CLADISTIC ANALYSES OF THE COCCINELLIDAE (COLEOPTERA)

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Abstract Numerical cladistic method was used for analyzing the phylogeny of ladybirds, based upon adult and larval characters. The analysis of adult characters for 21 tribes, representing all subfamilies proposed by various authors, exhibited 18 equally parsimonious cladograms with high level of homoplasy. Five lineages were roughly revealed in the strict consensus tree: Sticholotidinae, Epilachninae, Coccinellinae(including Singhikalini), Coccidulinae (excluding Noviini) and Scymninae+Chilocorinae. The taxonomic interpretation of the adult analysis was similar to the classification proposed by Chazeau *et al*. (1990). Comparison of a preliminary analysis based on the larval characters for 14 tribes revealed only one component consistently supported in both analyses (Serangiini+Sukunahikonini). Larval analysis showed that Epilachinae is the most primitive and highly derived group of the Coccinellidae. Larval characters might be more satisfactory in revealing the phylogeny.

Key words Coleoptera; Coccinellidae; cladistics

1 INTRODUCTION

The higher classification of the family Coccinellidae has long been the subject of study since the publication of Mulsant's remarkable world monograph titled " Species des Coleopteres Trimeres Securipalpes" in 1850. The subdivision of the family has given rise to much controversy: it might be divided into three (Korschefsky 1931, 1932, Kapur 1970, Bielawski 1984), six (Sasaji 1968a, 1971, Duang *et al.* 1974, Belicek 1976, Gordon 1985, Chazeau *et al.* 1989, 1990), or eight subfamilies (Pang *et al.* 1979).

Coccinellidae has not been analysed cladistically. Based upon available information on adults and larvae, this paper intends to probe the relationships on tribal level among the families by using numerical cladistics.

2 MATERIALS AND METHODS

2.1 Selection of OTUs

It attempted to include tribal members of every subfamily recognized in recently catalogues, and whenever possible a member of the type genus of each tribe was examined. The present study includes all tribes occurred in China except for tribe Epivertini. Appendix A is the list of genera selected for adult analysis (present taxonomic position from Chazeau *et al.* 1990, see Table 1).

The genera *Singhikalia* and *Scotoscymnus* were not examined by the author personally.

Kapur(1963), Miyatake(1972) and Sasaji(1968) have provided illustrations and descriptions of these two genera respectively.

In many groups of insects, studies of the immature stages have made great contribution to systematics, the phylogenetic relationships in particular. For comparing with the cladistic result based upon adult characters, the attempt to use available information of larvae, mainly from Kamiya(1965), Sasaji(1968a, 1968b) and Sasaji *et al.* (1982) was made for cladistic analysis. Appendix D and E are the lists of genera for larval cladistic analysis, the characters and the coding of the states respectively.

2.2 Selection and coding of characters

The primary source of adult characters was Sasaji's(1968a) phylogenetic study on Coccinellidae, with a small number of characters that came to light in my own examination of specimens. Character states were coded in graded linear series when possible, so that the most divergent states were at opposite extremes. Primitiveness or derivativeness was derived with slight change from Sasaji's (1968a) study on the comparative morphology of the adult Coccinellidae, by outgroup comparison with the closely related family Endomychidae. The affinity between Coccinellidae and Endomychidae is certainly recognizable as it is accepted by almost all the recent coleopterists (Sasaji 1971). Characters and the coding of the states are presented in Appendix B.

2.3 Data analyses

2.3.1 Computational procedures Relationships among taxa were explored through a numerical cladistic approach by using PAUP (Phylogenetic Analysis Using Parsimony, version 2.4.1, Swofford, 1985) implemented on an IBM PC/XT. The ADDSEQ=CLOSEST SWAP=GLOBAL F-VALUE MULPARS HOLD=10 were used in the analysis of data sets of adult and larval characters. Coding a character as 9 in the character data matrices indicates that it is unknown for the taxon, or it is no comparison data.

2.3.2 Unordered characters Prior hypotheses of character evolutions have overwhelming influence on the results of a taxonomic study. If a character has only two states, there is only one possible transformation; and it has been shown that polarity may be solved according to the parsimonious application of the outgroup method (Lungberg 1972, Farris 1982). But there are many possible transitions for characters with multiple states, which give rise to a significant and intractable problem, if lack of more general theories of character transformation to refer.

The PAUP provides a command UNORDERED, which can resolve the above problem. By using UNORDERED, no *a priori* transformation series is assumed; each character is at least potentially capable for transforming directly into any other character states (Swofford 1985).

2.3.3 Comparison of results For comparing phylogenetic hypotheses based on different data sets, we delete the taxa which are uncommon to the two sets before calculation. To compare the different cladograms, the consensus trees were constructed, which specify the common structure shared by two or more tree cladograms.

3 RESULTS

3.1 Monophyly of the Coccinellidae

Three characters (last segment of maxillary palpi securiform; tarsi cryptotetramerous and sternite of first visible abdominal segment with postcoxal line) are considered to be separated from the closely related families. However all of them are not unique to Coccinellidae. Postcoxal line, for example, is also presented in *Biphyllus japonicus* Sasaji of Biphyllidae, *Philothermys takasago* Sasaji and *Lapecautomus orientalis* Sasaji of Cerylonidae, *Edioreus japonicus* Sasaji of Endomychidae, *Sphaerosoma* of Spaerosomatidae, *Toramus* of Languriidae. On the other hand, not all species of Coccinellidae present the three characters. In members of Sticholotidinae and many of Scymninae, terminal segment of maxillary palpi is conical or parallel-sided; many groups of ladybirds have a tarsus of 3 segments. Still, in a few genera (*Hippodamia* of Coccinellini and *Epiverta* of Epivertini), the postcoxal line of first abdominal sternite is absent.

These three characters are presented in most species, while two of them are observed in many species. If all or two of these three characters are found in a beetle, we can determine the beetle as a member of Coccinellidae (Pang *et al*. 1979). However, some genrera (e.g. *Scotoscymnus*, *Shirozuella*) only present one character (postcoxal line). Therefore, at least two of them (securiform terminal segment of maxillary palpi and cryptotetramerous tarsi) could not be considered as synapomorphies of Coccinellidae.

The tentorium of Coccinellidae consists of very thin parallel tentorial arms which are usually convergent in middle but entirely separated, and always lacks a tentorial bridge. Such a structure of tentorium is uniform throughout the Coccinellidae and the absence of the tentorial bridge is a very stable character of the family. This fact seems to be important, because the tentorial bridge has been deliberately examined in almost all the genera of the other families related to Coccinellidae, such as Discolimdae, Endomychidae, Cerylonidae, Lathridiidae, Merophysiidae, Corylophidae, and many others of Clavicornia (Sasaji 1968a, Stickney 1923). The structure of tentorium may be considered as a synapomorphy of Coccinellidae.

The structure of male genitalia is proposed here as a strong synapomorphy of the family. The male genitalia proper of Coccinellidae is quite different from those of all the other Coleoptera in structure which is unique in this order (Sasaji 1968a). The structures of male genitalia are modified in many groups of Coccinellidae. However, they are all derivded from a common structure, namely, sipho (penis or aedeagus) very long and tubular; the tegmen consisting of a basal piece, paired paramera (lateral lobes) and distinct median piece, with a median strut (Trabes) further articulating with ventral side of the segment.

3.2 Analysis I: adult characters of 21 tribes

The existing classification of the Coccinellidae is based primarily upon adult characters, but these characters have not been analysed cladistically. This analysis employed 36 characters shown in Appendix B. All characters except 11,12,18,19 and 27 were coded as additive (or ordered). These five characters exhibited multiple states which could not be arranged in any obvious linear transformation series, so it is preferable to count any transformation between any of the alternate states as a single step. The data matrix for Analysis I is presented in Appendix C. This analysis found 18 equally parsimonious cladograms, with an overall length of 153 steps, consistency index of 0.373. The F-values of these parsimonious cladograms range from 0.545 to 0.608 (only apply to ordered characters). In other words, these characters exhibited a high level of homoplasy and showed relatively less resolution. The single cladogram with lowest F-value is reproduced in Fig. 1.

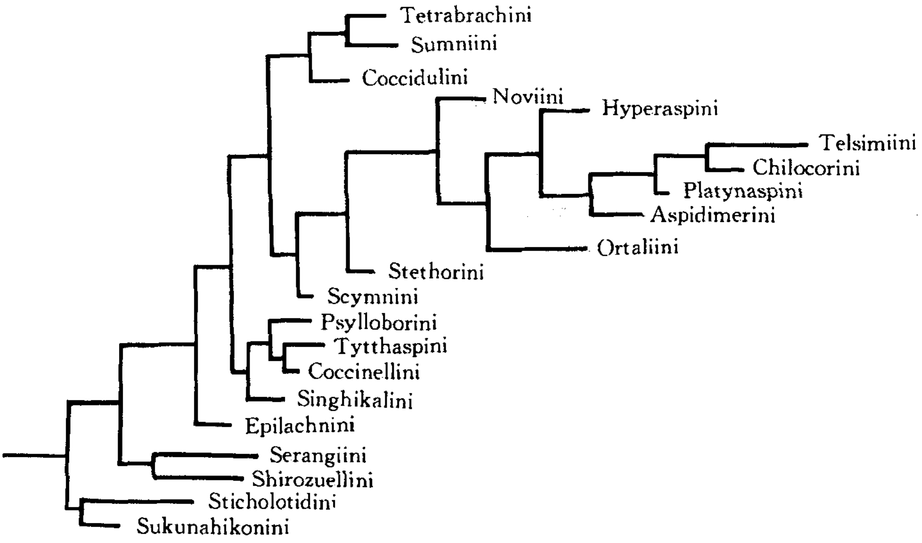

Fig. 1 The most parsimonious cladogram with lowest F-value(0.545) from adult analysis of 21 tribes.

The most noteworthy results of this analysis are (Fig. 3): 1) it may be roughly divided into five lineages: Sticholotidinae, Epilachninae, Coccinellinae, Coccidulinae, Scymninae +Chilocorinae; 2) Coccidulinae excludes two tribes: Noviini and Singhikalini; 3) Coccinellinae includes Singhikalini; 4) Chilocorinaeis a monophyletic group and closely relates with Scymninae (including Noviini); 5) the tree resembles the classification proposed by Chazeau *et al.* (1990) which divided the family into six subfamilies (Table 1).

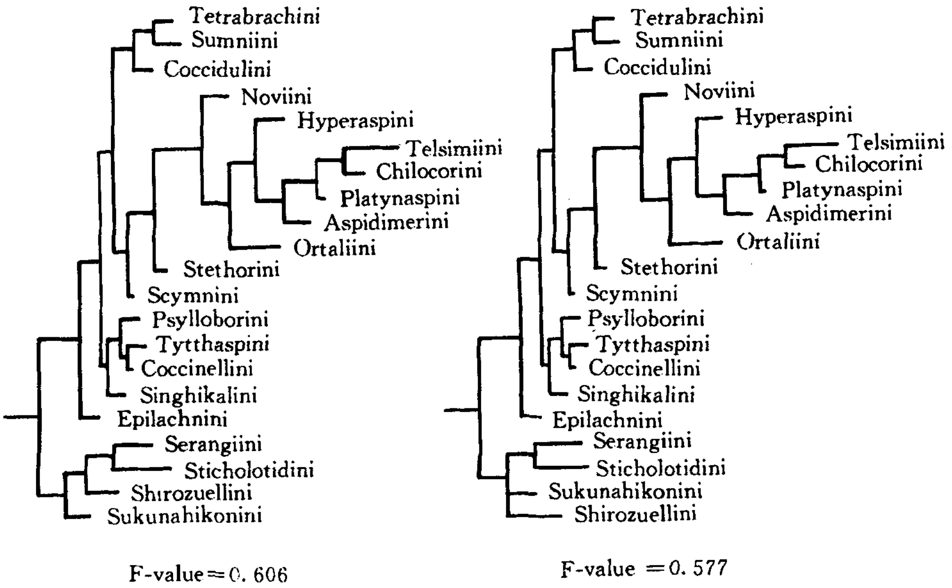

Fig. 2 Two examples of 18 most parsimonious cladograms from the adult analysis of 21 tribes.

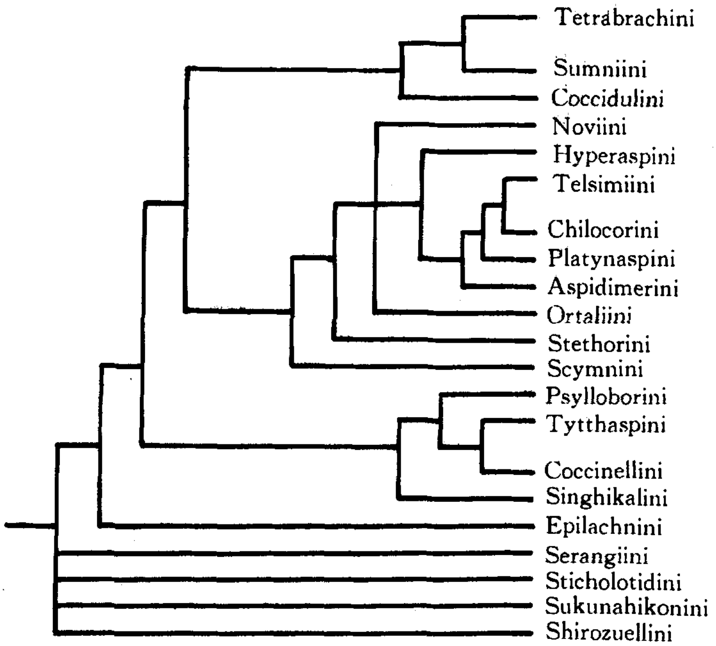

Fig. 3 Consensus tree for 18 cladograms based on adult characters for 21 tribes. Lengths of stems are arbitrary.

Table 1 Taxonomy of Coccinellidae (Chazeau *et al.* 1990)

Coccidulinae	Scymninae	Chilocorinae	Sticholotidinae	Coccinellinae	Epilachninae
* Tetrabrachini	* Aspidimerini	* Telsimiini	Cephaloscymnini	Oryssomini	* Epilachnini
Monocorynini	* Stethorini	* Platynaspini	Microweiseini	* Psylloborini	* Epivertini
* Coccidulini	* Scymnini	* Chilocorini	* Serangiini	* Tytthaspini	Madaini
* Sumniini	Scymnillini		* Shirozuellini	Bulaeini	Eremochilini
Exopletrini	Selvadiini		* Sticholotidini	* Coccinellini	
* Noviini	Cranophorini		* Sukunahikonini	Discotomini	
Azyini	* Hyperaspini				
* Singhikalini	* Ortaliini				
	Cryptognathini				

* Tribes occurred in China.

Singhikalini consists of a single genus *Singhikalia* Kapur 1963. Kapur(1963) placed *Singhikalia* in Coccidulini and Miyatake(1972) based on the shape of male and female genitalia moved Singhikalini to Coccinellinae near Coccinellini. Bielawski(1963) erected *Subepilachna* (syn. of *Singhikalia*) for a curious species, and put this genus under Epilachninae because of the dorsal pubescence. However, he noticed the Coccinellinae characters in *Subepilachna*, and concluded this genus being intermediate between Coccinellinae and Epilachninae. Now the dispute focuses on whether it belongs to Coccidulinae (Duverger1989, Chazeau *et al*. 1990) or Coccinellinae (Sasaji 1982, Chazeau *et al.* 1989, Jadwiszczak 1990). Analysis I supports the placement of Singhikalini in Coccinellinae, and it is more reasonable to consider Singhikalini as intermediate between Coccinellinae and Coccidulinae.

Sasaji(1968a, 1971) pointed out that Noviini is somewhat dissimilar to Coccidulini, Exoplectrini and Lithopilini altogether, and shows some affinities with Scymnini-Ortaliini. Nevertheless, he still considered it reasonable to include Noviini in Coccidulinae. The analysis indicates that Noviini is excluded from the Coccidulinae lineage, which is strongly supported by the relatively coarsely faceted eyes. The characters of eyes (finely faceted, slightly emarginate behind insertion of antenna), relatively short antenna, and moderately convex dorsum show strong affinities with Scymninae.

3.3 Analysis II: larval characters of 14 tribes

Information of fourteen tribes for which larvae have been described in sufficient detail to analysis cladistically was collected. Since the existing classifications are heavily based upon adult morphology, it is interesting to examine whether a numerical cladistic analysis based upon larval characters would support or contradict the phylogenetic hypothesis based upon adult characters, although the author did not examined majority of the fourteen tribes personally and the analysis was very preliminary. The data matrix and the coding for Analysis II are presented in Appendix E and D. All characters except 6,12,16 and 17 were coded as additive (or ordered), and the named four as unordered. This analysis found two equally parsimonious cladograms, with an overall length of 58 steps, consistency index of 0. 603. The F-values are 0. 180 and 0. 217 respectively (only apply to ordered characters)(Fig. 4).

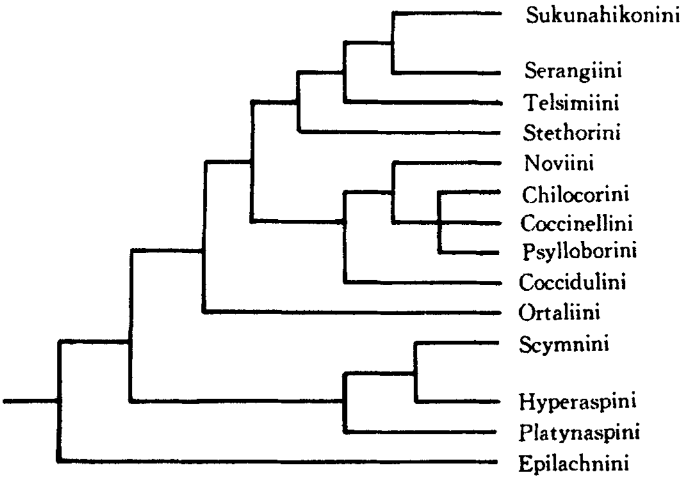

Fig. 4 Consensus tree for two cladograms based on larval characters for 14 tribes
Lengths of stems are arbitrary.

The strict consensus tree (Fig. 4) shows: 1) Epilachnini is the most primitive and highly derived group; 2) it is quite different to current classification of the family; 3) three members of Chilocorinae of current sense are scattered in the tree.

3. 4 Analysis III: adult characters of the same taxa as Analysis II

The next logical step is to perform a cladistic analysis with adult characters of the same tribes as used in analysis II. The data matrix is from Appendis C by deleting the tribes not used in Analysis II. The characters are the same as used in Analysis I. With the same five non-additive characters as in Analysis I, three equally parsimonious trees were found, with an overall length of 112 steps consistency index of 0. 509. F-values are 0. 265, 0. 265 and 0. 313 respectively. When we compare the results based upon larval (Fig. 4) and adult (Fig. 5) characters in fourteen tribes, it is interesting to find that there was almost no comparison in the two analyses. The monophyletic group consistently supported by adult characters, but not supported by larval characters is Chilocorinae (Telsimini, Chilocorini and Platynaspini). Therefore, this group is very equivocal. The close relationship between Serangiini and Sukunahikonini was supported by both analyses. Still, the close relationship between Coccinellini and Psylloborini was also supported by both analyses.

3. 5 Discussion

One of the central claim for cladistic methods is that they permit the formulation of testable hypothesis based upon one set of characters can potentially be falsified by examining an independent set of characters. For holometabolous insects such as labybirds, larval, pu-

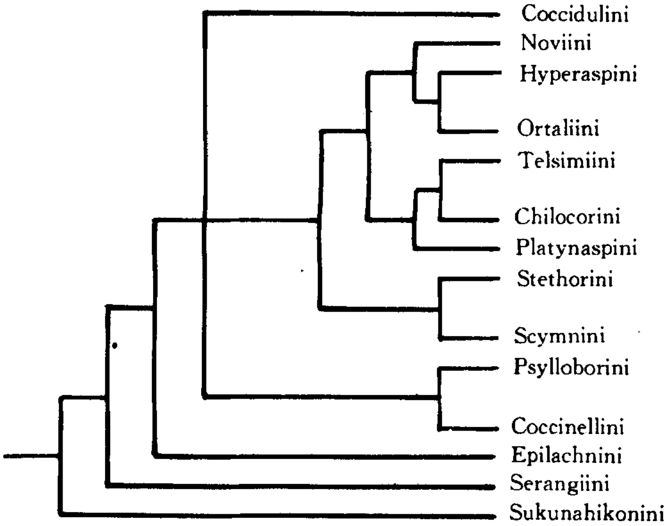

Fig. 5 Consensus tree for three cladograms based on adult characters for **14** tribes
Lengths of stems are arbitrary.

pal and adult stages provide independent sets of morphological characters upon which the phylogenetic hypotheses might be based.

We assume that results from different data sets should be concordant. When comparing phylogenetic hypotheses based upon larval (Fig. 4) and adult (Fig. 5) characters in fourteen tribes, we find only a few tribes showing similar relationships. There might be two explanations for this situation:

a) The selected characters perhaps are environmentally determined and do not accurately reflect phylogeny. The segments of tarsus is an important character in classifying the Coccinellidae on the level of tribe and genus. Generally speaking, the transformation series is from true tetramera to cryptotetramera, then to true trimera. The transformation from cryptotetramera to trimera is for certainty in the Coccinellidae. However, the tetramera of *Tetrabrachys* might not be primitive, perhaps caused by the change of the living environment. All ladybirds living on plant leaves present the tarsus with dilated second segment. On the other hand, those living underground (Tetrabrachini) have tetramerous tarsus with nearly cylindrical second segment. Thus, the state of tetramerous tarsus in Tetrabrachini might evolve from cryptotetramerous one. In a word, a more careful comparative morphological study of adult and a study of biology might well indicate that the codings of character states used in these analyses could be changed.

b) Abandonment of valuable characters which reveal the phylogeny. For example, the structure of the metendosternite is important in considering the inter-tribal relationships (Sasaji 1968a). Therefore, future studies should put more efforts on this aspect.

The analyses presented here indicate that larval characters exhibit considerably less homoplasy than adult characters. Similar result was also obtained in nomadine bee (Alexander 1990). Rates of evolutionary change in larval characters may be slower, so that any novel features that arise in a lineage will be retained with little or no material change through several specication events in that lineage. This would make them especially valuable for determining phylogenetic relationships. Some larval characters strongly reflect the evolutionary process. The frontal suture, for instance, is entirely wanting in the mature larvae of the genus *Hyperaspis* and some species of Scymnini, but their earlier instar larvae possess the frontal suture. Larval analysis might be more satisfactory in revealing phylogeny.

Unfortunately, larvae have been described for so few coccinellids that the cladistic analysis based on larval characters leaves the phylogenetic positions of many tribes of the family undetermined. Furthermore, cladograms based on adult characters did not show perfect concordance with those based on larval characters. Until more lauvae have been described, cladisic analysis of the entire family will have to base on adult characters. However, the knowledge about larvae has provided valuable insights into phylogenetic relationships.

Pupae of some species have been described in detail (Duang *et al.* 1974) and knowledge about pupae should be taken into consideration in the future cladistic studies of the family. It will be certainly proved valuable in assessing relationships amongst the Coccinellidae.

Detailed morphological studies of larvae and pupae, as well as adults, are needed for deciphering the phylogeny of the Coccinellidae. I hope that the above analyses have proved both the foundation and impetus for future cladistic studies of the family.

4 APPENDIX

4.1 Following is the list of genera selected for adult analysis (present taxonomic position from Chazeau *et al.* 1990).

Coccidulinae:
Tetrabrachini: *Tetrabrachys*
Coccidulini: *Coccidula*
Sumniini: *Sumnius*
Noviini: *Rodolia*
Singhikalini: *Singhikalia*
Scymninae:
Aspidimerini: *Cryptogonus*
Stethorini: *Stethorus*
Scymnini: *Scymnus*, *Pseudoscymnus*, *Nephus*
Hyperaspini: *Hyperaspis*
Ortaliini: *Ortalia*, *Amida*
Chilocorinae:
Telsimiini: *Telsimia*
Platynaspini: *Platynaspis*

Chilocorini: *Chilocorus*
Sticholotidinae:
Serangiini: *Serangium*
Shirozuellini: *Shirozuella*
Sticholotidini: *Sticholotis*, *Jauravia*
Sukunahikonini: *Scotoscymnus*
Coccinellinae:
Psylloborini: *Illeis*, *Vibidia*, *Psyllobora*
Tytthaspini: *Tytthaspia*
Coccinellini: *Alloneda*, *Calvia*, *Cheilomenes*, *Coccinella*, *Harmonia*, *Micraspis*, *Propylea*
Epilachninae:
Epilachnini: *Epilachna*, *Henosepilachna Afissula*

4.2 Adult characters and coding of the states

1. Body form: long, weakly convex(0); round, strongly convex(1).
2. Dorsal surface: pubescent or apparent glabrous(0); glabrous(1).
3. Anterior portion of head: projecting(0); no-projecting(1).
4. Size of eyes: small(0); medium(1); large(2).
5. Surface of eyes: faceted coarsely(0); finely(1).
6. Form of eyes: simple(0); slightly emarginate(1); widely of deeply emarginate(2).
7. Clypeus: normal(0); strongly expanded laterally(1).
8. Antenna inserted: dorsally(0); laterally(1); ventrally(2).
9. Length of antenna: longer than(0); about(1); shorter than(2); much shorter than (3) the width of head.
10. Antenna segments: 11(0); 10(1); 9(2); 8(3); 7(4).
11. Antenna club: bigger than(0); about(1); smaller than(2) its scape.
12. Mandible tip: simple(0); bifid(1); *Psyllobora*-type (2); *Epilachna*-type(3).
13. Basal teeth of mandible: absent(0); present(1).
14. Maxillary palpi: conical(0); almost parallel(1); securiform(2); strongly expanded apically(3).
15. Careoes of maxillae: about width of or narrower than(0); slightly wider than(1); distinct wider than(2) stipes.
16. Mentum articulated to submentum: narrowly(0); broadly(1).
17. Segments of labial palpae: three(0); two(1).
18. Labial palpi inserted at: apex(0); anterior(1); middle(2); and posterior(3) of prementum.
19. Prosternum: linear(0); T-shaped(1); expanded(2).
20. Inner hypermeral process: short(0); long(1).
21. Metepimeron: triangular(0); present(1).

22. Grooves of epipleura: absent(0); present(1).
23. Elytral epipleura: incomplete(0); complete(1).
24. Femora: long, cylindrical(0); short, flat(1).
25. Tibiae: simple(0); angulate externally(1).
26. Tarsal formula; 4(0); crypto-4(1); 3(2).
27. Scutellum: small(0); medium(1); large(2).
28. Visible abdominal segments(♀): six(0); five(1).
29. Visible abdominal segments(♂): six(0); five(1).
30. Coxites of female genitalia: longer than(0); about(1); shorter than(2) width.
31. Styli: distinct(0); small(1).
32. Ninth sternum of male: triangular(0); almost linear(1).
33. Tegmen: slender(0); thick or characteristic(1).
34. Sipho: nearly straight(0); weakly curved(1); strongly curved(2).
35. Apex of sipho: simple(0); complex(1).
36. Siphonal capsule: simple(0); developed(1).

4.3 Data matrix of adult characters

Outgroup	000000000000200090110000000100009999
Tetrabrachini	001100011101120101110000001110010101
Coccidulini	001100010001120101111000021000111101
Sumniini	101100011121120103111010011110091101
Noviini	101111012321120112011111121000110101
Stethorini	101111012001110102211000021000110100
Scymnini	101111012001110101111000011000011111
Hyperaspini	111110013321121102110101112002111111
Ortaliini	101212011221120102111001021102111210
Telsimiini	101112123411112101100111121110091010
Platynaspini	101112123201121101110101111000011101
Chilocorini	111112123311111102111111111100011101
Aspidimerini	101111023221122101110101021002011201
Serangiini	110110010200000001211101011110001000
Sticholotidini	110010001001100001000110110110000000
Sukunahikonini	100010000100000000000000010000001000
Psylloborini	111111000012130103111010011000011101
Tytthaspini	111111012011120101111010010000011101
Coccinellini	111111010011120101111010011000011111
Epilachnini	101111000023020101111000011001011000
Shirozuellini	000110111201910011000000021000001000
Singhikalini	101101000001120111111010011000091111

4.4 List of genera for larval cladistic analysis

Sukunahikonini: *Scotoscymnus*
Serangiini: *Serangium*
Ortaliini: *Amida*
Noviini: *Rodolia*
Coccidulini
Stethorini: *Stethorus*
Scymnini: *Scymnus*, *Pseudoscymnus*, *Nephus*
Hyperaspini: *Hyperaspis*
Telsiimini: *Telsimia*
Chiocorini: *Chilocorus*
Platynaspini: *Phymatosternus*
Coccinellini: *Micarspis*, *Phynocaria*, *Sospita*, *Calvia*, *Propylea*, *Oenopia*, *Harmonia*, *Coccinella*, *Lemnia*, *Menochilus*
Psylloborini: *Illeis*, *Vibidia*
Epilachnini: *Epilachna*, *Hensoepilachna*

4.5 Larval characters and coding of the states

1. Body form: elongate, slender(0); ellipsoidal(1).
2. Head sclerotized: very slightly(0); some areas(1);completely(2).
3. Frontal suture: Y-shaped(0); V-shaped(1); absent(2).
4. Front O-clypeus suture: well-developed(0); fused together(1).
5. Antenna segments:3(0);2(1);1(2).
6. Apex of mandible: simple(0); bifid(1); *Psyllobora*-type(2); *Epilachna*-type(3).
7. Retinaculum of mandible: absent(0); simple(1); complicated(2).
8. Maxillae segments: three(0); two(1).
9. Galea: with a pointed apex(0); with a round or truncate apex(1).
10. Galea: with numerous fine setae(0); with a few distinct styli(1).
11. Terminal segment of maxillary palpi: strongly convergent apically and elongate(0); mediate(1); shorter than wide(2).
12. Sclerotization of stipes: complete(0); semi-sclerotized(1); membranous(2).
13. Labial palpae segments: two(0);one(1).
14. Tibiotarsi: flat apical setae(0); clavate apical setae(1); normal setae(2).
15. Number of apical setae: one pair(0); two(1); five(2); numerous(3).
16. Sclerotized plates of pronotum: absent or slightly sclerotized(1); two plates(1); four plates(2).
17. Body projections: setae or chalazae(0); tubercules(1); strumae or parascoli(2); sentusi(3); scoli(4).
18. Body cover: absent(0); with wax-like exudation(1).

4.6 Data matrix of larval characters

Outgroup	000000001002029000
Sukunahikonini	001110000101000100
Serangiini	001100000109000200
Ortaliini	001110900109012001
Noviini	001111111122012210
Stethorini	011120101102011210
Scymnini	022100101101019111
Hyperaspini	012100101101111001
Telsimiini	001110101101010311
Chilocorini	001021100111012330
Platynaspini	112100111121012000
Coccinellini	001101200110012290
Psylloborini	001102100122012320
Epilachnini	000003001010012140
Coccidulini	001111109109019210

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References

Alexan,der B. 1990 A cladistic analysis of the nomadine bees. *Syst. Entomol.* **15**(2):121-152.

Belicek, J. 1976 Coccinellidae of Western Canada and Alaska with analyses of the transmontane zoogeographic relationships between the fauna of British Columbia and Alberta (Insect: Coleoptera: Coccinellidae). *Quaestiones Entomologicae* **12**:283-409.

Bielawski, R. 1963 Monographie der Epilachninae (Coleoptera: Coccinellidae) der Australischen Region. *Annales Zool. Warsz.* **21**(17):296-461.

Bielawski, R. 1984 Coccinellidae (Coleoptera) of Mongolia. *Annales Zool Warsz.* **38**(14):281-460.

Chazeau, J., H. Fursch and H. Sasaji 1989 Taxonomy of Coccinellidae. *Coccinella* **1**(1):6-8.

Chazeau, J., H. Fursch and H. Sasaji 1990 Taxonomy of Coccinellidae (Corrected version). *Coccinella* **2**(1):4-6.

Duang, T.H. and W.S. Frederick 1974 Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contrib. Amer. Ent. Inst.* **10**(6):1-125+vpp.

Duverger, Ch. 1989 In Errors and Corrections. *Coccinella* **1**(2):23, 24,27.

Farris, S. J. 1982 Outgroup and parsimony. *Syst. Zool.* **31**(3):328-334.

Gordon, R. D. 1985 The Coccinellidae of America North of Mexico. *J. New York Entomol. Soc.* **93**(1):1-912.

Jadwiszczak, A. 1990 On the systematic position of the genus *Subepilachna* Bielwaski (Coleoptera: Coccinellidae). *Coccinella* **2**(2):56-57.

Kapur, A. P. 1963 The Coccinellidae of the Third Mount Everest Expedition 1924 (Coleoptera). *Bull. Brit. Mus. (Nat. Hist.) Ent.* **14**:1-48.

Kapur, A. P. 1970 Phylogeny of ladybeetles. Proc. 57th Ind. Sci. Cong., II:1-14.

Korschefsky, R. 1931 Coccinellidae, I. *Junk's Coleopterorum Catalogus Par* **118**:1-244.

Korschefsky, R. 1932 Coccinellidae, II. *Junk's Coleopterorum Catalogus Par* **120**:1-435.

Lundberg, J. G. 1972 Wagner networks and ancestors. *Syst. Zool.* **21**:389-413.

Miyatake, M. 1972 A new Formosan species belonging to the genus *Singhikalia* Kapur, with proposal of a new tribe(Coleoptera: Coccinellidae). *Trans. Shikoku Ent. Soc.* **11**(3):92—98.

Mulsant, M. E. 1850 Species des Coleopteres Trimeres Securipes. *Ann. Sci. Phys. Nat. Lyon* **2**:1-1104.

Pang, X. F. and J. L. Mao 1979 Coleoptera: Coccinellidae. II. Beijing, 170pp. (in Chinese).

Sasaji, H. 1968a Phylogeny of the family Coccinellidae (Coleoptera). *Entizenia, Occ. Pub. Biol. Lab. Fukui Univ.* **35**:1-37.

Sasaji, H. 1968b Descriptions of the known Coccinellid larvae of Japan and the Ryukyus (Coleoptera). *Mem. Fac. Edu., Fukui Univ. Ser.* II **18**:93-135(II).

Sasaji, H. 1971 Fauna Japonica: Coccinellidae (Ins.: Coleoptera). Tokyo, 340pp.

Sasaji, H. and K. Tsubokawa 1982 Supplementary descriptions of coccinellid larvae of Japan (Coleoptera). *Men. Fac. Educ., Fukui Univ., Ser.* II(Nat. Sci.) **32**:33-66.

Stickney, F. S. 1923 The head-capsule of Coleoptera. *Illinois Biol. Mon.* **8**(1):1-51. (I)(not seen).

Swofford, D. L. 1985 PAUP(2.4) User's Manual. Illionis.

瓢虫科支序分析 （鞘翅目）

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根据成虫和幼虫的特征，应用数值支序方法探讨瓢虫科的系统发育。基于中国21族（包括不同学者提出的所有亚科）36个成虫性状，计算得到18个具有高度同质（homoplasy）的最简约的支序图。共同树显示5个支系：小艳瓢虫亚科，食植瓢虫亚科，瓢虫亚科（包括粗毛瓢虫族 Singhikalini）；红瓢虫亚科（不包括短角瓢虫族），以及小毛瓢虫亚科＋盔唇瓢虫亚科（包括短角瓢虫族）。这与 Chazeau 等（1990）提出的分六亚科系统相似。对14族幼虫18个性状初步分析，结果与相同14族成虫分析比较，只有一个组分即刀角瓢虫族和展唇瓢虫族的亲缘关系在两个分析中得到一致的支持。食植瓢虫是瓢虫科中最原始但高度衍化的一族。在揭示系统发育上，幼虫的研究或许更令人满意。