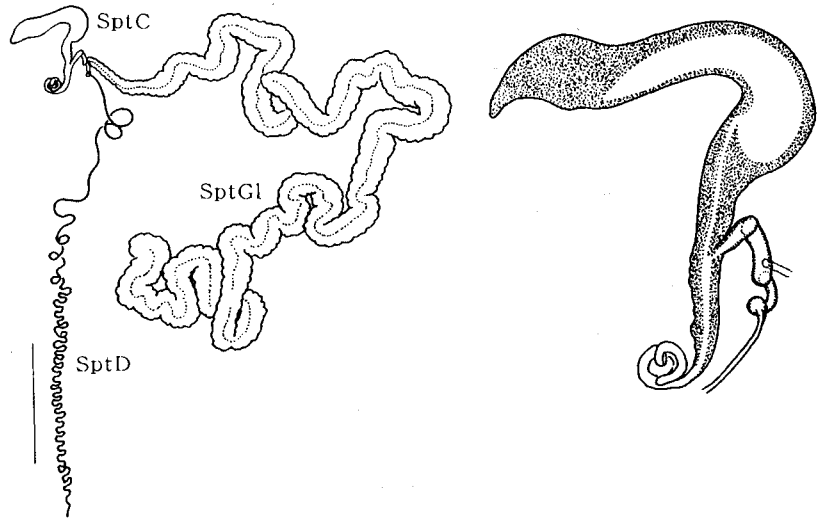

Fig. 4. The female SptO of *Mastostethus* sp. (Megalopodinae, 'Megalopodini') from Panama (Cerro Campana, 16-VII-1997, K. Suzuki and D. M. Windsor leg.). Scale bar 1.0 mm.

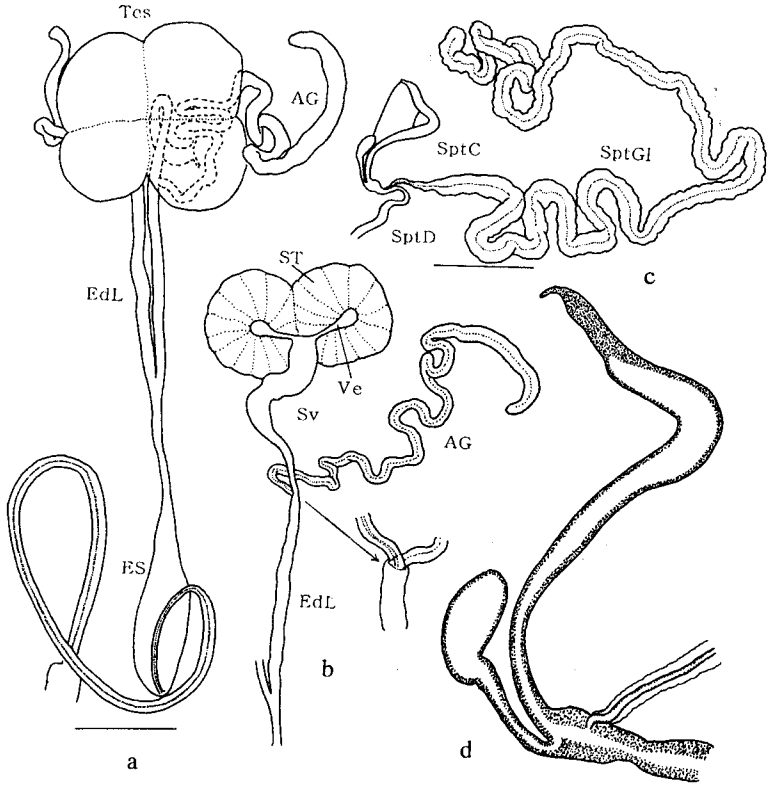

Fig. 5. The male IRS (a: whole system; b: a right half of Tes part, *peritoneal sheath* removed) and female SptO (c, d) of *Agathomerus* sp. (Megalopodinae, 'Megalopodini') from Panama (Cerro Campana, 16-VII-1997, K. Suzuki and D. M. Windsor leg.). Scale bar 1.0 mm.

Table 2. Main IRS characteristics in Megalopodinae *s. str.*

Male

1. Fused *testis*, including 4 *sperm tubes*
   Common in the three genera (*Megalopus*, *Agathomerus*, *Colobaspis*) and present in all Galerucinae+Alticinae.
2. A pair of tubular *accessory glands*
3. A very long *ejaculatory duct*, with a well-developed *ejaculatory sac*

Female

1. A very specialized *spermathecal capsule*
2. A very long *spermathecal duct*
3. A very long and well-developed *spermathecal gland*

A combination of the above three male characteristics is seen in only the subfamily Megalopodinae *s. str.* and a combination of the three female characteristics in only the subfamilies Megalopodinae *s. str.* and Zeugophorinae *s. str.* These characteristics are very stable in their fundamental morphological structures. Especially, I would like to point out the importance of the combination of these and

relative size of each of the elementary parts making up the system. The subfamily Megalopodinae *s. str.*, which has been generally accepted so far, should be regarded as one monophyletic group along with the generally accepted the subfamilies Zeugophorinae *s. str.* and Palophaginae *s. str.* In my system each of these three groups is treated as an independent 'tribe' within the subfamily Megalopodinae, respectively. Table 3 shows the previous studies of the IRS of the subfamilies Zeugophorinae *s. str.* and Palophaginae *s. str.*

Table 3. IRS studies of Zeugophorinae *s. str.* and Palophaginae *s. str.*

Zeugophorinae *s. str.*
- *Zeugophora (Pedrillia) annulata* (Baly) ♂ and ♀ Suzuki (1974, 1988)
- *Zeugophora (Pedrillia) bicolor* (Jacoby) ♂ and ♀ Suzuki (unpublished)
- *Zeugophora (Pedrillia) vitinea* (Oke) ♀: Reid, 1989
- *Zeugophora (Pedrillia) williamsi* Reid ♀: Reid, 1989

Palophaginae *s. str.*
- *Palophagus bunyae* Kuschel et May ♀: Kuschel and May (1990)
- *Palophagus australiensis* Kuschel et May ♀: Kuschel and May (1990)
- *Cucujopsis setifer* Crowson ♀: Kuschel and May (1990)

Fig. 6 shows the IRSs of both sexes of *Zeugophora (Pedrillia) annnulata* from Japan cited in Suzuki (1988). Besides non-fused *testis,* both male and female IRSs are basically identical with those of the previous four genera of the subfamily Megalopodinae *s. str.* Fig. 7 shows the female SptOs of two *Palophagus* species, *P. bunyae* and *P. australiensis*, and *Cucujopsis setifer.* Though those figures are schematic, they show well the fundamental characteristics, of members of the megalopodine groups.

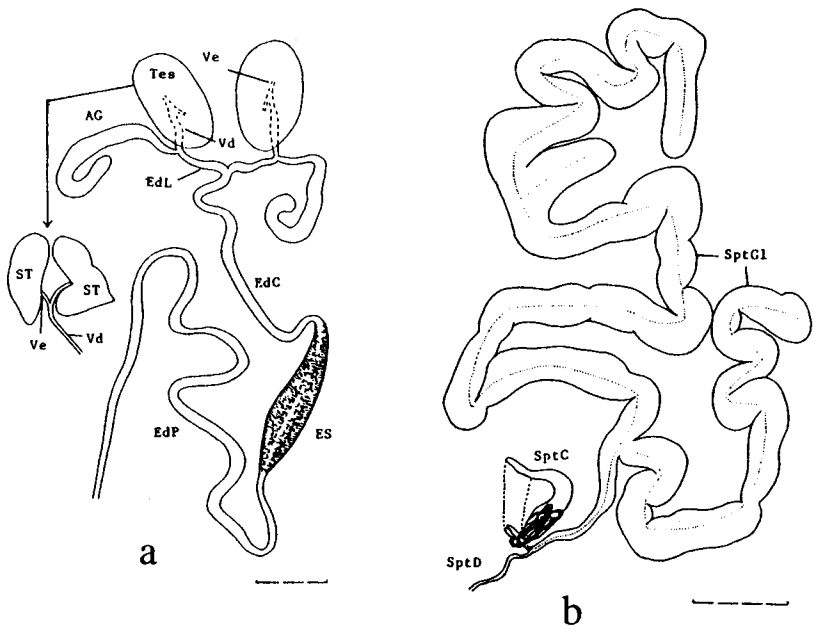

Fig. 6. The male IRS (a) and female SptO (b) of *Zeugophora (Pedrillia) annulata* (Baly) (Megalopodinae, 'Zeugophorini') from Japan. Scale bar 0.5 mm. (after Suzuki 1988).

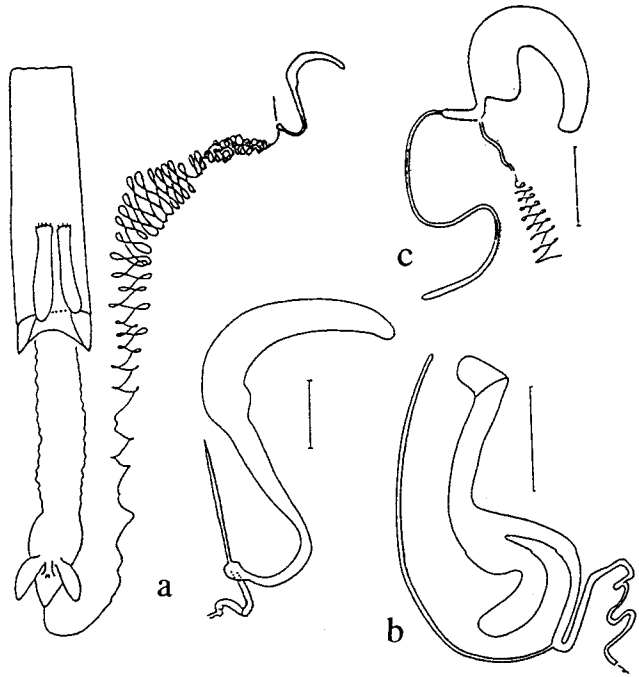

Fig. 7. The female SptOs of two *Palophagus* species, *P. bunyae* Kuschel et May (a) and *P. australiensis* Kuschel et May (b), and of *Cucujopsis setifer* Crowson (Megalopodinae, 'Palophagini'). Scale bar 1.0 mm. (after Kuschel and May 1990).

Subfamily Megascelinae

Table 4 shows the studies of the IRS of the subfamily Megascelinae *s. str.*, namely Suzuki's 'tribe Megascelini'.

Table 4. IRS studies of Megascelinae *s. str.*
Megascelis sp.1 ♀: Suzuki (1974, 1988)
Megascelis sp.2 ♂ and ♀: Suzuki (unpublished)
Megascelis puella Lacordaire, 1845 ♂ and ♀: Present study

Concerning the male and female IRSs of the 'tribe Megascelini' no reliable information has been obtained, except the SptO of *Megascelis* sp. studied by Suzuki (1974, 1988). The male IRS of the subfamily Megascelinae *s. str.* is reported here for the first time. I was able to dissect two (one Panamanian and one Mexican) species of the genus *Megascelis*. The main characteristics of both male and female IRSs in the two *Megascelis* species can be compiled as in Table 5.

Table 5. Main IRS characteristics in Megascelinae *s. str.*
Male
1. A long and thick *vas deferens*
2. Very long *accessory glands*

3. An *anterior ejaculatory duct* forming a weekly developed *ejaculatory sac* and a short *posterior ejaculatory duct*

Female

1. A very specialized proximal part of *spermathecal capsule*
2. A slender and long *spermathecal duct*
3. A long *spermathecal gland*

A combination of the above characteristics in both sexes is seen in only the subfamilies Megascelinae *s. str.* and Eumolpinae auct. Fig. 8 shows both male IRS and female SptO of *Megascelis puella* from Panama. The IRS of another Mexican species is almost same as that of *M. puella* in both sexes. Fig. 9 shows the male IRS and female SptO of *Colposcelis variabilis* of the subfamily Eumolpinae *s. str.*, Suzuki's 'tribe Eumolpini', from Japan cited in Suzuki (1988). One can quickly find that no fundamental difference is seen in the IRSs of either sex of the species belonging to the subfamilies Megascelinae *s. str.* and Eumolpinae auct.

DISCUSSION

Based on the results of the comparative morphology of the IRS, I would like to consider the systematic position of the subfamilies Megalopodinae *s. str.* and Megascelinae *s. str.* and the phylogenetic relationships among them and their relatives. I propose the following two hypotheses about the phylogenetic relationships among the three subfamilies studied.

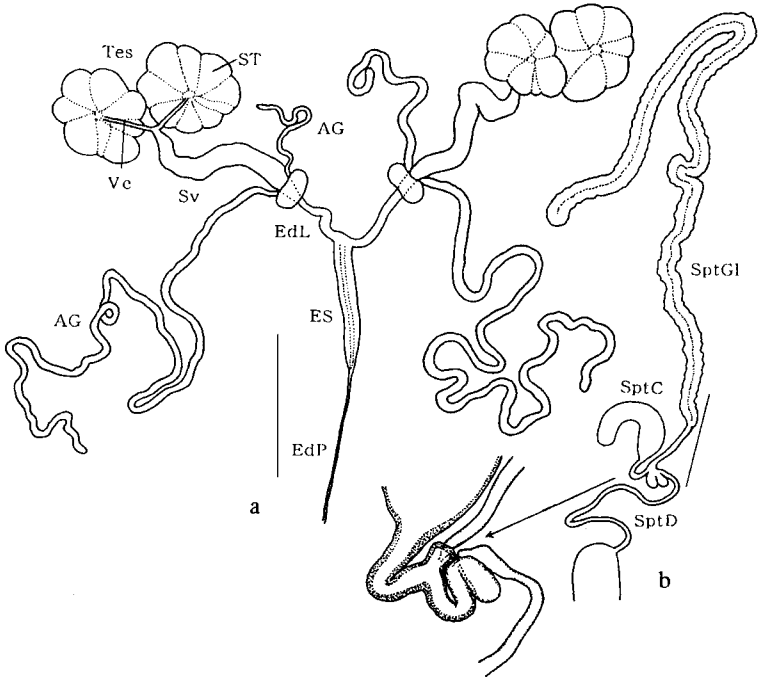

Fig. 8. The male IRS (a) and female SptO (b) of *Megascelis puella* Lacordaire (Eumolpinae, 'Megascelini') from Panama (Gamboa, 15-VII-1997, K. Suzuki and D. M. Windsor leg.). Scale bar 1.0 mm for a, 0.5 mm for b.

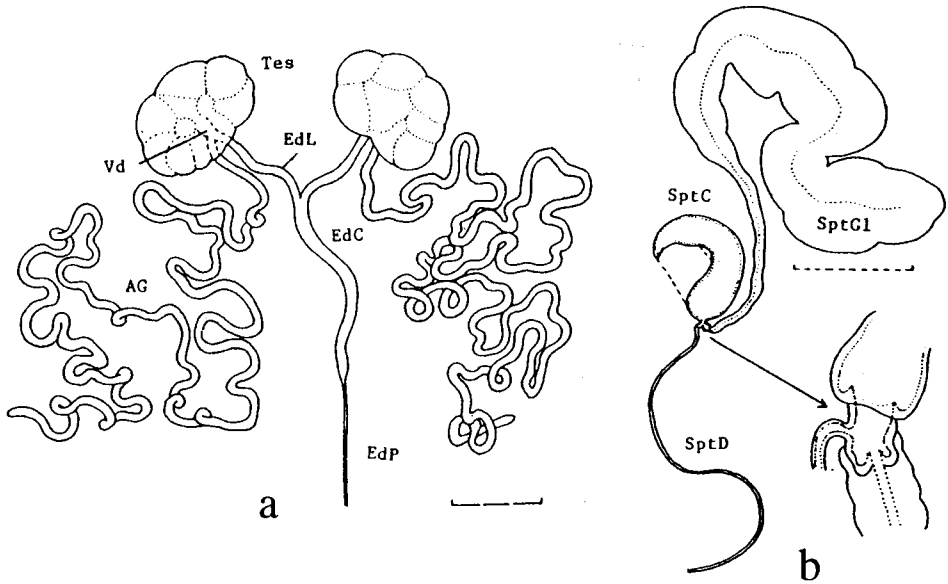

Fig. 9. The male IRS of *Colposcelis variabilis* (Baly) (a) and female SptO of *Basilepta fulvipes* (Motschulsky) (b) (Eumolpinae, 'Eumolpini') from Japan. Scale bar 0.5 mm for a, 0.25 mm for b. (after Suzuki 1988).

1. The subfamily Megalopodinae *s. str.*, together with the subfamilies Zeugophorinae *s. str.* and Palophaginae *s. str.*, constitutes a monophyletic group (Suzuki's 'subfamily Megalopodinae'), but they have a close phylogenetic relationship with some ancestral forms of the family Cerambycidae (e.g. Lamiinae) rather than with any other groups of the family Chrysomelidae.
2. The subfamilies Megascelinae and Eumolpinae are sister groups which might have originated from an ancestral form and constitute a monophyletic group (Suzuki's 'subfamily Eumolpinae').

The two hypotheses proposed here are basically consistent with my higher classification system of the family Chrysomelidae proposed since Suzuki (1980) and with the results of the comparative morphology of external genitalia and hind wing venation (Suzuki, 1994a). For the results of comparison of the IRS with other phylogenetic and/or systematic characters like external genitalia, hind wing venation, and so on, refer to my recent papers listed in the References section below.

Finally, I would like to take this opportunity to mention briefly the phylogenetic relationship of the subfamilies Orsodacninae and Aulacoscelinae. Recently I have published the results of IRS studies of the subfamily Aulacoscelinae (Suzuki, 1994 b; Suzuki and Windsor, 1999). Table 6 shows the previous studies, which have been made for the IRSs of the subfamilies Orsodacninae and Aulacescelinae.

Table 6. IRS studies of Orsodacninae and Aulacoscelinae

Orsodacninae

Orsodacne arakii Chûjô ♂ and ♀: Suzuki (1974, 1988)

Orosodacne lineola Panzer ♂ and ♀: Mann and Crowson (1981)

Aulacoscelinae

Aulacoscelis melanocephala Jacoby ♀: Suzuki (1994b)

Aulacoscelis confusa Monrós ♀: Suzuki (1994b)
Aulacoscelis costaricensis Bechyné ♀: Suzuki (1994b)
Aulacoscelis tibialis Jacoby ♀: Suzuki (1994b)
Aulacoscelis variabilis variabilis Jacoby ♀: Suzuki (1994b)
Aulacoscelis candezei Chapuis ♀: Suzuki (1994b)
Aulacoscelis sp. ♂ and ♀: Suzuki and Windsor (1999)
Janbechynea (Janbechynea) elongata (Jacoby) ♀: Suzuki (1994b)

Fig. 10 shows the male IRS and female SptO of *Aulacoscelis* sp. from Panama cited in Suzuki and Windsor (1999). Fig. 11 shows the male IRS and female SptO of *Orsodacne arakii* from Japan cited in Suzuki (1988). It can easily be recognized that these two groups have many characteristics in common in both sexes. Until I examined the male IRS of *Aulacoscelis* sp. from Panama, I retained my previous opinion of the systematic position of the subfamily Aulacoscelinae (Suzuki, 1996). But, their IRS obviously indicated a direct relationship to the subfamily Orsodacninae.

Through comparative morphological studies of the hind wing venation and male and female IRSs, I have confirmed the effectiveness of these morphological characters in considering the phylogenetic relationships among higher taxa. I would like to retain my previous phylogenetic system, which is a revised version of that of Suzuki (1994a) paper as shown in Fig. 12 (Suzuki 1994a, 1996; Suzuki and Windsor, 1999). I am convinced that this system is consistent with the data, which have been obtained from morphological as well as other aspects of biology.

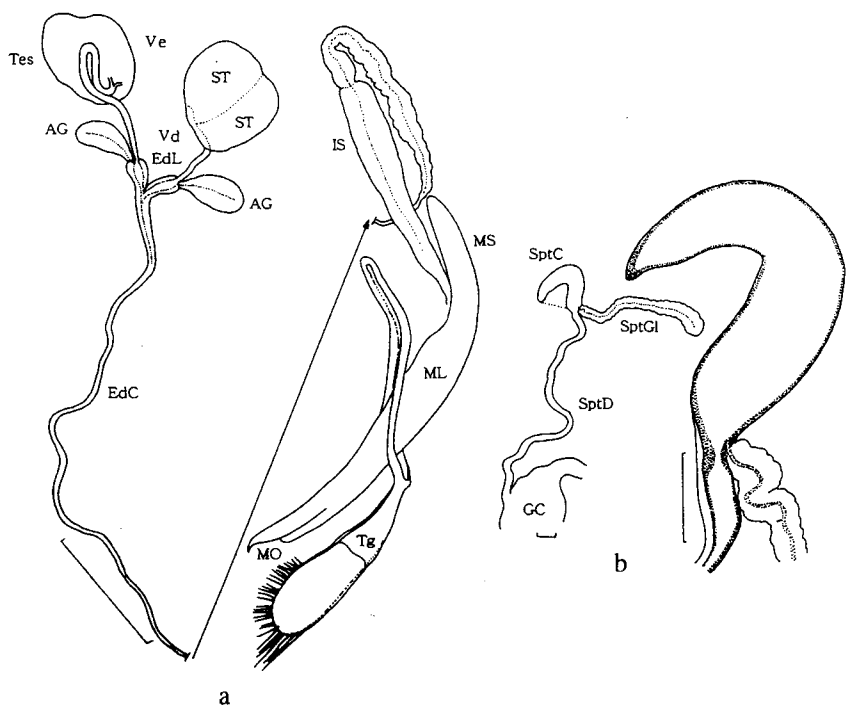

Fig. 10. The male IRS (a) and female SptO (b) of *Aulacoscelis* sp. (Orsodacninae, 'Aulacoscelini') from Panama. Scale bar 1.0 mm. (after Suzuki and Windsor, 1999).

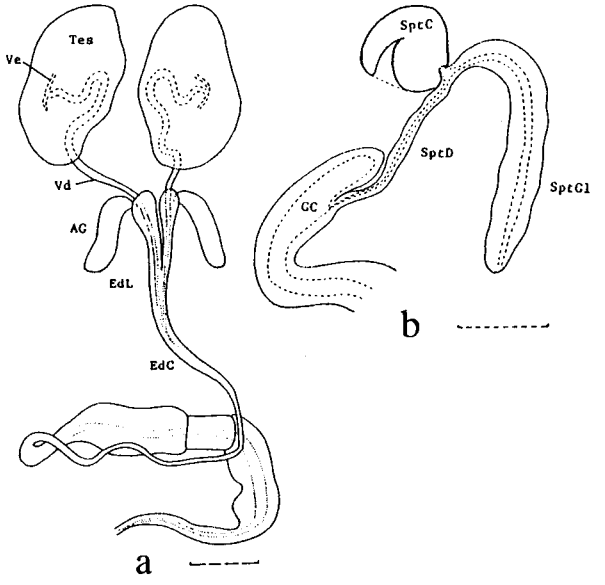

Fig. 11. The male IRS (a) and female SptO (b) of *Orsodacne arakii* Chûjô (Orsodacninae, 'Orsodacnini') from Japan. Scale bar 0.5 mm for a, 0.25 mm for b. (after Suzuki 1988).

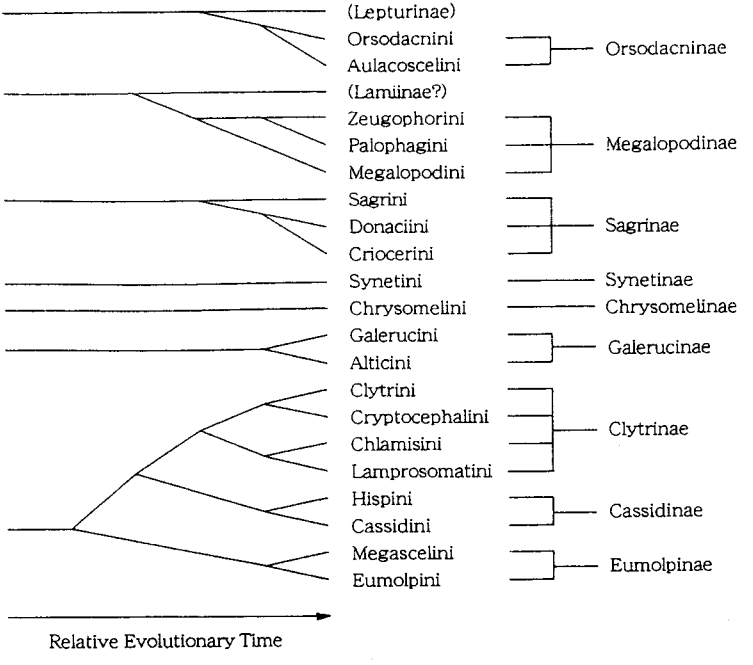

Fig. 12. Supposed phylogenetic relationships among the 'subfamilies' and 'tribes' of the family Chrysomelidae (after Suzuki and Windsor 1999).

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LEGEND FOR FIGURES

Abbreviations for the male internal reproductive system (IRS) and female spermathecal organ (SptO) used in Figures 1-12: AG: *accessory gland*; EdC: *common ejaculatory duct*; EdL: *lateral ejaculatory duct*; EdP: *posterior ejaculatory duct*; ES: *ejaculatory sac*; GC: *genital chamber*; IS: *internal sac*; ML: *median lobe*; MO: *median orifice*; MS; *median strut*; SptC: *spermathecal capsule*; SptD: *spermathecal duct*; SptGl: *spermathecal gland*; ST: *sperm tube*; SV: *seminal vesicle*; Tes: *testis*; Tg: *tegmen*; Vd: *vas deferens*; Ve: *vas efferens*. (see also Suzuki 1988)