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NUMERICAL TAXONOMIC STUDIES ON THE ASIRACINAE AND TROPIDOCEPHALINI (FULGOROIDEA: DELPHACIDAE) FROM TAIWAN

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Yang Jeng-Tze, Chung-Tu Yang and Kwang-Tsao Shao (1987) Numerical taxonomic studies on the Asiracinae and Tropidocephalini (Fulgoroidea: Delphacidae) from Taiwan. *Bull. Inst. Zool., Academia Sinica* **26**(3): 215-230. Different numerical taxonomic techniques including both phenetic and cladistic methods were used analyzing the phylogeny of the ten genera of Asiracinae and Tropidocephalini from Taiwan. A total number of sixty-two characters in binary states were divided into three character suits. They are external morphology, genitalia, and host-plant. The taxonomic congruence among these three character suits was investigated by using consensus tree method. The consensus results among above different phenograms and cladograms shown that *Ugyops* is the most primitive group. The two most closely related pairs are the group of *Arcofacies* and *Belocera*, and the group of *Bambusiphaga* and *Epeurysa*. The genera *Arcofaciella* and *Purohita* are closed to the former group, and forming a monophyletic group but the relationships among them is not clear. The genus of *Specinervures* joints with the latter group as a monophyletic group. The relationship between *Malaxa* and the above two monophyletic groups is not clear. However, they all form a monophyletic group as non-*Tropidocephala* group which then joints with *Tropidocephala* as a sister group.

Although Wagner (1962) and Asche (1962) have studied the phylogenetic relationship of Delphacidae on the generic category, they applied only the cladistic analysis. The present paper used both of the cladistic and phenetic analysis, in hoping that a more objective phylogenetic relationships among the 10 genera of Taiwanese Delphacidae including Asiracinae and Tropidocephalini (Yang and Yang 1986) could be proposed.

In general, classical taxonomist prefers to assign some particular morphological characters in constructing and explaining the genealogical relationship. This phenomenon was shaken since 1960' when numerical taxonomy was prevailed by using computer to analyze massive biological data more efficiently and objectively. However, the proliferation of various numerical taxonomic methods discourage many applicants later since it is too difficult to make a choice among many different resulting phylogenetic trees as well as to summarize a consensus result from all incongruent results. This problem was partially solved in 1980 when the consensus methods were becoming established. To obtain the consensus tree from both phenetic and cladistic studies as well as to test the nonspecificity hypothesis by congruence studies among three different character suits, some consensus methods were applied in the present paper also.

HISTORICAL RESUME

For the phylogenetic relationship of delphacids, Wagner (1962) firstly proposed a hypothesis of 42 taxa belonging to Asiracinae and Delphacini from central Europe. His cladistic analysis was based on 20 multistate characters and assigned the Cixiidae as the outgroup for Delphacidae. The resultant cladogram shows that the genus *Asiraca* (Asirasinae) is the most primitive taxon. Recently, Asche (1982) provided a cladogram by using many valuable characters including apodeme of abdominal segments to interprete the phylogenetic relationship among the 12 OTUs of delphacids. The results found no proof that the "Asiracinae" (Muir and Fennah) as a whole is a monophyletic group since there is no any new reliable synapomorphic character. The Ugyopini Fennah (excluding *Tetrasteira* Muir and *Platysystatus* Muir) seems to be monophyletic group. Delphacinae Muir should be a monophyletic group based on several synapomorphic characters. *Tropidocephala* Muir form one monophyletic group as well with its related genera.

MATERIALS AND METHODS

Data matrix

Sixty-two binary characters were coded (Appendix I) for numerical taxonomic studies. The overall original data matrix of 62 characters [hereafter call it complete character suit (C suit)] were subdivided into three submatrices based upon three different character suits. They are external morphological characters (M suit) (1–33); genitalic characters (G suit) (34–52); host-plant characters (H suit) (53–62). A total number of 10 OTUs were studied in this part which consist of one genus of Asiracinae and nine genera of Tropidocephalini of Delphacinae from Taiwan (Appendix II). (Yang and Yang, 1986) The original data matrix is given in Table 1.

TABLE 1

Binary data matrix of the genera of Asiracinae and Tropidocephalini. The number of 9=no comparison. Row numbers correspond to those given genera in Appendix II; column numbers correspond to the characters listed in Appendix I

	1 62
1	00011000000000001000100110100011100000010010011000000000000010
2	01101101110010000000001000011100001010119900010100001011000000
3	11001101000011000000010010011099001010019900100000111010000000
4	00000001001000100010010010000110011010019900100010101000010000
5	11000001111000010001001001010100000000019900010100111010000000
6	11000001100000100100000010010190011100009110100010101001001100
7	00000000101000000010100100010190010110001110100000011010000000
8	01000011000100110001101000010100000000000100010000111101010000
9	00000001000000010010010000001910010001000100100011011000100000
0	00110000100000000100011000000100000000010101010000110000000001

Data analysis

Program packages used in this study were provided by KTS and run on the VAX computer at the Institute of Information Engineering, Academia Sinica.

Phenetic analysis

For phenetic analysis, seven resemblance coefficients and three clustering methods in the CLUSTAR program package (Romesburg, 1984) were used to construct the phenograms and their corresponding cophenetic correlation coefficient values (CPCC). The formula for computing the resemblance coefficients were furnished in the User's manual for CLUSTAR/CLUSTID package (Romesburg and Marshall, 1984). For further information about these resemblance coefficients and clustering methods please refers to some clustering textbooks (Sneath and Sokal, 1973; Romesburg, 1984).

Cladistic analysis

The cladistic analysis based on the binary data matrix, and out-group Wagner in the WAGNER78 (Farris, 1978) were used to construct the cladograms and their corresponding total tree length. Because the WAGNER78 program does not accept the no comparision data (NC), those characters with NC state were deleted, transformated to 0, or 1 before computation, only H suit data matrix had no NC. Because delete NC will reduce the number of characters which will sacrifice some valuable information in the data set, thus delete the character with NC directly was not taken into account.

Consensus analysis and taxonomic congruence

The maximun consensus tree (MCT) (Shao, 1983) and consensus index of CIc (Rohlf, 1982) and SCI (Stienbrickner, 1984) were applied on the above resultant phenograms and cladograms for the following comparisons: 1) The consistency of phenograms and cladograms based on the complete data matrix of 62 characters. 2) The congruence among three different character suits with respect to the phenetic and cladistic analysis seperately. For easy to make the above second comparison, the consensus methods was applied on the first two trees originated from the data sets of M and G suits, and then compare the resulting consensue trees against the third tree from H data matrix.

The CI value indicates the degrees of congruence of two character suits when compaired. The table of significance test of consensus index in Shao & Sokal (1986) was used to make the decision of whether the taxonomic congruence among different character suits is significant or not.

RESULTS

Phenetic analysis

Table 2 shows the CPCC value of each character suit with various combination of resemblance coefficients and clustering methods. It is apparent that the CPCC value in the combination of Russell and Rao's resemblance coefficient and UPGMA clustering method is the highest one among all of them. The CPCC value of the C, M and G character suits are 0.9107, 0.8366, and 0.9086 respectively. But of the H character suit it is lower in such combination case than the other cases. The average of CPCC values of different combinations averaged from each suit (Table 2) is shown in Table 3. The average value resulted from each clustering method shows that the Jaccard resemblance coefficient (CPCC=0.8405) is the best one among the seven different coefficients. The UPGMA clustering method (CPCC=0.8594) is the best among three clustering methods in the analysis. The phenograms of each character suit constructed from the UPGMA based on the Jaccard resemblance coefficient were shown in Fig. 1.

Cladistic analysis

The different cladograms of each character suit and their associated total tree

TABLE 2

The cophenetic correlation coefficient (CPCC) values of various phenograms computed from seven resemblance coefficients in combination with three different clustering methods. C suit data matrix based on complete characters; M suit data matrix based on external morphological characters (1–33 characters); G suit data matrix based on genitalic characters (34–53 characters); and H suit data matrix based on characters of host plant (54–62)

Resemb. coef.	Cluster. methods	C suit CPCC	M suit CPCC	G suit CPCC	H suit CPCC
Jaccard	Single	.8039	.7210	.8215	.9214
	Comple.	.8222	.7054	.7629	.9770
	UPGMA	.8848	.8159	.8680	.9813
Sorensen	Single	.8271	.7184	.8338	.8374
	Comple.	.8347	.6818	.7819	.9495
	UPGMA	.8918	.7980	.8667	.9593
Simple matching	Single	.7249	.7250	.6328	.8222
	Comple.	.7491	.7587	.5463	.9014
	UPGMA	.8217	.7730	.6928	.9365
Yule	Single	.8268	.7153	.7264	.7065
	Comple.	.8471	.6795	.6825	.9053
	UPGMA	.8811	.7418	.7685	.9219
Russell & Rao	Single	.8848	.7224	.8947	.5714
	Comple.	.8620	.7401	.7741	.8030
	UPGMA	.9107	.8366	.9086	.8494
Ochiai	Single	.8263	.7240	.8329	.8383
	Comple.	.8361	.6793	.7815	.9504
	UPGMA	.8907	.7945	.8610	.9598
Pearson	Single	.8072	.7653	.7512	.9459
	Comple.	.8396	.7336	.7217	.9841
	UPGMA	.8750	.7869	.7995	.9862

TABLE 3

The overall effects of different resemblance coefficients and clustering methods on CPCC values. The table values are the means averaged from the CPCC values in Table 2. The indices values of all character suits were sum up when calculated the means

	Single	Complete	UPGMA	Average
Jaccard	.8170	.8169	.8875	.8405*
Sorenson	.8042	.8120	.8790	.8317
Simple matching	.7262	.7389	.8060	.7570
Yule	.7438	.7786	.8283	.7836
Russell & Rao	.7683	.7948	.8763	.8131
Ochiai	.8054	.8118	.8765	.8312
Pearson	.8174	.8198	.8619	.8330
Average	.7832	.7961	.8594**	

* The best one among seven resemblance coefficients.

** The best one among three clustering methods.

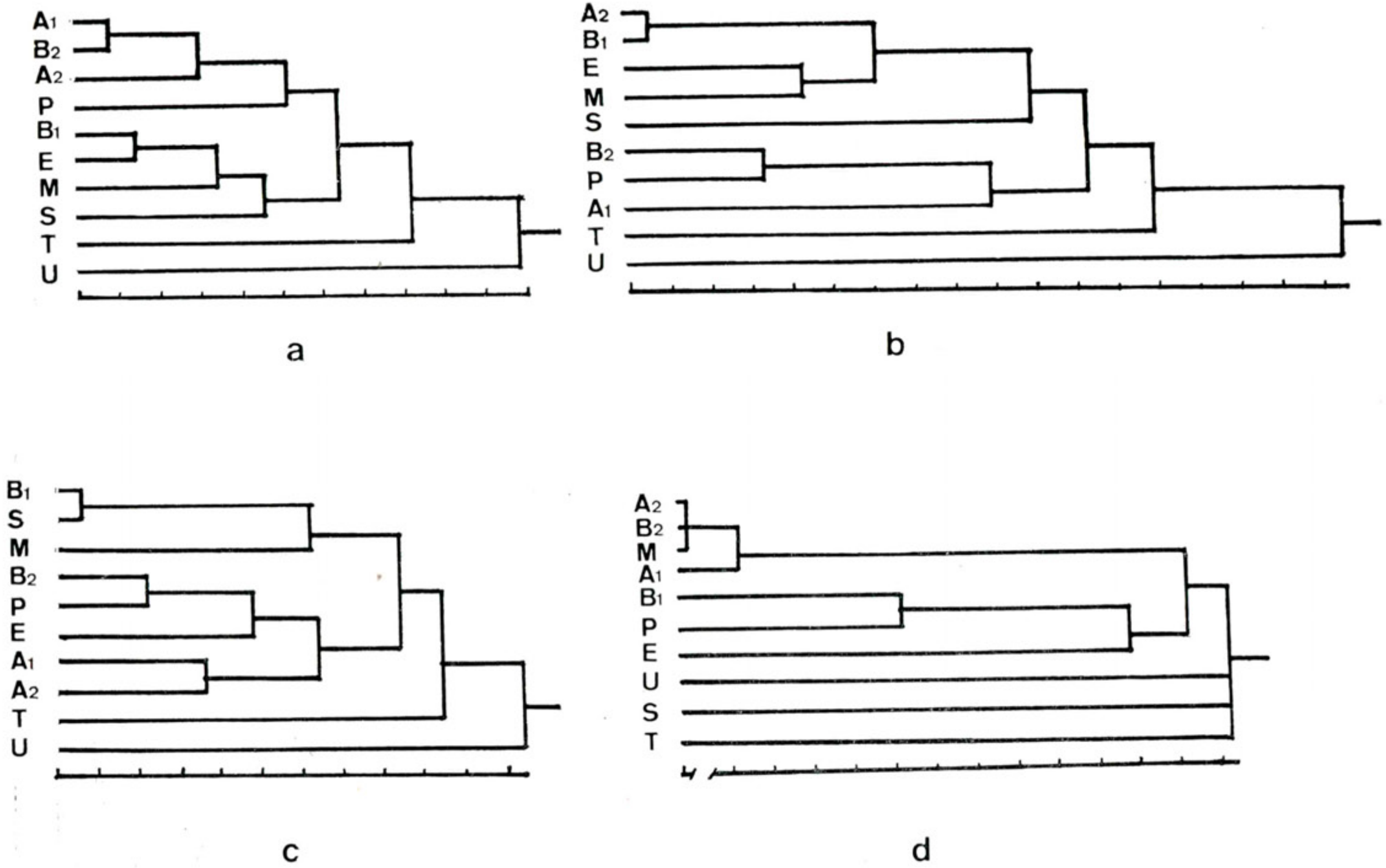

Fig. 1. Phenograms constructed from the Jaccard similarity matrix by UPGMA based on (a) complete characters (C suit); (b) external morphological characters (1-33) (M suit); (c) genitalic characters (34-53) (G suit); and (d) host plants (54-62).

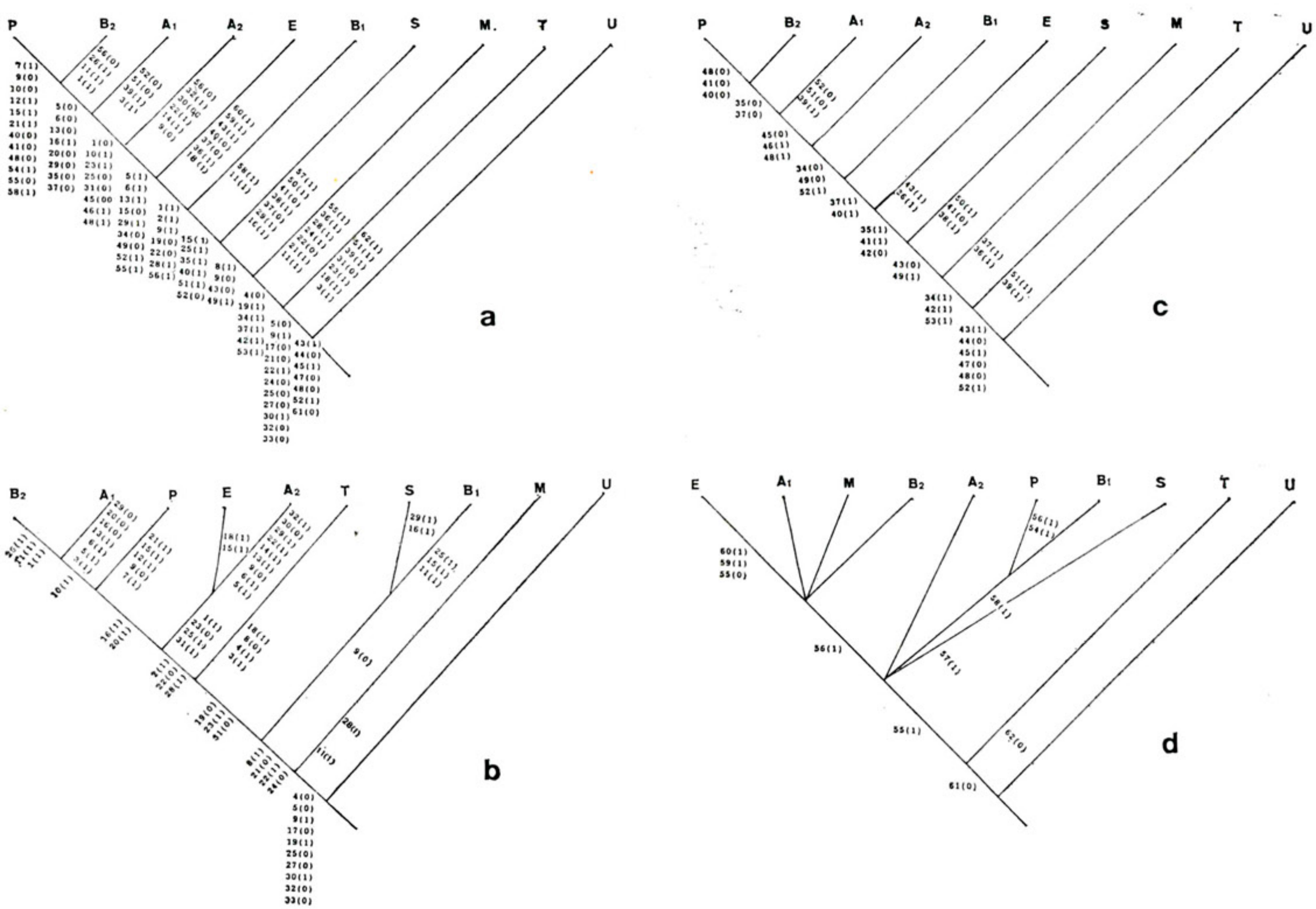

Fig. 2. Cladograms (a) based on C suit data matrix; (b) based on M suit data matrix; (c) based on G suit data matrix; and (d) based on H suit data matrix.

TABLE 4

Total tree length based on three different treatments of NC state from four different original data matrice. The value in parenthesis is the total character numbers used in the analysis

Treatments of NC state	Total tree length			
	C suit	M suit	G suit	H suit*
NC (9) → 0	126 (62)	65 (33)	40 (20)	10 (9)
NC (9) → 1	122 (62)	65 (33)	39 (20)	10 (9)

* H suit data matrix has no NC state.

length (Table 4) were obtained by treating the NC state differently. The shortest tree resulted from the treatment of transformed NC to 0 or to 1 was chosen as our result based on the principle of parsimony. The resultant cladograms were shown in Fig. 2, based on the treatment of NC transformated to 1.

Consensus analysis and taxonomic congruence

After comparing the phenogram and the cladogram based on the complete data matrix (Fig. 1a and 2a) the consensus tree (Fig. 3a) and its associate SCI value shows that the taxonomic congruence between the two trees is 51.6%. For CIc value the congruence is 75.0%. This consensus tree also shows that the generas in tribe Tropidocephalini (OTU 2–10) formas a monophyletic group when the genus *Ugyops* of Asirasinae (OTU 1) was used as the outgroup. Based on the hiearchical level between the second and third groups in Fig. 1, authors would like to suggest that the tribe should be divided into four generic groups (I) *Arcofacies* group consists of *Arcofacies*, *Arcofaciella*, *Belocera*, and *Purohita*; (II) *Bambusiphaga* group consists of *Bambusiphaga*, *Epeurysa*, and *Specinervures*; (III) *Malaxa* group and (IV) *Tropidocephala* group.

The consensus tree of compairing the

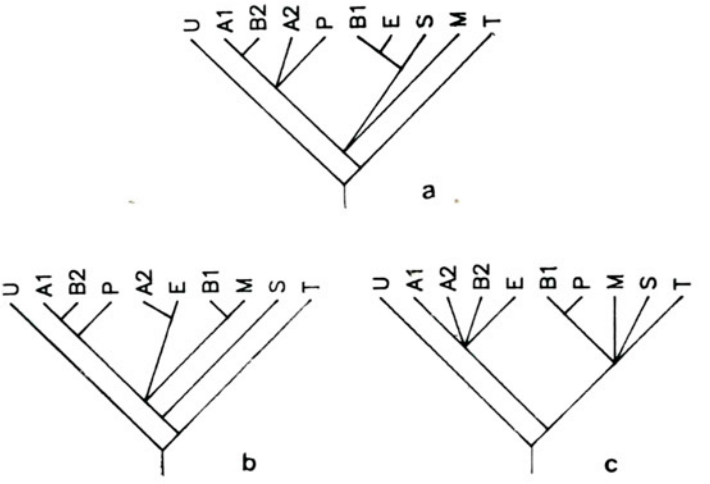

Fig. 3. Consensus trees indicating common information and components for phenograms and cladogram. (a) C suit with phenogram versus cladogram; (b) phenogram of M suit versus G suit then versus H suit; (c) cladogram of M suit versus G suit then versus H suit.

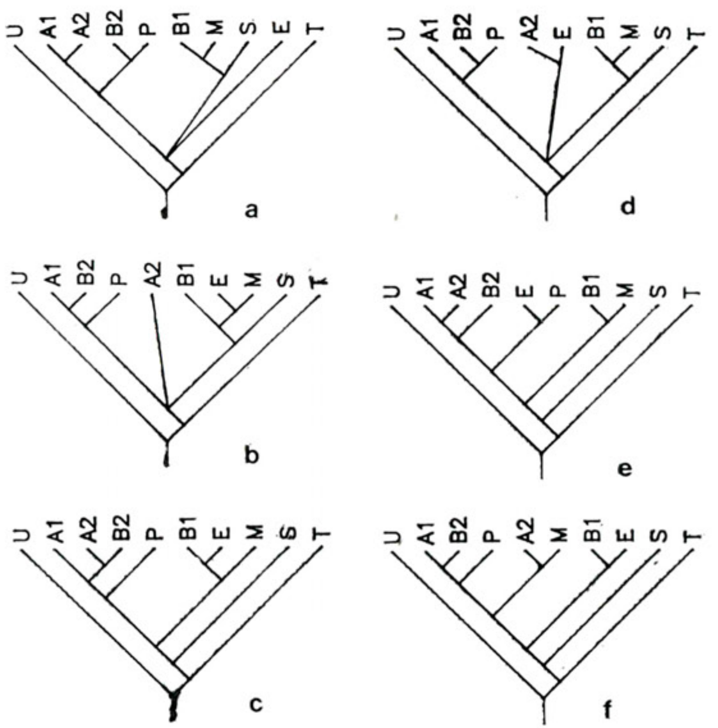

Fig. 4. Consensus tree for comparision of phenogram among different couple character suits.

(a) C suit versus M suit
(b) C suit versus G suit
(c) C suit versus H suit
(d) M suit versus G suit
(e) M suit versus H suit
(f) G suit versus H suit

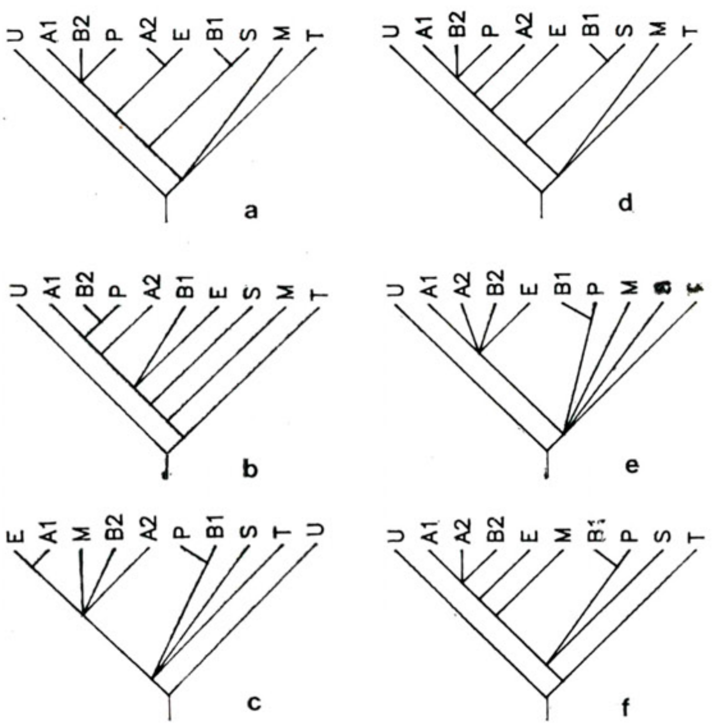

Fig. 5. Consensus tree for comparision of cladogram among different couple character suits.

(a) C suit versus M suit
(b) C suit versus G suit
(c) C suit versus H suit
(d) M suit versus G suit
(e) M suit versus H suit
(f) G suit versus H suit

TABLE 5
Colless consensus index (CIc) and Stinebricker consensus index (SCI) of the maximun consensus tree of couple comparison among various phenograms (p) (based on Complete data (C); Morphological suit (M); Genitalic suit (G) and Host plant suit (H))

	Cp		Mp		Gp	
	CIc	SCI	CIc	SCI	CIc	SCI
Mp	.875*	.640*	——			
Gp	.875*	.665*	.875*	.606*	——	
Hp	1.000*	.650*	1.000*	.639*	1.000*	.589*

* The value with asterisks are significantly higher than 0.05 critical value of CIc (0.875) and SCI (0.474) based on maximum consensus tree in multifurcating model of 10 OTUs.

phenograms of M suit (Fig. 1b), G suit (Fig. 1c), and H suit (Fig. 1d) is shown in Fig. 3b. The associate consensus index (SCI=0.502, CIc=0.875) are equal or higher than the significance level at 0.05 (SCI=0.474, CIc=0.875) which indicates that the evolutionary trend among external morphological characters, genitalic characters and host-plant characters in phenetic analysis is relatively consistent.

The consensue tree of comparing the cladograms of M suit (Fig. 2b), G suit (Fig. 2c), and H suit (Fig. 2d) is shown in Fig. 3c. It shows that Tropidocephalini as a whole is a monophyletic group. The associate consensus index (SCI=0.244, CIc=0.375) is quite low.

As to the consensus trees from compairing different phenograms or comparing different cladograms among different two character suits are shown in Fig. 4 and 5. The consensus index values of above comparisons are listed in Table 5 and Table 6.

DISCUSSION

Phylogenetic relationships among genera

The consensus tree of Fig. 3a was made by comparing the phenograms (Fig. 1a) and cladograms (Fig. 2a) based on the complete data matrix. It shows that the two most closely related groups are the group of *Arcofacies* and *Belocera*, and group of *Bambusiphaga* and *Epeurysa* are more closely related than in other groups. The genus *Arcofaciella* and *Purohita* are closed to the former group, and forming a monophyletic group but the relationships among them is

TABLE 6
Colless consensus index (CIc) and Stinebricker consensus index (SCI) of the maximun consensus tree of couple comparison among various cladograms (c) (based on Complete data (C); Morphological suit (M); Genitalic suit (G); Host plant suit (H))

	Cc		Mc		Gc	
	CIc	SCI	CIc	SCI	CIc	SCI
Mc	.625	.508*	——			
Gc	.875*	.875*	.875*	.606*	——	
Hc	.250*	.439	.375	.240	.750	.489*

* see Table 5.

not clear. The genus of *Specinervures* joints with the latter group as a monophyletic group. The relationship between *Malaxa* and the above two monophyletic groups is not clear. However, they all form a monophyletic group as non-*Tropidocephala* group which then joints with *Tropidocephala* as a sister group.

What is the most primitive group of Delphacidae? Wagner (1962) and Asche (1982) have proposed a cladogram using Cixiidae as an outgroup and pointed out that the Asiracinae is the most primitive taxa among their OTUs. In Asche's paper (1982) showed that Ugyopini Muir is a monophyletic group, and the other groups could not be proved as a monophyletic group. It is evident that *Ugyops* is a primitive group based upon several sympleisiomorphic characters. From this point of view, the authors would assign *Ugyops* as an outgroup and the resulted cladogram is shown in Fig. 2a. Despite the outgroup of *Ugyops* it is apparent that *Tropidocephala* is the most primitive group and *Malaxa* is the next. It also shows that Tropidocephalini as a whole is a monophyletic group which agree with the conclusion of Asche (1982).

Phenogram of Fig. 1a shows that Tropidocephalini can be classified into three subsets based on the similarity level of 0.265. The first subset is made up by *Arcofacies*, *Belocera*, *Arcofaciella* and *Purohita* in sequence. The second subset is made up by *Bambusiphaga*, *Epeurysa*, *Malaxa*, and *Specinervures*. The third subset is the *Tropidocephala* as a singlton. *Ugyops* (Asiracinae) is the root of the phenogram. *Arcofacies* and *Belocera* are highly similar to each other, the similarity value is about 0.466 (Fig. 1a). It is different from the traditional view-point that *Arcofacies* was clustered with *Arcofaciella* instead of with *Belocera*. Because of the latter result of phylogenetic tree was adopted from the key of traditional classification (Yang and Yang, 1986) in which *Arcofacies* is grouped with *Arcofaciella* based upon the character of external features of the frons bend into postclypeus in right angle. The difference may be resulted from the incongruence of different character suits. In general, *Tropidocephala* is a monophyletic group but much less similar to the most parts in Tropidocephalini, the similarity coefficient is about 0.265. The most closely related groups are the group of *Arcofacies* and *Belocera* (similarity coefficient about 0.466) and the group of *Bambusiphaga* and *Epeurysa* (similarity coefficient about 0.460). The former group plus *Arcofaciella* has the similarity coefficient about 0.309, the latter group plus *Malaxa* has the similarity coefficient about 0.380. Based on the similarity level of 0.3438, the authors would recommend that the 10 genera should be classified into six subsets. They are (1) *Arcofacies*, *Belocera*, and *Arcofaciella*; (2) *Purohita*; (3) *Bambusiphaga*, *Epeurysa*, and *Malaxa*; (4) *Specinervures*; (5) *Tropidocephala*, and (6) *Ugyops*. Because of the numbers of character of host-plant is less than OTUs number, that make *Ugyops*, *Specinervures*, and *Tropidocephala* and the group of *Arcofaciella*, *Belocera* and *Malaxa* unresolved in the Fig. 1d. The *Specinervures* which forced into the unresolved group of non-bamboo host may due to *Bambusa edulis* is a specific host plant.

Character analysis

The cladogram of Fig. 2a is similar to the result of Asche (1982) but Tropidocephalini could be proved as a monophyletic group based on several synapomorphic characters (rostrum has three segments; mesonotum not five-carinate; post-tibia has 2 lateral spines, genital styles not convergent apically, aedeagus non-coiled like, and not feeding on the plant of Pteridophyta). However, those characters also support *Tropidocephala* as the sister group of the rest eight genera of Tropidocephalini except *Tropidocephala*. The autapomorphy of *Tropidocephala* is the character of feeding on grasses of Graceae, especially on the two genera of *Miscanthus* and *Imperata*. The rest of eight genera are all feeding on the various species of Bambusoidea. This character is useful to seperate Tropidocephalini into two major monophyletic groups. The 10 genera as a whole could be discussed from coevolutionary trend between insects and their host plants. Based on the character of host plant, the 10 genera could be subdivided into 3 major groups of *Ugyops*, *Tropidocephala*, and non-*Tropidocephala* Tropidocephalini.

The synapomorphy of eight genera of Tropidocephalini excluding *Tropidocephala*, are as following: Vertex rounding into frons in obtusely angle, medioventral process of pygofer more than one, and aedeagus not protruding beneath or even through the anal segment. In fact, *Epeurysa*, *Malaxa*, *Purohita*, and *Specinervures* have more than one medioventral process, and *Arcofacies*, *Arcofaciella*, *Bambusiphaga* and *Belocea* have no any process at all.

Since the lack of medioventral process was coded as NC in the data matrix and then transfered it into state 1 in order to run outgroup rooting method of WAGNER78, the character of medioventral process should not be included in the synapomorphic characters to avoid possible error.

The synapomorphic characters of *Malaxa* in Fig. 2a are the character 11, 21, 22, 24, 28, 36, and 55. They are all advanced characters except character 22. Nevertheless these characters have homoplasy. For instance, character 11 of *Bambusiphaga* is convergent. Other characters also show somewhat reversal evolutionary process in the whole tree. Although, these characters supporting *Malaxa* and the rest 7 genera as sister groups, no autapomorphy stands for it, even the synapomorphy is not clearly neither. So that there is no any character strongly enough to support them as a monophyletic group.

The median length of frons shorter than or subequals to the broadest width is one of the synapomorphic character which is taxonomically important to the next hierachical level. This character also supports that *Specinervunes* is a sister group of the rest 6 genera, *Purohita*, *Belocera*, *Arcofacies*, *Arcofaciella*, *Epeurysa* and *Bambusiphaga*. Three synapomorphic characters of *Specinervures* are two genitalia characters: non-membraneous diaphragm and phallus with minute spines apically, and the hostplant character of feeding on *Bambusa edulis*. Since the sclerolization of diaphragm is a very particular synapomorphy in Tropidocephalini, and the character of phallus with teeth on apical margin are common in Delphacini of Delphacinae, the genus *Specinervures* is therefore suggested to be the close relative of Delphacini.

The next hierachy including *Purohita*, *Belocera*, *Arcofacies Arcofaciella*, *Epeurysa* and *Bambusiphaga* have no definite synapomorphic characters. For example, the character of anal margin of anal segment inclined to caudoventrad was reversed in *Purohita* and *Belocera*. The character of the pygofer with medioventral process and the character of the postclypeus wider at base than frons at apex were reversed in *Purohita*. The character of the pronotum with lateral carinae not reaching at hind margin was reversed in the group of *Purohita*, *Belocera* and *Arcofacies*, and the character of distinct phallobase was reversed in *Arcofacies*. In addition, several synapomorphies of *Bambusiphaga* are also convergent in other genera. For example, the character of frons with median carina not forked is convergent to *Belocera*. To *Ugyops* the character of distinct phallobase is an advanced character. Asche (1982) had mentioned that less sclerolized and less distinct of phallobase are more primitive characters. Thus the whole group except *Arcofacies* with synapomorphic character of well sclerolized phallobase is advanced character.

Although, the character of host plant is the same as *Purohita* that feeding on *Dendrocalamus latiflorus*, but *Bambusiphaga* has never been found in feeding on shoots or young culms. Instead, *Bambusiphaga* feed on leaf of *D. latiflorus*. Thus different feeding site on the plants between these two genera should be a good character to distinguish them. And the former state is the autapomorphy of *Purohita* and the latter state is the apomorphy of *Bambusiphaga*.

As to the character of the frons with median carina unforked in *Bambusiphaga*, Wagner (1982) had suggested that it is derived state since the nymphal stage always with two median carinae is the primitive state and unicarina is the advanced state, and biforked median carina is intermediate. According to the character of the stem length of Y-shaped median carina, the evolutionary history of the 10 genera are as following sequence: (1) forked near to apex of frons (*Ugyops*) (2) forked near to base of frons including *Arcofaciella*, *Epeurysa*, *Purohita* and *Specinervures*, (3) Unicarina (not forked), including *Tropidocephala*, *Arcofacies*, *Bambusiphaga*, *Belocera* and *Malaxa*.

The character of short vertex is the synapomorphic character supports *Purohita*, *Belocera*, *Arcofacies*, *Arcofaciella* and *Epeurysa* to form one monophyletic group, and *Epeurysa* is suggested to be the sister group of the rest members of the group. The two synapomorphies of *Epeurysa* are the characters of host plant. Although the host range of *Epeurysa* is widely distributed to several host plants only *Epeurysa* can feed on *Phyllostachys makinoi* and *Cinobambusa*.

Although the length of the antenna is usually the valuable character for generic classification the ratio of the second to the first segments of antennae, is higher in nymphal stage than in adults. Take the nymph of *Purohita* (*Purohita*) *taiwanensis* as an example, the ratio of the third instar nymphs ranged from 1.2 to 1.3, and of the fourth instar nymphs it ranged from 1.1 to 1.2.

According to the criterion of "the earliest ontogenetic state is the most primitive" among nine criteria of evolutionary polarity proposed by Criscis and Stuessy (1980), higher ratio of antennae is more primitive. In other words, the evolutionary direction of ratio of the length of antennae should be from the value higher than 3.00 to that lower than 3.00. If this assumption is true, *Ugyops* should be recongnized as advanced group by the character of antennae. This is in contravercy to the classical result and should be futher studied.

Distinct suspensorium (=supporting plate) is an important synapomorphic character, that support *Purohita*, *Belocera*, *Arcofacies* and *Arcofaciella* as a monophyletic group. The other important character, which usually grouped *Arcofacies* and *Arcofaciella* together in traditional taxonomy, is the frons that curved into postclypeus in right angle. Because this character is reversed in *Purohita* and *Belacera* it can only be regarded as a synapomorphy of *Arcofacies* and *Arcofaciella* as in the classical taxonomy. However, *Arcofaciella* is different from *Arcofacies* by having an autapomorphy of distinct postclypeus tricarinated.

The character of genital style which parallel with each other is an important synapomorphy which support *Purohita*, *Belocera* and *Arcofacies* as a monophyletic group.

The terminal group of *Purohita* and *Belocera* share same character state of non-cylindrical first segment of antennae. The first segment of antenna is cylindrical among 10 genera. But *Belocera* is sagittated and *Purohita* is elongated and flattened foliately. Thus, the character state of non-cylindrical antennae makes *Purohita* and *Belocera* a monophyletic group.

The autapomorphy of *Belocera* is the lateral carinae of pronotum raised behind eyes. It differs from other genera which raised from post-margin of vertex and between eyes. *Purohita* also has three important autapomorphic characters: lateral carinae of vertex and lateral carinae of frons raised and foliated, and the character of feeding on shoots and young culms of bamboos.

Consensus analysis and taxonomic congruence

In general, the consensus indices of CIc and SCI listed in Table 5 and 6 are significant (0.875 and 0.474 for CIc and SCI). But those consensus indices from comparing cladograms of hostplants (Hc) with cladograms of other character suits (Cc, Mc, and Gc) are low (significant level at 0.05). The reason for such low consensus indices requires further studies.

For comparing both phenetic versus cladistic method based on the taxonomic congruence studies, it is clear that the congruence is higher in phenetic (Table 5) than in cladistic (Table 6). Although the consensus index value are mostly significant in Table 5 and 6, the nonspecificity hypothesis is not shong supported in this case.

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APPENDIX I

Characters and their states used in the analysis. Zero is plesiomorphy, and one is apomorphy.

I. External morphology (M suit)

Head

1. Head including eyes/pronotum, <1 (0); ≥ 1 (1).

Vertex

2. Median length/basal width, >1 (0); ≤ 1 (1).
3. Apical margin convexed in obtusely angle, yes (0); no (1).
4. Vertex curved into frons, ≥ 90 (0); <90 (1).
5. Median carina distinct, yes (0); no (1).
6. Submedian carinae convergent apically, yes (0); no (1).
7. Lateral carinae foliaceous, no (0); yes (1).

Frons

8. Median length/the width of widest part, >1 (0); ≤ 1 (1).
9. The widest part submedially, yes (0); no (1).
10. Median carina strong, yes (0); no (1).
11. Median carina forked, yes (0); no (1).
12. Lateral carinae foliaceous, no (0); yes (1).
13. Curved into postclypeus in right angle, no (0); yes (1).

Postclypeus

14. Tricarinate, yes (0); no (1).
15. Basal width/apical width of frons, ≤ 1 (0); >1 (1).

Rostrum

16. Surpassing mesotrochanters, no (0); yes (1).
17. 3 segments (0); seems 4 segment (1).
18. Apical segment length/width, >1 (0); ≤ 1 (1).

Antennae

19. 2nd segment/1st segment, <3 (0); ≥ 3 (1).
20. First segment cylindrical, yes (0); no (1).
21. First segment with length/width, ≤ 2 (0); >2 (1).
22. 2 segments surpassing frontoclypeal suture, yes (0); no (1).

Eyes

23. Lateral margin emarginated (dorsal view), no (0); yes (1).

Pronotum

24. Lateral carinae decurved laterally, no (0); yes (1).
25. Lateral carinae attaining hind margin, yes (0); no (1).
26. Lateral carinae arising behind eyes, no (0); yes (1).

Mesonotum

27. Tricarinated (0); pentacarinated (1).

Tegmina

28. Apical margin obtusely rounded, yes (0); no (1).
29. Cross vein beset subbasally, no (0); yes (1).
30. Sc+R befor furcation/Sc befor furcation, ≤ 2 (0); >2 (1).

Wings

31. M+Cul present, yes (0); no (1).

Hind legs

32. Basal tarsus with 5 spines, (0); 4 spines, (1).
33. Tibia with 3 lateral spines, no (0); yes (1).

II. Genitalic characters (G suit)

Anal segment

34. Anal style not sunked, yes (0); no (1).

35. Anal segment reclined caudal ventrally, no (0); yes (1).
36. Lateroapical angles produced, no (0); yes (1).

Pygofer

37. Depressed anterioposteriorly, no (0); yes (1).
38. Diaphragm membraneous, yes (0); no (1).
39. Ventral angles produced, no (0); yes (1).
40. Medioventral process absent, no (0); yes (1).
41. Medioventral process single, no (0); yes (1).
42. Medioventral processes more than one, no (0); yes (1).

Genital styles

43. Basal angle produced; no (0); yes (1).
44. Convergent apically, no (0); yes (1).
45. Divergent apically, no (0); yes (1).
46. Parallel, no (0); yes (1).

Aedeagus

47. Coile, no (0); yes (1).
48. Curved downward, yes (0); no (1).
49. Phallus tubular, simple, yes (0); no (1).
50. Apical part of phallus with minute spines, no (0); yes (1).
51. Phallobase recongnizable, no (0); yes (1).
52. Supporting plate recongnizable, yes (0); no (1).
53. Aedeagus protruding through or enveloped in anal segment, yes (0); no (1).

III. Host-plant (H suit)

54. Feeding on shoots or culms, no (0); yes (1).
55. *Bambusa multiplex*, yes (1); no (0).
56. *B. oldhamii*, yes (1); no (0).
57. *B. edulis*, yes (1); no (0).
58. *Dendrocalamus latiflorus*, yes (1); no (0).
59. *Phyllostachys makinoi*, yes (1); no (0).
60. *Yushania* sp. or *Sinobambusa* spp., yes (1); no (0).
61. Pteridophyta, yes (1); no (0).
62. Graminaceae, yes (1); no (0).

APPENDIX II

Generic names of 10 OTUs and their denotation which were used in this analysis.

1. *Ugyops* (U).
2. *Arcofacies* (A_1).
3. *Arcofaciella* (A_2).
4. *Bambusiphaga* (B_1).
5. *Belocera* (B_2).
6. *Epeurysa* (E).
7. *Malaxa* (M).
8. *Purohita* (P).
9. *Specinervures* (S).
10. *Tropidocephala* (T).

臺灣錐距飛蝨亞科及凹距單齒飛蝨族（飛蝨總科：稻蝨科）數值分類之研究

楊正澤　楊仲圖　邵廣昭

本文利用表型分析及分歧分析等數值分類方法分析臺灣的錐距飛蝨亞科及凹距單齒飛蝨族共計 10 個屬的類緣關係。全部 62 個二態形質共分成外部形態、生殖器、寄主植物等三個形質組，以便探討三組間有關分類一致性之問題。分析結果 *Ugyops* 是其中最原始的一屬。基於公同樹分析 *Arcofacies* 和 *Belocera* 以及 *Bambusiphaga* 和 *Epeurysa* 分別是近緣的兩羣；*Arcofaciella* 和 *Purohita* 兩屬與前者類緣較近，形成一單源羣，但親緣關係不明。*Specinervures* 加入後者也形成另一單源羣。*Malaxa* 與前述兩單源羣間之親緣關係不明，但全部均歸屬成一 non-*Tropidocephala* 之單源羣與 *Tropidocephala* 屬是姊妹羣。