한국동물분류학회지 제11권 제4호
The Korean Journal of Systematic Zoology
Vol. 11, No. 4: 485-495 (December 1995)

Cladistic Taxonomy of the Tribe Errhomenini (Insecta: Homoptera: Cicadellidae)

Eun Yeop Huh and Yong Jung Kwon
(Dept. of Agricultural Biology, Coll. of Agric., Kyungpook Nat. Univ., Taegu 702-701, Korea)

ABSTRACT

A cladistic analysis is conducted to establish the phylogenetic relationship of the 6 genera in the Errhomenini, and 2 monophyletic groups are represented as the result.

Key words: Cladistics, taxonomy, phylogenetics, Errhomenini, Cicadellidae, Homoptera.

INTRODUCTION

Most of the genera in the tribe Errhomenini frequently have brachypterous adults, and especially, no macropterous forms in females have been known in any of these genera throughout the world. Consequently, the short winged condition is presumed to be genetically fixed in the female of the tribe. The structural evidence of evolutionary changes is most pronounced in males, whereas there have been relatively little evidence in case of females. There is a remarkable resemblance among genera belonging to the tribe, and naturally also as in case of species, for example, between females of *Bathysmatophorus shabliovskii* and the components of *Diodontophorus*.

These situations suggest that in the alone groups the brachypterous condition of the female would have survival value at a sufficiently early period in their evolutionary development to become fixed through selective pressure. While, the same selective pressures would work the primary means for intra- and interpopulation dissemination of genetic materials (Oman and Musgrave, 1975). This alary dimorphism is one of the environmental adaptation for the habitats such as bushes or herbs of rocky area in high altitude, moss and under stones (Kwon, 1983). These confined habitats would provide a disadvantageous ecological niche to the long winged species.

Among the tribes of Cicadellinae, the Errhomenini is a unique group having such particular structural features.

However, approaches to the phylogeny of the tribe Errhemenini have not been attempted substantially on the basis of the world fauna as well as that of Far East Asia, so far. Accordingly this analysis is conducted to establish the phylogenetic relationships between the component genera of the Errhomenini, and this can be used as one of the basis for the evolutionary classification.

MATERIALS AND METHODS

The 3 constituent subtribes of the tribe Errhomenini which currently recognized by many authors, represented by the 6 genera, were used to assess the evolutionary progress in combination with the phylogenetic interpretation (Appendix 1).

The selected characters of each genus represented the common component ones within the subtribe, and the abroad specimens were examined by the loan, or some others were adopted from the previous authors' articles (Oman and Musgrave, 1975; Oman, 1987; Anufriev and Emel'yanov, 1988). Accordingly, the given characters of the subtribe Bathysmatophorina in this investigation included those of the other exotic genera such as *Errhomus, Ankosus, Thatuna, Lystridea*, and *Carsonus* etc., which is generally distributed in North America.

Foreign specimens examined

**Errhomenus brachycephala*: 1 ♂ and 1 ♀, 4-12.VIII.1978, Yugoslavia (Centre for Land and Biological Resources Research, Ottawa, Canada).

**Errhomus lineatus*: 4 ♂♂ and 4 ♀♀, 30.IV.1990, U.S.A. (Centre for Land and Biological Resources Research, Ottawa, Canada).

**Lystridea uhler*: 1 ♂ and 3 ♀♀, 30.V.1987, Canada (Centre for Land and Biological Resources Research, Ottawa, Canada).

**Bathysmatophorus shabliovskii*: 1 ♀ and 1 ♂, 31.V-3.VI.1984, North Korea (Slovakia Natural History Museum): 1 ♂ and 4 ♀♀, 10-13.VII.1939, China 2 (Institute of Zoology, Academia Sinica, Beijing, China).

A total of 10 characters, consisting of both 5 external and genitalic characters were used for the present comparative study (Table 1).

The data matrix based on the character polarization was scorded by multistate steps (0, 1, 2), which were hypothesized to form a linear transformation series. Character polarity was evaluated by outgroup comparision.

The outgroup chosen was the tribe Pagaroniini of this subfamily, following Oman's classification (1949, 1975), as the Pagaroniini is closely related to the Errhomenini as a rather primitive groups in the Cicadellinae (Oman and Musgrave, 1975), which was previously treated as a member of the tribe Errhomenini (= Errhomenellini).

The cladistic analysis procedures were carried out using Hennig86 (Farris, 1988, V.1.5), which employs parsimony algorithms. All the characters employed were unweighted, multistate, additively and non-additively coded.

Table 1. Character polarization for the tribe Errhomenini.

Characters	Character states 0	1	2
1. Male style; distal part	short, curved ventrad	elongate, curved dorsad	
2. Crown	produced	truncate	
3. Fore wing	macropterous (both sex)	♀: brachypterous ♂: macropterous	brachypterous (both sex)
4. Hind wing	well developed (both sex)	♀: vestigial ♂: well developed	vestigial (both sex)
5. Aedeagus; apical process	present	vestigial	absent
6. Ocellus	prominent	vestigial	absent
7. Subgenital plate	dull	slightly pointed	sharply pointed
8. Style; apical process	dull (partly absent)	pointed	
9. Style; subapical process	absent	present	
10. Pygofer; dorsal process	absent	single	bifurcate

0: Plesiomorphic; 1, 2: apomorphic

RESULTS

All of 6 genera representing each tribe of the Errhomenini were analyzed for the cladistics. The out group chosen was the tribe Pagaroniini which is closely related to the Errhomenini as a sister group. This work was also drawn with the character analysis and considerations of the geographical distribution for the background of cladistic philosophy.

1. Character analysis

A total of 10 morphological characters were selected and analyzed in this work to designate primitive or derived states in the possible evolutionary progress (Table 2).

1) External characters

Crown: within the Cicadellinae, the produced crown is unique and plesiomorphic. The crown is truncate in the Errhomenini, and it is presumed to be a apomorphic.

Ocellus: the loss, or only vestigial ocellus is apomorphy naturally, and between them, the absence of ocellus is further apomorphy (Figs. 1-4).

Fore wing: more specialized characters than general charcters are usually apomorphic. The brachypterous condition in females are considered as synapomorphy that defines the Errhomenini.

Table 2. Data matrix for the tribe Errhomenini based on the character polarization.

Taxa	Characters									
	1	2	3	4	5	6	7	8	9	10
Pagaroniini	0	0	0	0	0	0	0	0	0	0
Bathysmatophorus	1	1	1	1	0	0	0	0	0	1
Diodontophorus	1	1	1	1	1	0	0	0	0	2
Errhomenus	1	0	2	2	0	0	0	0	1	0
Koreotettix	1	1	2	2	2	1	1	0	0	0
Bannalgaechungia	1	1	2	2	2	2	2	1	1	0
Malmaemichungia	1	1	2	2	2	2	2	1	1	2

0: Plesiomorphic; 1, 2: apomorphic

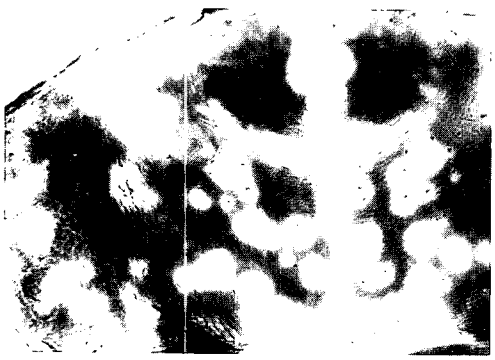

Fig. 1. Optical micrograph of the vertex lacking ocelli in *Bannalgaechungia hallasana*.

Fig. 2. Optical micrograph of the vertex showing vestigial ocelli in *Koreotettix parvus*.

Fig. 3. Scanning electron micrograph of the vertex showing prominent ocelli in *Diodontophorus japonicus*.

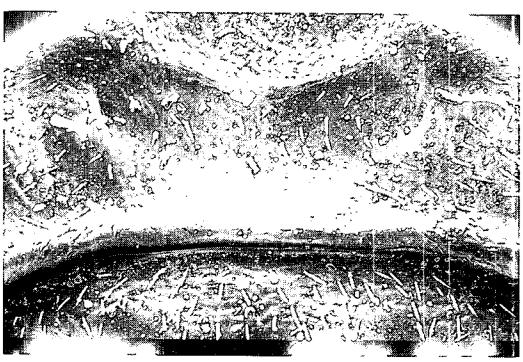

Fig. 4. Scanning electron micrograph of the vertex showing prominent ocelli in *Koreotettix parvus*.

Moreover, the brachypterous degeneration in both sexes are regarded as further apomorphy.

Hind wing: fully developed condition of the hind wing is generally common characters in leafhoppers. But, reduced hind wing with atrophied venation is regarded as a structural modification for the adaptation of the disadvantageous environment. This is considered as synapomorphy, and the rudimentary hind wing in both sexes is further apomorphy.

2) Genitalic characters

Aedeagus: the apical processes clearly present usually both in the Errhomenini and the outgroup Pagaroniini. However, they are only vestigial in the *Diodontophorus* which treated in apomorphy, and *Malmaemichungia* and *Bannalgaechungia* completely lost the structure which considered further apomorphy.

Subgenital plate: the component species of the tribes Pagaroniini and Errhomenini examined are dull in the apical part. Whereas, *Koreotettix* is slightly pointed at apex. Also, both *Bannalgaechungia* and *Malmaemichungia* are strongly constricted apically and pointed at tip. These structural conditions of the latter 2 genera can be treated as apomorphies in their evolutionary trends.

Pygofer: in *Bathysmatophorus*, the dorsal process terminates in a single hooked point. But in *Diodontophorus*, it is broadly subtruncate or bidentate, a trend toward the bifurcate condition in *Malmaemichungia* in which the ventrad ramus is greatly attenuated. The bidentate, or bifurcate condition is derived character state naturally.

Style: the styles of the Pagaroniini are short and curved ventrad, but the Errhomenini examined was very long and curved dorsad. The unique condition of the latter considered as a derived character state. The apical process of the *Pagaronia* is dull, and lack in the most Errhomenini. On the other hand, in the *Bannalgaechungia* and *Malmaemichungia*, the apical process is sharply pointed and directed ventrad which is apomorphy. The primitive pattern of the style has a nearly uniform diameter throughout (Oman, 1987), but in some genera, the style has a subapical process in ventral part, and this is apomorphic.

2. Cladistic computation

This analysis using Farris' Hennig86 package was analyzed by enumeration (*ie*) and mhennig (*mh*) algorithms, and induced a single tree from the both methods.

This cladogram with 6 terminal taxa and 10 characters had a consistency index of 76 and retention index of 79. After this initial running, the extended branch swapping (*bb*) on this cladogram was followed to locate all minimum-length cladograms. However, this analysis could found no more parsimonious cladograms (Fig. 5).

Also, when the characters coded additively, the results were same with the nonadditive character states. The optimization to determine where character state changes occur on the internal branches of a cladogram was diagnosed (Table 3). And to examine how well an individual character is fit by a tree, the length, consistency index, and retention index of individual characters were measured (Table 4).

3. Cladistic relationships

The purpose of the present study is to know whether the component genera in the Errhomenini make a natural monophyletic group, and to establish and analyze the phylogenetic relationships

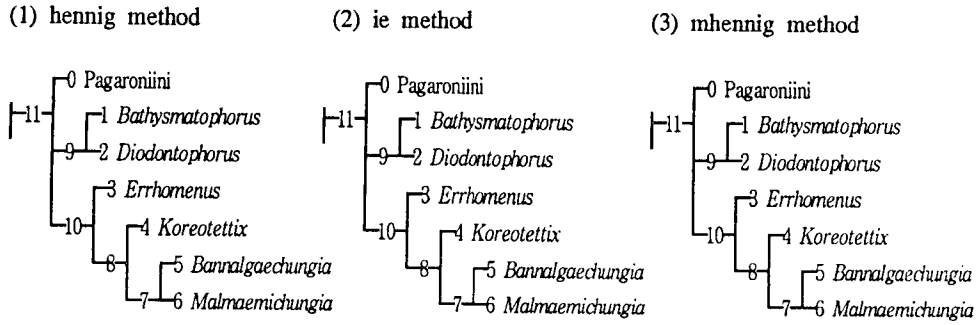

Fig. 5. Test of the cladogram of the Errhomenini using the Farris' method with tree length 21, consistency index (*ci*): 76, and retention index (*ri*): 79.

Table 3. Character state changes on the internal branches of a cladogram.

Internal branch	Character									
	1	2	3	4	5	6	7	8	9	10
7	1	1	2	2	2	2	2	1	1	0
8	1	1	2	2	2	1	1	0	0, 1	0
9	1	1	1	1	0	0	0	0	0	1
10	1	0, 1	2	2	0	0	0	0	0, 1	0
11	1	0, 1	1	1	0	0	0	0	0	0

Table 4. The length, consistency index, and retention index of individual characters.

Character	Step	Consistency index	Retention index
1	1	100	100
2	2	50	0
3	2	100	100
4	2	100	100
5	3	66	75
6	2	100	100
7	2	100	100
8	1	100	100
9	2	50	50
10	4	50	33

among them. In this analysis, the tree length of 21 (character states changes) were required as the most parsimonious cladograms, those requiring the fewest convergences or reversals are shown in figs. 6 and 7.

As the result, several characters support the existence of 2 monophyletic groups in the Errhomenini. The first group encompasses *Bathysmatophorus* and *Diodontophorus* of the subtribe

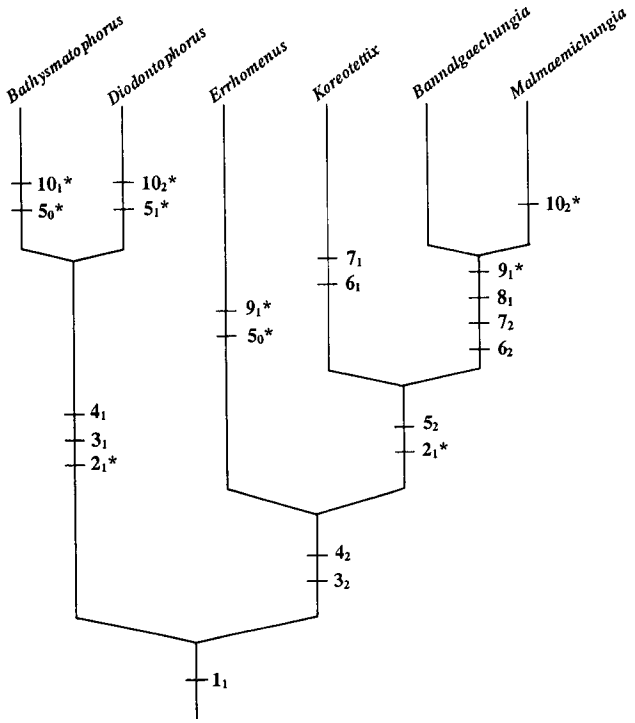

Fig. 6. Cladistic relationships of the genera based on synapomorphies in Errhomenini [bar: synapomorphies, number and subscript: character and states listed in table 1, asterisk: character convergences, consistency index (*ci*): 76, retention index (*ri*): 79].

Bathysmatophorina which shared several synapomorphies (3_1, 4_1) such as macropterous in male and brachypterous only in female condition, and contains the most plesiomorphies.

The second group incomporates the following component genera: *Errhomenus* of Errhomenina and *Koreotettix*, *Bannalgaechungia* and *Malmaemichungia* of Malmaemichungiina. The both subtribes were supported by 2 synapomorphies (3_2, 4_2) exposed as a brachypterous group in both sexes. Hence, the Errhomenini represented as a inter-group between more primitive Bathysmatophorina group and further derived Malmaemichungiina group. Moreover, *Bannalgaechungia* and *Malmaemichungia*, both endemic to Korea, were turned out to be the most derived group within the tribe Errhomenini supported by 3 synapomorphies (6_2, 7_2, 8_1).

4. Distribution

The Errhomenini mainly represents in vast continental area of the northern hemisphere, occurring throughout the Holarctic region ranging from Far East Asia, Europe to western part of North America. The only genus of the subtribe Errhomenina, *Errhomenus* is known from the Central and South Europe.

This member has been known to occur on moss and under stones (Oman and Musgrave, 1975), and the wings are typically reduced to brachypterous condition in this habitat as discussed previously. Furthermore, the 3 endemic genera of the subtribe Malmaemichungiina, such as *Malmaemichungia*,

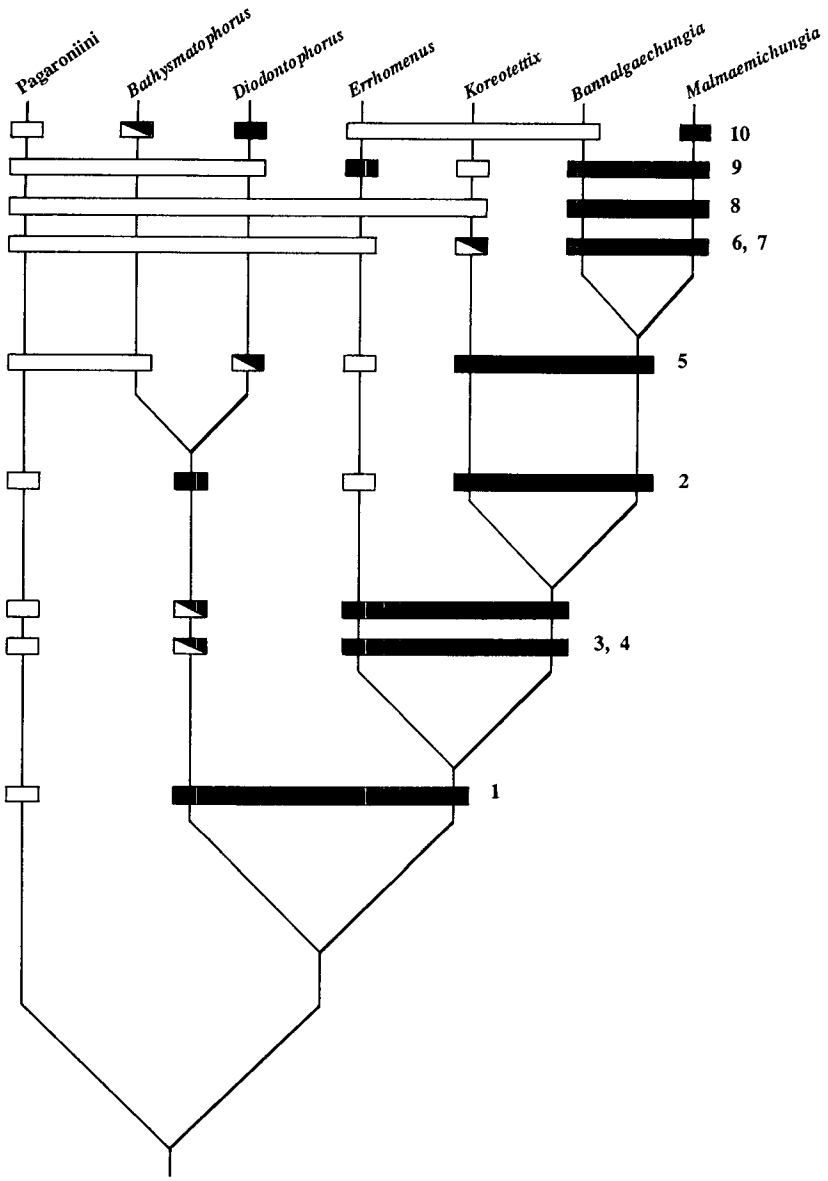

Fig. 7. Cladogram to illustrate a proposed phylogeny of Errhomenini (black square: apomorphic, open square: plesiomorphic).

Bannalgaechungia and *Koreotettix* are geographically isolated only to Korean peninsula.

Also, they are usually found at bushes with shrubs of rocky area in high altitude (Kwon, 1983), and thus, such confined and specialized ecological niches apparantly seem to have no need for the fully developed conditions of wings as well.

Among the genera of the subtribe Bathysmatophorina, *Bathysmatophorus commonly* occurs in Japan, China, Russia (Maritime Territory, Kazakhstan, North Russia, North East Siberia) of Far East Asia, Fennoscandia in Europe, and North America; *Diodontophorus* occurs in Korea and Japan; while many of the other genera in this subtribe are generally known from North America.

DISCUSSION

As the basis of classification, the monophyly of Errhomenini was tested by cladistic analysis and the most parsimonious hypothesis of phylogenetic relationships within this tribe was also determined.

When the analyses were done by '*ie* (implicit enumeration)' and '*mh* (mhennig)' methods with branch sweeping as well as non-additively coded characters, the results were all completely resembled as a single tree with the tree length 21 (character state changes), which consisted of 76 consistensy index (*ci*) and 79 retention index (*ri*). This is the most parsimonious cladogram, requiring the fewest convergences or reversals.

The 2 monophyletic groups in the tribe Errhomenini represented as the support of several characters. They consist of the first group as the Bathysmatophorina and the second one as the Malmaemichuniina including the Errhomenina. The former subtribe, analyzed by the representatives of the genera *Bathysmatophorus* and *Diodontophorus* has macropterous wings in males, and brachypterous ones only in females.

Hence, they can be more easily movable than the other leafhoppers belonging to the 2 subtribes, which principally have brachypterous conditions in both sexes. For this reason, the monophyletic group is revealed as more primitive taxa than the others. And, zoogeographically the distributional range is represented in Far East Asia, Fennoscandia and North America. Nevertheless, most genera of these subtribes in the world are usually restricted within North America.

On the other hand, the latter monophyletic group consisting of more derived 2 subtribes, the Errhomenina and the Malmaemichungiina, has brachypterous conditions in both sexes so as to adapt for the special environment. Where they can inhabit without evolutionary selective pressure for the necessity of the long distance migration through flying, as discussed above.

The genus *Errhomenus* of the subtribe Errhomenina was reported to occur on moss and under stones in Central South Europe. Whereas, all the component species of the genera *Malmaemichungia, Bannalgaechungia* and *Koreotettix* have been known as endemic to Korean peninsula only. These 3 derived genera are closely related one another. Moreover, both *Malmaemichungia* and *Bannalgaechungia* are more closely related each other consisting as the most derived group. And they are usually found at apparently specialized ecological niches such as bushes of rocky area confined in high altitude, as mentioned above.

REFERENCES

Alexander, B., 1990. A cladistic analysis of the nomadine bees (Hymenoptera: Apoidea). Syst. Ent. **15:** 121-152.

Anufriev, G.A. and A.F. Emel'yanov, 1988. 1. Suborder Cicadinea (Auchenorrhyncha). Keys to insects of the Far East USSR **2:** 12-495 (in Russian).

Farris, J.S., 1970. Methods for computing Wagner trees. Syst. Zool. **19:** 83-92.

Hamilton, K.G.A., 1983. Classification, morphology and phylogeny of the family Cicadellidae (Rhynchota: Homoptera). *In*: 1st international workshop on leafhoppers and planthoppers of economic importance. C.

I.E., Knight, W.J. *et al.* (eds.), London, pp. 15-37.

Huh, E.Y., 1993. Taxonomic revision of the subfamily Cicadellinae from Korea (Homoptera: Cicadellidae). Ph.D. Thesis. Kyungpook Nat. Univ. 324 pp.

Kwon, Y.J., 1983. Classification of leafhoppers of the subfamily Cicadellinae from Korea (Homoptera: Auchenorrhyncha). Korean J. Ent. **13**(1): 15-25.

Mayer, E. and P.D. Ashlock, 1991. Principles of systematic zoology 2nd ed. McGraw-Hill Book Co., New York, 475 pp.

Norrbom, A.L. and K.C. Kim, 1985. Taxonomic and phylogenetic relationships of *Copromyza* Fallén (s. s.) (Diptera: Sphaeroceridae). Ann. Entomol. Soc. Am. **78:** 331-347.

Oman, P., 1987. The leafhopper genus *Errhomus* (Homoptera: Cicadellidae), systematics and biogeography. Occ. Publ., Syst. Ent. Lab., Dep. Ent., Oregon State Univ. **1:** 1-72.

Oman, P. and A. Musgrave, 1975. The nearctic genera of Errhomenini (Homoptera: Cicadellidae). Melanderia **21:** 1-14.

Oman, P., W.J. Knight and M.W. Nielson, 1990, Leafhoppers (Cicadellidae): a bibliography, generic chedk-list and index to the world literature 1956-1985. CAB Int. Inst. Ent., London, 368 pp.

Triplehorn, B.W. and L.R. Nault, 1985. Phylogenetic classification of the genus *Dalbulus* (Homoptera: Cicadellidae), and notes on the phylogeny of the Macrostelini. Ann. Ent. Soc. Am. **78:** 291-315.

Wiley, E.O., 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons Inc., New York, 439 pp.

RECEIVED: 23 September 1995
ACCEPTED: 23 October 1995

민숭머리말매미충족의 分枝論的 分類(곤충강: 매미목: 매미충과)

허 은 엽 · 권 용 정
(경북대학교 농과대학 농생물학과)

요 약

分枝論的 分類方式을 이용하여 Errhomenini族의 6屬에 대한 系統 進化關係를 조사한 結果, 2개의 單配列系統群을 보였으며, 이 분석을 分類 體系化의 기초로 이용하고자 하였다.

Appendix 1. Current subtribial and generic classification of the tribe Errhomenini, with estimated number of species and adopted references in each genus.

Taxon	No. of sp.	Reference
Errhomenina		
Errhomenus	1	Lauter (1983), Lauter and Bures (1984), Nast (1972, 1976), Ossiannilson (1981)
Malmaemichungiina		
Malmaemichungia	1	Huh (1993), Huh and Kwon (1994), Kwon (1983)
Bannalgaechungia	2	Huh (1993), Huh and Kwon (1994), Kwon (1983)
Koreotettix	1	Huh (1993), Huh and Kwon (1994)
Bathysmatophorina		
Bathysmatophorus	3	Anufriev (1971, 1977, 1978), Anufriev and Emelyanov (1968), Bliven (1957), Emelyanov (1977), Emmrich (1974), Ishihara (1957, 1968), Kwon (1983), Lee and Kwon (1977, 1979), Mityayev (1967, 1968, 1971), Nast (1972, 1982), Oman and Musgrave (1975, 1987), Vilbaste (1968, 1980)
Errhomus	15	Oman and Musgrave (1975, 1987)
Ankosus	1	Oman and Musgrave (1975, 1987)
Thatuna	1	Oman and Musgrave (1975, 1987)
Lystridea	2	Kramer (1967), Oman and Musgrave (1975, 1987)
Carsonus	6	Oman and Musgrave (1975, 1987)
Diodontophorus	2	Huh (1993), Huh and Kwon (1994)