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Phylogenetic Studies on the Larvae of the Chrysomelidae (Coleoptera) from Japan[1)]

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Abstract The larvae of the family Chrysomelidae inhabiting Japan are examined on 77 species and 2 subspecies in 45 genera and 16 subfamilies. The phylogenetic relationships among subfamilies are inferred on 34 characters of the larvae by the WAGNER tree method on a computer after the evaluation of every character and the inference of its polarity. The cladogram obtained by this method suggests the phylogenetic positions of the Orsodacninae and Megalopodinae on the first branch as sister taxa from the rest. Next branch is the Bruchidae, which should be treated as a subfamily of the Chrysomelidae. The Donaciinae constitute the third branch. The remaining subfamilies can be divided into 2 phyletic groups: one comprises the Zeugophorinae, Criocerinae, Synetinae, Eumolpinae, Chlamisinae, Clytrinae, Cryptocephalinae, and Lamprosomatinae, and the other includes the Alticinae, Galerucinae, Chrysomelinae, Cassidinae, and Hispinae. This cladogram is not concordant with the previous systems proposed based mainly on the adult characters for the systematic positions of the Criocerinae, Cassidinae, and Hispinae.

Key words: Chrysomelidae; larva; phylogeny; systematic position.

Introduction

The Chrysomelidae are commonly known as leaf beetles, and constitute one of the most abundant and diverse families among herbivorous insects. All of them are phytophagous and some of them are serious pests. With few exceptions, adults feed on foliage and flowers and their larvae on leaves and roots. This family comprises at least 35,000 species from the world and some 500 species from Japan at present.

The foundation of the classification system of this family was first laid by CHAPUIS (1874), who divided the family into 4 sections and 15 tribes. After that, his tribes have been elevated to the subfamily rank and 4 subfamilies have been proposed by the subsequent authorities. Each of 19 subfamilies is currently recognized as a monophyletic taxon and recent classification is largely based on this system.

In contrast to the system below the subfamily level, higher classification above subfamily level can be said to be in a state of chaos. Namely, the recent higher

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systems proposed by Jolivet (1957), Monrós (1959), Mann and Crowson (1981), and Chen (1986) are markedly different from one another from the view point of phylogeny on the relationships of the subfamilies.

The present paper is aimed to infer the phylogenetic system of higher categories from the obtained larval character states on Japanese material.

Materials and Methods

Materials examined. The present study was based on 77 species and 2 subspecies of the chrysomelid larvae from Japan, together with 8 species of Bruchidae from literatures. They were mainly obtained by my extensive collectings and rearings from various parts of Japan during 1986–1989. The outgroup chosen for cladistic analysis was the Cerambycidae, which is the group most closely related to the family Chrysomelidae in the same superfamily, and a total of 8 species in 8 genera was examined.

List of species examined

I. Ingroup:

Chrysomelidae:

Orsodacninae: *Orsodacne lineola* Panz, 1942.

Zeugophorinae: *Zeugophora annulata* (Baly, 1873).

Megalopodinae: *Megalopus jacobyi* Bruch, 1949.

Donaciinae: *Donacia* (*Donacia*) *fukiensis* Goecke, 1944; *Donacia* (*D.*) *hirtihumeralis* Komiya et Kubota, 1987; *Donacia* (*D.*) *hiurai* Kimoto, 1983; *Plateumaris* (*Plateumaris*) *constricticollis babai* Chûjô, 1959; *Plateumaris* (*P.*) *c. chugokuensis* Tominaga et Katsura, 1984; *Plateumaris* (*Euplateumaris*) *sericea* (Linnaeus, 1768).

Criocerinae: *Lema adamsii* Baly, 1865; *Lema cirsicola* Chûjô, 1959; *Lema concinnipennis* Baly, 1865; *Lema decempunctata* Gebler, 1830; *Lema diversa* Baly, 1873; *Lema honorata* Baly, 1873; *Lilioceris subpolita* (Motschulsky, 1860); *Oulema oryzae* (Kuwayama, 1929).

Clytrinae: *Clytra arida* Weise, 1907.

Cryptocephalinae: *Cryptocephalus approximatus* Baly, 1873; *Cryptocephalus nigrofasciatus* Jacoby, 1885; *Cryptocephalus nobilis* Kraatz, 1879; *Cryptocephalus obliquostriatus* Motschulsky, 1866; *Cryptocephalus signaticeps* Baly, 1873.

Chlamisinae: *Chlamisus laticollis* (Chûjô, 1942); *Chlamisus* sp.

Lamprosomatinae: *Oomorphoides cupreatus* (Baly, 1873).

Eumolpinae: *Basilepta fulvipes* (Motschulsky, 1860); *Colposcelis signata* (Motschulsky, 1858); *Demotina fasciculata* Baly, 1874; *Demotina modesta* Baly, 1874; *Hyperaxis fasciata* (Baly, 1874); *Lypesthes ater* (Motschulsky, 1860); *Lypesthes lewisii* (Baly, 1878); *Nodina sauteri*

CHÛJÔ, 1956; *Xanthonia placida* BALY, 1874.

Synetinae: *Syneta adamsi* BALY, 1877.

Chrysomelinae: *Chrysomela populi* LINNAEUS, 1758; *Chrysomela vigintipunctata* (SCOPOLI, 1763); *Gastrolina depressa* BALY, 1859; *Gastrolina peltoidea* (GEBLER, 1832); *Gastrophysa atrocyanea* MOTSCHULSKY, 1860; *Gonioctena* (*Gonioctena*) *japanica* CHÛJÔ et KIMOTO, 1960; *Gonioctena* (*Brachyphytodecta*) *rubripennis* BALY, 1862; *Gonioctena* (*Gonioctena*) *springlovae* (BECHYNÉ, 1947); *Linaeidea aenea aenea* (LINNAEUS, 1758); *Plagiodera versicolora distincta* BALY, 1874.

Galerucinae: *Agelasa nigriceps* MOTSCHULSKY, 1860; *Agelastica coerulea* BALY, 1874; *Atrachya menetriesi* (FALDERMANN, 1835); *Aulacophora femoralis* (MOTSCHULSKY, 1857); *Exosoma flaviventre* (MOTSCHULSKY, 1860); *Fleutiauxia armata* (BALY, 1874); *Galeruca vicina* SOLSKY, 1874; *Galerucella grisescens* (JOANNIS, 1961); *Galerucella nipponensis* (LABOISSIÈRE, 1922); *Gallerucida bifasciata bifasciata* MOTSCHULSKY, 1860; *Gallerucida b. nigromaculata* (BALY, 1861); *Lochmaea capreae cribrati* (SOLSKY, 1872); *Pyrrhalta* (*Pyrrhalta*) *annulicornis* (BALY, 1874); *Pyrrhalta* (*P.*) *humeralis* (CHEN, 1942); *Pyrrhalta* (*P.*) *maculicollis* (MOTSCHULSKY, 1853); *Pyrrhalta* (*Tricholochmaea*) *semifulva* (JACOBY, 1885).

Alticinae: *Altica caerulescens* (BALY, 1874); *Altica cirsicola* OHNO, 1960; *Alitica* sp.; *Argopistes biplagiatus* MOTSCHULSKY, 1860; *Argopistes coccinelliformis* CSIKI, 1940; *Luperomorpha funesta* (BALY, 1874); *Sangariola punctatostriata* (MOTSCHULSKY, 1860).

Hispinae: *Dactylispa issikii* CHÛJÔ, 1938.

Cassidinae: *Aspidomorpha indica* BOHEMAN, 1854; *Cassida* (*Odontionycha*) *erudita* BALY, 1874; *Cassida* (*Cassida*) *fuscorufa* MOTSCHULSKY, 1886; *Cassida* (*C.*) *nebulosa* LINNAEUS, 1758; *Cassida* (*Alledoya*) *vespertina* BOHEMAN, 1862; *Cassida vibex* LINNAEUS, 1767; *Thlaspida cribrosa* (BOHEMAN, 1855).

Bruchidae: *Bruchidius atrolineatus* (PIC, 1921); *Bruchidius baudoni* (CAILLOL, 1908); *Bruchus brachialis* FÅHRAEUS, 1839; *Bruchus pisorum* (LINNAEUS, 1758), *Bruchus rufimanus* BOHEMAN, 1833; *Caryedon albonotatum* (PIC, 1898); *Caryedon cassiae* (GYLLENHAL, 1833); *Caryedon palaestinicus* SOUTHGATE, 1976.

II. Outgroup:

Cerambycidae:

Prioninae: *Eurypoda unicolor* HAYASHI, 1956; *Megopis sinica* WHITE, 1853; *Prionus coriarius* (LINNAEUS, 1758); *Psephactus remiger* HAROLD, 1879.

Parandrinae: *Parandra shibatai* HAYASHI, 1963.

Lepturinae: *Caraphia lepturoides* (MATSUSHITA, 1933); *Leptura rubra* (LINNAEUS, 1758); *Rhagium japonicum* BATES, 1884.

Methods of dissection and observation. The larvae were mostly killed and preserved in 70% ethanol/glycerin solution (9: 1), and partly killed by injecting a fixative (equivalent mixture of 95% ethanol and 30% formalin) from the pleural region of the body to prevent decomposition and shrinkage. These materials were macerated in 10% KOH solution for several minutes, rinsed in water, and then dissected under a stereoscopic microscope using a sharp needle and pointed forceps. For a detailed morphological study, the antenna, epipharynx, stipes, galea, lacinia, prementum, and spiracles were mounted on slides and observed under the phase-contrast microscope. Drawings were made with the aid of an ocular grid micrometer attached to an eye piece of the stereoscopic microscope.

Methods of the phylogenetic analysis. The phylogenetic relationships among the subfamilies of the Chrysomelidae were examined by the cladistic method. Numerical ways of the cladistic analysis were done on a personal computer with SAWADA's program (1988), which adopts a parsimony algorithm of the WAGNER tree method. The apomorphic (=derived or less general) and plesiomorphic (=primitive, ancestral, or more general) character states have been determined by the outgroup comparison method on the principles that "the primitive state of a character for a particular group is likely to be present in many of the representatives of closely related groups" (KLUGE & FARRIS, 1969, p. 5), or that "if one of two or more character states in one group occurs in other closely related groups, it is probably the ancestral one" (ROSS, 1974, p. 153).

Historical Review

The history of the classification of the Chrysomelidae is relatively uncomplicated. Various systems and modification of these systems have been proposed. The first mention of the Chrysomelidae as a discrete entity was made by LATREILLE (1802). DUMERIL (1806) proposed the name Phytophages for the family instead of Chrysomelidae. CHAPUIS (1874) proposed a system which is the foundation of the modern classification in use today. His system used LATREILLE's idea of grouping these beetles into a single family, and then further divided the family into 4 "sections" and 15 "tribes". JACOBY (1908) modified CHAPUIS' system to include 5 "divisions" and 16 subfamilies. The superfamily Chrysomeloidea was proposed by PIERCE (1916). BÖVING and CRAIGHEAD (1931) established a classification of the Coleoptera based on the morphology of larvae rather than adults. They followed the previously proposed system of PIERCE (1916) and the Zoological Record in which the family Chrysomelidae was elevated to the superfamily rank and the various subfamilies of JACOBY (1908) to the family level. Included therein are the Bruchidae. CHEN (1934, 1940) proposed a slight modification to the JACOBY's system, and a new classification for the leaf beetles. His conclusions were largely based on the following characters: 1) adult external characters, 2) hind wing venation, 3) male genitalia, and 4) larval structures and bionomics. The old family Chrysomelidae

was rearranged into 6 "divisions," each of which was elevated to the family rank. GRESSITT (1942) moved the Megalopodinae from the "Camptosomes" to the "Eupodes" and placed the subfamily Chrysomelidae by itself between the "Cyclica" and the "Trichostomes". CHÛJÔ (1952, 1953–54) proposed the subfamily Zeugophorinae, and re-grouped the family Chrysomelidae into 14 divisions based on adult morphology. EDWARD (1953) proposed the family Synetidae for the genera *Syneta* DEJEAN and *Tricolema* CROTCH. Various works on all families of Coleoptera were done by CROWSON (1955). MONRÓS (1959) proposed a system of classification of the Cerambycoidea in which the "Eupoides" is suppressed as an unnatural assemblage of primitive genera in several subfamilies of different evolutionary trends. GRESSITT and KIMOTO (1961, 1963) produced the first of the large monographs on the Chrysomelidae of various parts of Asia by separating the family into 17 subfamilies. CHEN (1964) proposed a system of classification of the Chrysomeloidea including 6 families and 18 subfamilies. CHEN (1973) also proposed the new superfamily Cassidoidea and compared the taxa in this new system to those in the old one. MANN and CROWSON (1981) offered views and proposal involving various chrysomelid subfamilies relative to the genera *Orsodacne* LATREILLE and *Syneta* LACORDAIRE, based on the internal anatomy and tarsal vestiture of the adult as well as larval characters. CROWSON (1981) divided the traditional family into the Megalopodidae (including Zeugophorinae), Bruchidae (including Sagrinae, Donaciinae, Criocerinae), and Chrysomelidae. SEENO and WILCOX (1982) proposed 19 subfamilies based on the literature.

As stated above, an agreement has largely been reached on the subfamily classification by the authors, but not on the higher grouping of the family.

Historical Review of the Works on the Larvae of Chrysomelidae

The comprehensive study on the chrysomelid larvae was first carried out by SANDERSON (1901) who gave notes on the classification of the Chrysomelidae. More detailed morphological descriptions and illustrations of the galerucine and donaciine larvae were presented by BÖVING (1927) who also gave some information on larval habits. PATERSON (1930, 1931) furnished notes on the bionomics and comparative morphology of the early stages of certain Chrysomelidae including the Galerucinae, Alticinae, Chrysomelinae, Criocerinae, Donaciinae, Cryptocephalinae, and Cassidinae. BÖVING and CRAIGHEAD (1931) established a classification of the order Coleoptera based on the larval morphology. HENNIG (1938) described the setae, tubercles, and chaetotaxy on the basis of the chrysomeline larvae. The comparative morphology and taxonomy of some larvae in the Criocerinae were made by SAILSBURY (1943). Brief notes on 2 species of the megalopodine larvae were presented by MONRÓS (1954). A new key to the chrysomelid larvae was provided and a phylogenetic dendrogram of the family with palaeontological data were figured by MANN and CROWSON (1981). MAULIK (1930) described the larvae and pupae of some

Table 1. The characters and character states used in the cladistic analysis. Zero indicates plesiomorphic state and numbers greater than 0 indicate progressive and more apomorphic states.

Character	Character states
1. Shape of head:	(0) Ovoid
	(1) Round
2. Number of frontal setae:	(0) More than 3 pairs
	(1) Less than 4 pairs
3. Papillate seta on frons:	(0) Absent
	(1) Present
4. Number of antennal segments:	(0) 2 or 3 segments
	(1) 1 segment
5. Coronal suture:	(0) Absent
	(1) Present
6. Endocarina:	(0) Present
	(1) Absent
7. Frontal suture:	(0) Present
	(1) Absent
8. Hind corners of epicranium:	(0) Produced
	(1) Not produced
9. Head:	(0) Retracted into prothorax
	(1) Protracted from prothorax
10. Length of pronotal setae:	(0) Minute
	(1) Long
11. Frons and clypeus:	(0) Not fused
	(1) Fused
12. Anterior margin of labrum:	(0) Not incised
	(1) Incised
13. Number of setae on labrum:	(0) More than 4 pairs
	(1) 3 or 4 pairs
	(2) 0 to 2 pairs
14. Shape of mandible:	(0) Gouge-like
	(1) Palmate
15. Number of mandibular teeth:	(0) Less than 3
	(1) More than 2
16. Number of mandibular setae:	(0) 2
	(1) 1
17. Penicillus:	(0) Absent
	(1) Present
18. Type of pronotum:	(0) D-DL-Ep type
	(1) D-DL-type
19. Number of maxillary palpal segments:	(0) 3 segments
	(1) 1 or 2 segments
20. Galea and lacinia:	(0) Fused
	(1) Not fused
21. Number of labial palpal segments:	(0) 2 segments
	(1) Rudiment or 1 segment
22. Number of setae on stipes:	(0) More than 4

Table 1. (Continued.)

Character	Character states
	(1) Less than 5
23. Number of setae on postmentum:	(0) Less than 3 pairs
	(1) 3 pairs
24. Cardo:	(0) Present
	(1) Absent
25. Urogomphi:	(0) Present
	(1) Absent
26. Seta on claw:	(0) Absent
	(1) Present
27. Pulvillus:	(0) Absent
	(1) Present
28. Shape of claw:	(0) Falciform
	(1) Sickle-like
29. Dorsal tubercle:	(0) Not sclerotized
	(1) Sclerotized
30. Ambulatory wart:	(0) Present
	(1) Absent
31. Shape of body:	(0) Elongated or plumped
	(1) J-or C-shaped, not plumped
32. Defensive glands:	(0) Absent
	(1) Present
33. Shape of spiracle:	(0) -Annuliform
	(1) Biforous
	(2) Bicameral
34. Egg bursters:	(0) Present
	(1) Absent

Hispinae. Immature stages of some Chlamisinae and Cryptocephalinae were described by LESAGE (1982, 1984 a, b, 1985, 1986). Many works on the chrysomelid larvae were done by MARSHALL (1979, 1880), HOUSTON (1982), COX (1982), and others.

In Japan, the detailed description of the larva was first mde on *Cryptocephalus signaticeps* by FUJITA (1958). Some chrysomelid larvae were also described and illustrated by HAYASHI (1959). KIMOTO (1962) described the morphological change in the course of larval growth in the Chrysomelinae, especially the arrangement of tubercles rather than that of setae, and gave phylogenetic accounts based on the immature stages. Recently, descriptions of the last instar larvae and pupae of glanduliferous group of the Galerucinae and Chrysomelinae were given by TAKIZAWA (1972, 1976).

Phylogeny

Cladistic relationships were assessed with the WAGNER tree method of SAWADA

(1988) based on 34 character data sets (Fig. 1), and their plesiomorphic and apomorphic states are listed in Table 1. In SAWADA's program on this method, the length of each segment or stem is changed along it. The branching is determined by minimizing the total number of character state changes over the entire tree. The trees shown here were all rooted by including the hypothetical OTUs (operational taxonomic units). Tables 2 and 3 show the character state matrix and the character change matrix in point of each intervals, respectively.

Results and Discussion

Cladistic analysis. This analysis partitioned the 17 taxa into 2 groups, one with the Orsodacninae and Megalopodinae, the other with the remaining subfamilies. The recognition of the Orsodacninae and Megalopodinae as a monophyletic group rests on the characters of the frons, number of setae on the labrum and teeth on the mandible (characters 11, 13, and 15). In both subfamilies the frons are not fused with the clypeus, the labrum is furnished with or without 2 pairs of labral setae and the mandible with more than 3 teeth. The remaining 15 taxa are characterized primarily by the number of segments of the labial palp, the number of setae on the postmentum and absence of the urogomphi (characters 21, 23, and 25). For the Bruchidae, additional data are needed to resolve their systematic position.

The positions of the Synetinae-and Eumolpinae on the cladogram are based on relatively minor differences in the structures of the antennae, endocarina and spiracle. The recognition of the Clytrinae, Cryptocephalinae and Lamprosomatinae as sister taxa rests on 2 characters: type of the sclerite on the pronotum (character 18), and the number of setae on the stipes (character 22). Cladistic analysis justifies treatment of the Orsodacninae and Megalopodinae, the Alticinae and Galerucinae, and the Chrysomelinae and the Cassidinae as sister groups, respectively. These are delimited from all the other chrysomelids by 3, 2, and 4 synapomorphies, respectively. Although I think that Fig. 1 presents a hypothesis of the phylogenetic relationships, there is a need for additional data. Limitations to the current analysis include the number of segments of the labial palp, the employment of traits at different levels in the cladogram that are not independent but simply increasingly derived states of the same feature (*e.g.* characters 13, 15) and the assumptions of taxa from the limited information (Orsodacninae, Megalopodinae and Bruchidae).

According to CROWSON (1955) the *Orsodacne* (Orsodacninae) larva obtained by VAN EMDEN had considerable similarities to the larval types of the Eumolpidae and Galerucinae. In respect to its biforous spiracles, it resembles larvae of the Criocerinae, and in the straight simple tarsungulus it resembles *Sagra* (Sagrinae), *Clytra* (Clytrinae), and the Eumolpinae. In the possession of the mandibles with pluridentate apices, it is similar to the larvae of the Galerucinae. The larvae of *Orsodacne* share with that of the genus *Megalopus* (Megalopodinae) the straight, cerambycid-like shape, and distinct short thoracic legs, and is different from *Zeugophora* (Zeugo-

Table 2. Distribution of the character states of the larvae of the family Chrysomelidae. Zero indicates plesiomorphic state and numbers greater than 0 indicate progressively more apomorphic states (Ancestor: Cerambycidae).

No.	Taxa/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1	Bruchidae*	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
2	Orsodacninae*	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
3	Zeugophorinae	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	0	0	0
4	Megalopodinae*	0	1	0	0	0	1	1	0	0	0	1	0	2	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0
5	Donaciinae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	1	0	0	0	1
6	Criocerinae	1	0	0	0	1	0	0	1	1	0	0	1	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	0
7	Clytrinae	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0
8	Cryptocephalinae	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0
9	Chlamisinae	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0
10	Lamprosomatinae	1	0	0	0	0	1	0	1	1	1	1	1	2	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	2	0
11	Eumolpinae	1	0	0	0	1	1	0	1	1	1	0	0	1	1	1	0	0	1	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
12	Synetinae	1	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1
13	Chrysomelinae	1	1	0	0	1	0	0	1	1	1	0	1	2	1	1	0	0	1	0	1	0	1	1	0	0	1	0	1	1	1	1	1	0	0
14	Galerucinae	1	1	0	1	1	0	0	0	1	1	0	0	2	1	1	0	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	1	0	1
15	Alticinae	1	1	0	1	0	0	0	0	0	1	0	0	2	1	1	0	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0
11	Hispinae	0	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	1	1	0	0	0	1
17	Cassidinae	1	0	0	0	1	0	1	1	0	1	0	1	2	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	1
18	ANCESTOR*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* I have not seen larvae of Bruchidae, Orsodacninae, Megalopodinae and Ancestor (outgroup=Cerambycidae) but indications as to the state of these characters are found in PREVETT (1971), MANN & CROWSON (1981), MONRÓS (1954) and KOJIMA & HAYASHI (1969), respectively.

Table 3. A matrix of character change in point of each intervals (IT,

IT (N)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
2	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·
3	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	+	·	·
4	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·
5	·	+	·	·	+	·	+	+	·	·	·	·	·	·	·	·	+	·	+
6	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
7	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
8	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
9	·	+	·	·	·	+	+	·	·	·	·	·	+	+	·	·	·	·	·
10	·	·	·	·	·	·	·	·	·	·	+	·	+	·	+	·	·	·	·
11	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
12	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·
13	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·
14	+	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·
15	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	—	·
16	·	·	·	·	+	·	·	+	+	·	·	·	·	·	·	·	·	·	·
17	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·
18	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
19	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
20	·	·	·	·	—	·	·	·	·	·	·	·	+	·	·	·	·	·	·
21	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	—	·
22	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
23	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
24	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·
25	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·
26	·	+	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·	·	·
27	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·
28	+	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·
29	·	—	·	·	·	·	+	·	·	·	·	·	·	·	·	+	·	·	+
30	·	·	·	·	+	·	·	+	·	·	·	+	·	·	·	·	·	·	·
31	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·
R (N)	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1
L (N)	2	4	1	2	5	3	3	3	4	2	2	3	5	3	3	1	3	3	3
H (N)	1	3	0	1	4	2	2	2	3	1	1	2	3	2	2	0	2	2	2

phorinae) in having a fully developed labium (CROWSON, 1955).

Thus, the larvae of *Orsodacne* share most character with those of the Galerucinae and Alticinae. However, these similarities of the larvae in remote taxa have probably arisen by convergence as a result of adaptation to the same living habitat.

The genus *Syneta* had usually been classified in the subfamily Orsodacninae until the establishment of the Synetinae by EDWARDS (1953). CROWSON (1953) excluded *Syneta* from the Orsodacninae and discussed on the evolutionary line from the Orsodacninae to the Galerucinae on the adults structures. JOLIVET (1957) con-

interval; PT, point; HTU, hypothetical taxonomic unit; H, homoplasy).

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	PT (2)=5 Donaciinae
.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	PT (3)=2 Orsodacninae
.	.	+	.	.	.	+	.	.	.	+	.	.	.	.	PT (4)=HTU 18
.	.	−	.	.	.	−	.	.	.	−	.	.	.	.	PT (5)=1 Bruchidae
.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	PT (6)=HTU 19
.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	PT (7)=3 Zeugophorinae
.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	PT (8)=HTU 20
.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	PT (9)=4 Megalopodinae
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	PT (10)=HTU 21
.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	PT (11)=16 Hispinae
.	.	.	--	.	.	.	.	.	.	.	.	.	.	.	PT (12)=HTU 22
.	.	.	.	.	.	.	+	.	.	−	.	.	.	.	PT (13)=6 Criocerinae
.	.	.	.	.	.	−	.	.	.	.	.	.	.	.	PT (14)=HTU 23
.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	PT (15)=12 Synetinae
.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	PT (16)=HTU 24
.	.	.	+	.	.	.	.	.	.	.	.	.	−	.	PT (17)=11 Eumolpinae
.	.	.	.	.	.	+	.	−	.	.	+	.	.	.	PT (18)=HTU 25
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	PT (19)=7 Clytrinae
.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	PT (20)=10 Lamprosomatinae
.	.	−	.	.	.	.	.	.	.	.	.	.	.	.	PT (21)=HTU 26
.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	PT (22)=8 Cryptocephalinae
.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	PT (23)=9 Chlamisinae
.	−	.	.	.	.	.	.	.	.	.	.	.	.	.	PT (24)=HTU 27
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	PT (25)=15 Alticinae
.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	PT (26)=HTU 28
.	−	.	.	.	.	.	.	.	.	.	.	+	.	.	PT (27)=13 Chrysomelinae
+	.	.	+	.	−	.	.	.	.	.	+	.	.	.	PT (28)=HTU 29
−	.	.	.	+	+	.	.	.	.	.	−	.	.	+	PT (29)=17 Cassidinae
.	.	.	.	.	.	.	−	.	.	.	.	.	.	.	PT (30)=HTU 30
.	−	.	.	.	.	.	.	.	.	.	.	+	.	+	PT (31)=14 Galerucinae
1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	RANGE R=36
2	4	4	4	2	4	4	3	3	1	3	3	2	5	5	LENGTH L=104
1	3	3	3	1	3	3	2	2	0	2	2	1	3	4	H=68

sidered the direct origin of the Synetinae from the Orsodacninae based on the wing venation. CHEN (1964) placed the Synetinae in his "Crioceridae" but he (1973, 1986) changed his previous opinion and transferred it to his "Chrysomelidae". KURCHEVA (1964, 1967) described the larvae of *Syneta betulae* F. for the first time and placed the Synetinae in or close to the Eumolpinae on the larval character. MANN and CROWSON (1981) proposed a phylogenetic system of the superfamily Chrysomeloidea and placed the Synetinae in a monophyletic group with the Eumolpinae, Galerucinae and Alticinae on the larval and adult characters. By the

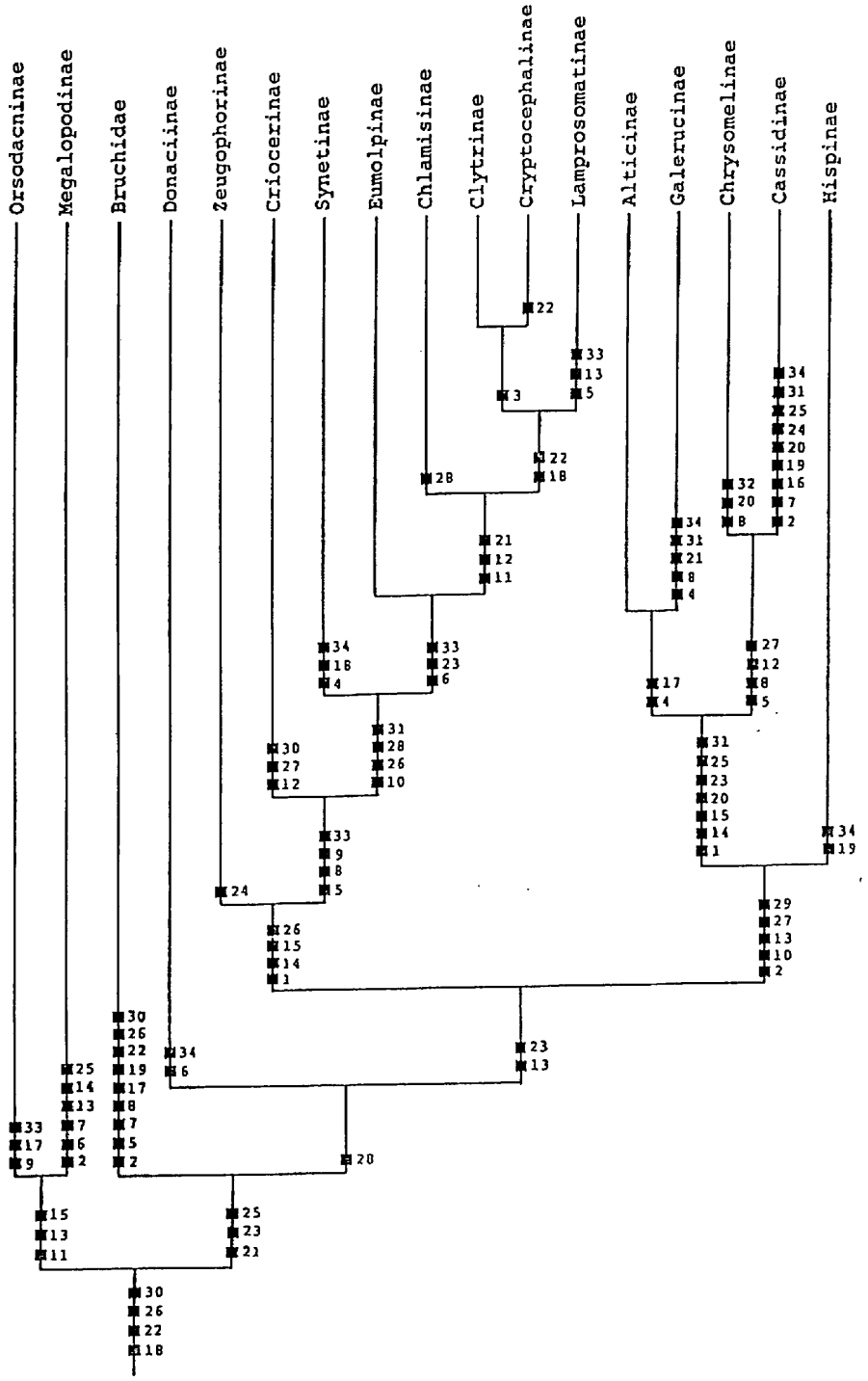

Fig. 1. Cladogram of relationships among the 17 subfamilies based on 34 larval characters. Numbers refer to apomorphic character states as described in text.

larval characters, *Syneta* is close to the Eumolpinae in having the similar head capsule, mandibles, labial palpi, claws, spiracles and chaetotaxy, but is characteristic in the sclerotized tergites of the abdominal segements 9 and 10, one-segmented antennae, and fused trochanters and femora (Table 3). Furthermore, the larvae of the Synetinae occupy the same ecological niche as those of the Eumolpinae feeding on root in the soil.

The subfamily Lamprosomatinae had been classified in the 'Cyclica' including the Eumolpinae by such old authors as CHAPUIS (1874), JACOBY (1908), CHEN (1934) and GRESSITT (1942). BÖVING and CRAIGHEAD (1931) transferred the Lamprosomatinae from the "Cyclica" to the "Camptosomata" based on the morphology of the larvae. MONRÓS (1959) proposed a new system placing the Lamprosomatinae in his division "Alticae Clytriformes". CHEN (1964, 1973, 1986) placed the Lamprosomatinae in his family "Eumolpidae" together with the Eumolpinae, Chlamisinae, Clytrinae and Cryptocephalinae. CROWSON (1955) classified the Lamprosomatini in the Clytrinae, which are equivalent to the "Camptosomata". KASAP and CROWSON (1976) and again MANN and CROWSON (1981) fixed the phylogenetic position of the Lamprosomatinae in the camptosomatan line. Present study supports the conclusion of MANN and CROWSON on the larvae (Fig. 1).

The subfamily Criocerinae was treated by MONRÓS (1959) in his Chrysomelae Crioceriformes including the Sagrinae, Bruchinae and Donaciinae, and MANN and CROWSON (1981) placed it in a branch from the Orsodacninae-Chrysomelinae line. But, present sudy concludes the position of the Criocerinae in a branch from the Zeugophorinae-Eumolpinae-Cryptocephalinae line, and not in the group including the Chrysomelidae.

The Cassidinae and Hispinae have been classified as sister subfamilies in an isolate group within this family, or in the other independent family. But, present study draws the conclusion from the larval characters that they belong to the group including the Chrysomelinae.

On the systematic position of the subfamily Chrysomelinae, there are various opinions. MONRÒS (1959) placed it in his Chrysomelae Chrysomeliformes, a distant group from the the Galerucinae. But, CHEN (1940, 1964, 1973, 1986) was consistent to classify it in the same group with the Galerucinae and Alticinae. MANN and CROWSON (1981) treated it in an independent branch from the primitive group of the Cassidinae-Clytrinae line. Present study supports CHEN's treatment.

The cladograms of the subfamily relationships depicted in Fig. 1 is drawn primarily on the limited information from the Japanese materials. So, it is strongly hoped that further information will be added and the system will be reconstituted by many entomologists in the various regions of the world in the future.

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