

REVIEW

**What is a Classification?
A Case Study in Insect Systematics: Potential
Confusion before Order**

KUNIO SUZUKI¹ and DAVID G. FURTH²

¹*Department of Biology, College of Liberal Arts, Toyama University, Gofuku,
Toyama City, 930 Japan;* ²*Museum of Comparative Zoology, Harvard
University Cambridge, Massachusetts 02138, U.S.A.*

ABSTRACT—A case study is presented of the Leaf Beetle genus *Orthalica* (Coleoptera: Chrysomelidae) as an example of a group involved in a variety of taxonomic problems and controversies demonstrating many of the technical and philosophical complexities of systematics that often make the derivation of a classification difficult and confusing. The history of *Orthalica* is reviewed providing discussion and illustration of the concepts of: multiple synonymy and homonymy; the genus and subgenus; lumping and splitting; and a systematic character, especially morphological, and its application in formulating higher classifications. Based on morphological characters *Orthalica* provides a good vehicle for considering the classification of the two largest subfamilies of the Leaf Beetles, the Galerucinae and the Alticinae (approximately 500 genera each). The primary difference between the Galerucinae and the Alticinae is the absence or presence, respectively, of the jumping organ (metafemoral spring), although some secondary differences exist in varying degrees. These two chrysomelid subfamilies are so diverse and relatively unstudied systematically that deriving a higher classification or speculating on their phylogeny, including their derivation from one (monophyletic) or many (polyphyletic) lineages, is premature and needs a considerable amount of study of many characters.

INTRODUCTION

One purpose of systematics is to recognize the existence of all organisms on the earth, to describe and order them, and to establish a good classification system. A well-organized classification system may be useful in deepening our understanding of the organic world. If we have no reliable system established by systematists, we cannot find any order in the biologically diverse organic world. This can be easily understood if we go to a zoo, a botanical garden or a natural history museum. If animals and plants are displayed without any consideration of their inter-relationships, we know only that these various organisms exist. The inter-relationship among organisms is the key to

organizing them. What is the “inter-relationship” among organisms? The authors use this term in the sense of evolutionary relationship; that is, they assume that all organisms on the earth have evolutionary relationships, and that they are descended from the first organism about 4 billion years ago. One purpose of systematics is to organize all organisms by such evolutionary relationships, and even though exact evolutionary history may be impossible to reconstruct completely, we can use systematic methods to make limited approximations. The authors do not adopt the viewpoint of numerical taxonomy (phenetics) which generally ignores historical perspectives. The authors also do not completely follow cladistics, a type of systematics which often forces taxonomists to make premature choices based on a restricted methodology oriented toward producing phy-

logenetic (lineage) results. In this context the authors follow more the methodology of 'evolutionary systematics' (sensu Mayr, 1963 [1]). Evolutionary relationships may be recognized based on close analysis of systematic characters in a broad sense. Much of this paper will address the question "what is a systematic character?" and its application.

What is a phylogenetic classification? Most of the problems discussed here are interconnected and relate to this question. To answer this question is not a simple matter, as with a dictionary definition, but rather a complex multi-faceted issue with arguably different viewpoints concerning both present and past relationships of organisms. We attempt here to recognize the various aspects and problems in answering such a question. The term "phylogenetic classification" in this question refers to a classification of a particular group which will reflect evolutionary history. Readers should note that the authors use the term "phylogenetic" instead of "natural" classification. This is a conscious usage in order to avoid confusion because the term "natural classification" has also been used by numerical taxonomists in a restricted sense to mean a clustering of groups based on overall similarities of many characters. The authors' usage of this term (natural classification) actually agrees more with its usage by cladists. One goal of systematics, and the taxonomists who practice it, is to establish a better phylogenetic classification system which will be acceptable to more systematists and will result in a more consistent understanding and usage of scientific names for taxa.

One of the intentions of this paper is to demonstrate to other non-systematist biologists and other scientists some of the issues, problems and logic present in the field of taxonomy/systematics. Although the examples used from insect (beetle = Coleoptera) systematics are at times somewhat complicated and some problems are left unresolved, nevertheless, they illustrate some of the fundamental complexities of biological systematics. In this paper the authors discuss some of their opinions about phylogenetic systematic procedure (theory and methods) based on recent studies. As with most basic systematic research, the authors are studying a specific group, the Leaf

Beetles (Chrysomelidae) from a particular viewpoint. In systematic studies there are different problematic situations with theoretical and/or methodological viewpoints that differ from systematist to systematist and from taxon to taxon. This is occasionally an important obstacle to communication among systematists. Using these specific studies, the authors attempt here to present their awareness of the issues in systematics. The authors would also like to help correct or improve the present unfortunate situation which underestimates the role and importance of systematic study as compared with other experimental biological disciplines. Such an attitude is based on scientific ignorance and/or a glaring misunderstanding or prejudice about the practice and significance of systematics. Unfortunately there are even some systematists who do not understand the significance of systematics. This is all the more reason for a clear and consistent explanation of biological systematics and its role in basic science. In order to stimulate further development of biosystematics, it is essential to cooperate with other biological disciplines. This has been occasionally pointed out but has not been practiced effectively. One possible reason for this scarcity of interdisciplinary cooperation may be the lack of mutual awareness of the issues existing between systematics and those other disciplines. Systematists are at least partially to blame for this because they have not often stated their awareness of such interdisciplinary issues or the significance of systematics as a basic empirical science, and as a stepping stone to other modern aspects of biological sciences.

The authors have recently conducted research together concerning several topics in insect systematics. There are even differences in theoretical and/or methodological approaches between the authors even though they both have studied the same insect group for many years. However, it has become increasingly apparent through discussion and mutual criticism that both authors have a common recognition of the above-mentioned problems of cooperative efforts in systematics. Through this mutual and reciprocal interaction the authors have managed to complete many systematic studies within a relatively brief period that could not have been accomplished in the same

broad-spectrumed way, if each of us had studied the same topics individually. The authors hope that such cooperative studies will serve as an example to systematists studying different groups or using different methodologies, and to biologists of different disciplines who might mutually augment their individual research through cooperative discussion and studies.

In this paper, we are going to focus on a problem which we call the "GA Problem". G and A refer to the chrysomelid subfamilies Galerucinae and Alticinae, respectively. The core of the "GA Problem" may be summarized as follows: "How can we classify the Galerucinae and Alticinae?" or more specifically "How should the Galerucinae and Alticinae be defined?"—this form of question may show that this problem is one of group/taxon recognition or establishment. Most systematists have accepted the view that the family Chrysomelidae should be classified into 19 subfamilies; Galerucinae and Alticinae are the largest. Various opinions have been proposed concerning the systematic position or phylogenetic relationships of these two groups (e.g. Crowson, 1955, 1982 [2, 3]; Lawrence & Britton, 1991 [4]) but it is generally accepted that they are closely related to each other. However, within these two groups there are several taxa (mostly genera) whose true systematic position (even subfamily placement) has not been decided. So that, the above question may be better expressed as: "How should the Galerucinae and Alticinae be distinguished?". There is a variety of possible ways to express this problem depending on differences in the awareness of the issues and/or which points are emphasized. Various practical aspects derived from this GA Problem may be included in this type of question. The authors will introduce these aspects using examples wherever possible because they involve many typical problems encountered in systematic study of other organisms.

Systematics has, of course, an essential purpose to deepen our recognition of a particular taxon. However, if we are satisfied with only this aspect of systematics one might ask "why is systematics needed?", especially when such a huge number of organisms exists on the earth. In other words, if we say that a purpose of systematics is to know all

organisms, is this not an endless task, how can this be sensibly planned and how can this survey of organisms be justified? Such questions are often used as arguments against systematists; Sibatani (1960) [5] asked such an essential question to systematists in Japan. Some systematists may reply that the people who laugh at such a biotic inventory do not know the world and they cannot understand the significance of organic diversity on our earth. Yet systematists are convinced that giving meaning to organic diversity on the earth from various aspects should be one of the most important priorities in biology.

Even though systematics has its own issues and perspectives, it also gives a kind of a bird's eye view to other biological disciplines. The bird's eye view which systematists offer resembles a topographical map. The precision (scale) of the map depends on the area (organic group). If we do not have any map, we cannot walk even one step. At the same time, even if we have a map we may lose our way because of disagreement between the map and our present spot. We must make an effort to improve the map in order to reflect our present position; this analogy resembles the relationship between systematics and other biological disciplines. The opinion that systematics is a synthetic discipline in biology may have originated from the viewpoint that both systematics and other biological disciplines should be mutualistic. Extensive survey of our present position will be necessary in order to improve the map to the point of maximum usefulness. The opinion that we do not need so many kinds of organisms for biological research shows gross misunderstanding of science. Biological inventory studies have limitations and, because of rapid destruction of natural ecosystems by humans in recent years and the resulting extinction of many organisms, there is an intense crisis and urgency that systematists realize more than any scientists. Systematists are the only ones who can record the great biological diversity that exists and that which is being lost forever. Therefore, systematists should play a leading role in alerting others (scientists, politicians, etc.) to the current crisis and in devising plans for conservation of this organic diversity.

GA PROBLEM

Orthaltica: History and Confusion

In order to consider "GA Problem" (Galerucinae—Alticinae Problem) the authors have chosen the genus *Orthaltica* as a good example to demonstrate many of the problems of systematics, beginning with a brief historical review. The authors would like to give an explanation of the present problem based on Scherer (1974) [6] and using the following table (list of synonymous names) from his article:

<p>Genus <i>Orthaltica</i> Crotch, 1873</p> <p><i>Orthaltica</i> Crotch, 1873:69 (type-species: <i>Crioceris copalina</i> Fabricius; N. America); Horn, 1889:236, 247; Blatchley, 1910:1206, 1215; Heikertinger, 1924–25 (1925): 65; Arnett, 1963:914, 938.</p> <p><i>Leptotrix</i> Horn, 1889:236, 249 (type-species: <i>L. recticollis</i> LeConte; N. America (nec Menge, 1868; Araneae) see <i>Leptotrichaltica</i>).</p> <p><i>Livolia</i> Jacoby, 1903:15 (type-species: <i>L. sulcicollis</i> Jac.; Africa); Scherer, 1961:268; 1969:10, 19, 118, 242; 1971:1–37. New Synonym.</p> <p><i>Leptotrichaltica</i> Heikertinger, 1924–25 (1925): 68 for <i>Leptotrix</i> Horn. New Synonym.</p> <p><i>Micrepitrix</i> Laboissière, 1933:205 (type-species: <i>M. coomani</i> Lab.; Tonkin); Gressitt, 1955:35 (Alticinae); Gressitt & Kimoto, 1963:404, 575; Samuelson, 1965:215; Scherer, 1969:10, 19, 98; 1971:10 (as synonym.)</p> <p><i>Serraticollis</i> B. E. White, 1942:17 (type-species: <i>S. rhois</i> White; Calif.); Arnett, 1963:938 (as synonym.)</p>
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The essence of the history of systematic treatment of *Orthaltica* is compiled in the above table. A trained systematist can easily understand not only the formal meaning but also the fact that beyond the nomenclature this group may contain many systematically difficult problems. The main information that should be deduced from this table may be arranged as follows (supplemental comments in brackets).

This genus was established by Crotch (1873) [7] based on *Crioceris copalina* described by Fabricius

from North America. [The genus *Crioceris* currently belongs to the subfamily Criocerinae. Crotch considered *O. copalina* as a member of a previously unknown genus currently in the Alticinae. However, even by Crotch's time higher classification of the family Chrysomelidae had been only gradually and not well established. Chapuis (1874) [8] was the first to propose a higher classification system; this was the basis of our modern system. However, not until Jacoby (1908) [9] was an actual subfamily system established. So that, we should understand that Crotch regarded the species *copalina* as a member of a close relative of many genera which are included in the Alticinae today]. After Crotch, Horn (1889) [10], Blatchley (1910) [11], Heikertinger (1925) [12], and Arnett (1963) [13] followed his treatment. [This also means that all of them recognized the genus *Orthaltica* as valid].

Until now the following have been considered synonyms of *Orthaltica*:

Leptotrix: This genus was established by Horn (1889) [10] based on the species *recticollis* described by LeConte from North America. However, this genus name (*Leptotrix*) was a homonym, in other words, the name was already preoccupied by Menge (1868) [14] as a name of a spider genus (see also *Leptotrichaltica*). [Here, some readers may think that Horn should have recognized the independence of *Orthaltica* from *Leptotrix* within his 1889 article [10]. This suggests the following two possibilities: (1) Horn positively recognized the independence of both genera or (2) he established *Leptotrix* because he did not recognize the identity of *Orthaltica*. In order to judge which possibility is probable, we have to examine Horn's 1889 paper [10]. In this paper, Horn pointed out that *Orthaltica* was similar to other genera like *Crepidodera* and *Pseudoepitrix*. He then described *Orthaltica melina* as a new species and, following the description of *O. melina*, he established *Leptotrix* and pointed out that this new genus resembles *Orthaltica* and *Pseudoepitrix* but did not belong to any genus of the tribe Crepidoderides. Subdivision of Alticinae into tribes has been partially attempted by Leng (1920) [15] and Bechyné and Bechyné (1975) [16] but remains very confusing and invalid. According to the above facts, the authors judge

that Horn took the first possibility mentioned above. Moreover, we should pay attention to the fact that in Horn's era a genus was likely to have been defined more typologically than in recent times. In other words, a genus was established based on a comparison with type-species and, in general, it was likely to be more subdivided. Of course, this may vary from worker to worker and from group to group].

Livolia: This genus was established by Jacoby (1903) [17] based on a new species *sulcicollis* from Africa. Scherer (1961, 1969, 1971) [18, 19, 20] followed this but synonymized it with *Orthaltica* in his 1974 article [6].

Leptotrichaltica: Heikertinger (1925) [12] gave a new name to *Leptotrix* Horn because the existence of a homonym (mentioned above); this genus was also synonymized with *Orthaltica* by Scherer (1974) [6].

Micrepitrix: This genus was established by Laboissière (1933) [21] based on the type-species *M. coomani* from Tonkin. [Laboissière described this genus as a member of the Galerucinae but Gressitt (1955) [22] transferred it to the Alticinae. After that, Gressitt & Kimoto (1963) [23], Samuelson (1965) [24], and Scherer (1969) [19] followed this, but Scherer synonymized it with *Orthaltica* in his 1974 paper [6]].

Serraticollis: This genus was established by White (1942) [25] who described the type species (*S. rhois*) from California. After that, Arnett (1963) [13] synonymized this genus with *Orthaltica*. [Though his opinion cannot be determined from this synonym list, this was suggested to Arnett by J. A. Wilcox, an authority of the Galerucinae]. The items mentioned above are the things which are summarized in Scherer's (1974) [6] synonym list. One should examine further each of the previous worker's opinions; this is an important routine for many systematists.

The authors will now examine some of the details of the confusion in the systematic treatment of *Orthaltica*. Scherer (1974) [6] synonymized five genera with *Orthaltica*. In considering whether his treatments are reasonable or not one has to examine all the literature involved and often to examine original type-specimens, depending on the situation. Seeno and Wilcox (1982) [26] listed

Leptothrix Heikertinger et Csiki (1940) [27] as a synonym of *Orthaltica*; however, such a difference in spelling between *Leptotrix* and *Leptothrix* is not significant. Because *Leptotrix* is a homonym of a spider genus, the species belonging to it should be automatically transferred to *Leptotrichaltica* established by Heikertinger (1925) [12] as a new name for *Leptotrix*. This merely follows proper systematic treatment in accordance with the international rules of zoological nomenclature. We have to consider the other four genera *Livolia*, *Micrepitrix*, *Leptotrichaltica* and *Serraticollis*, the first three of which were synonymized with *Orthaltica* by Scherer (1974) [6].

1. *Livolia*:

When this genus was established, Jacoby (1902) [28] mentioned that this genus may be transitional between the Alticinae and Galerucinae. In his revisional study of this genus, Scherer (1971) [20] treated the following 20 species, which included seven known and 13 new species. Also in this 1971 paper Scherer synonymized *Micrepitrix* with *Livolia* species ([20]; see also Scherer, 1981 [29]). In the list below "nov. comb." (new combination) means a new change of genus assignment of the species in question, "nov. spec." (new species) a new species is described and in brackets is the original locality (type-locality).

- vestita* (Baly, 1877) nov. comb. [W. Australia]
- sulcicollis* Jacoby, 1903 [Mashonaland: Salisbury]
- **africana* nov. spec. [W. Africa]
- coomani* (Laboissière, 1933) nov. comb. [China: Tonkin; Hainan I.]
- carolina* (Chûjô, 1943) nov. comb. [Yap; Palau]
- minuta* (Jacoby, 1887) [Ceylon]
- **minor* nov. spec. [Singapore]
- **fulva* nov. spec. [W. Sarawak]
- **nigripennis* nov. spec. [Singapore]
- **sarawakensis* nov. spec. [W. Sarawak]
- **parva* nov. spec. [Singapore]
- **malayaensis* nov. spec. [Malaya]
- **perakensis* nov. spec. [Malaya]
- **assamensis* nov. spec. [India: Assam]
- **serraticollis* nov. spec. [Burma] [= *impresiceps*: Scherer, 1974]
- **tenasserimensis* nov. spec. [S. Burma]

**ceylonensis* nov. spec. [Ceylon]
minutiuscula (Csiki, 1940) [Sumatra]
 **laticollis* nov. spec. [Singapore]
laboissierei (Chen, 1935) nov. comb. [E. China:
 Kiangsi]

Of these 20 species, we exclude here the 13 species with asterisks described by Scherer in this paper [20] from our present discussion because they were originally described as members of *Livolia*; we will examine the seven remaining species. Naturally in such cases systematists have to examine all the original literature involved, even though in a practical sense this is sometimes quite difficult for taxonomists who do not have easy access to good libraries.

vestita: This species was described by Baly (1877) [30] as a member of *Crepidodera*. This means that in Scherer's opinion at least some species which belong to *Livolia* have been mixed in *Crepidodera* (see also Scherer, 1982 [29]).

sulcicollis: This is the type-species of *Livolia*. Thus, as far as the genus continues to exist this species plays an important representative role.

coomani: This species was described by Laboissière (1933) [21] as a member of *Micrepitrix*. If we regard this species as a member of *Livolia*, this means that at least some species of *Livolia* have been mixed in *Micrepitrix*. If we agree with Scherer's (1971) [20] opinion that *Micrepitrix* is a synonym of *Livolia*, this problem is eliminated immediately; this is discussed below.

carolina: This species was described by Chûjô (1943) [31] as a member of *Epitrix* (= *Epitrix*). If we regard this species as a member of *Livolia*, this means that some species have been mixed in *Epitrix*. Gressitt (1955) [22] treated this species as a member of *Micrepitrix*. Therefore, as in the case of *coomani*, at least some species which should belong to *Livolia* have been mixed in *Micrepitrix*. Here, we experience the following two derived problems: (1) what kind of systematic relationship is there between *Epitrix* and *Livolia* and (2) how should we treat the systematic position of *carolina*. For the first problem, one possible answer may be that if *Micrepitrix* should be regarded as a synonym of *Livolia*, we have to consider systematic treatment of *Epitrix* separately; that is, because *Epitrix*

is a very big group, even if there are systematic changes for some species treated as members of this genus, all other species are not necessarily transferred to *Livolia*. For the second problem, as with other species which have been treated as members of *Micrepitrix*, the true systematic position of this species cannot be determined automatically.

minuta: This species was described by Jacoby (1887) [32] as a member of *Crepidodera* and, thus, the same situation as in *vestita* can be pointed out. Scherer (1969) [19] already pointed out that this species should belong to *Livolia*.

minutiuscula: Concerning systematic treatment of this species, there is a problematic history. The author of this species is Csiki (1940) [33] in Heikertinger and Csiki (1940) [27]. But, the taxon corresponding to this species was first described by Jacoby (1895) [34] under the name of *minuta* as a member of *Crepidodera*. But, as above, Jacoby (1887) [32] already used the name *minuta* as a member of *Crepidodera*. That is, Jacoby produced a new homonym to his other species in the same genus! This is a very unusual example of a homonym. By discovering this fact, Csiki (1940) [33] became the author of this species without describing even one line about this species.

laboissierei: This species was described by Chen (1935) [35] as a member of *Micrepitrix*. This is the same situation as in the above cases of *coomani* and *carolina*.

Scherer (1974) [6] changed the name of his *L. serraticollis* to *impressiceps* because of homonymy; that is, the name was preoccupied by Samuelson (1965) [24] as a name for one of three species of *Micrepitrix* from New Guinea. Such homonymy produces a quite confusing history that seems to be mysterious for workers of other fields of biology.

The authors summarize above items as follows. In analyzing Scherer's (1971) [21] opinion, the systematic relationships between three genera (*Crepidodera*, *Epitrix* and *Micrepitrix*) and *Livolia* are: (1) in the first two genera, only some species belonging to *Livolia* had been mixed; so that, their systematic assignment to a genus needed to be changed and; (2) *Micrepitrix* should be regarded as a synonym of *Livolia*; so that, all species described as members of *Micrepitrix* should be automatically

transferred to *Livolia*. After all these changes, Scherer (1974, 1982b) [6, 29] ultimately regarded *Livolia* as a synonym of *Orthaltica*.

2. *Leptotrichaltica*:

Concerning the systematic treatment of this genus, we completely agree with Scherer's opinion that it should be regarded as a synonym of *Orthaltica*. That is, *Leptotrix* (= *Leptotrichaltica*) *recticollis* described by Horn (1889) [10] can be treated as a member of *Orthaltica* according to the original description.

3. *Micrepitrix*:

Scherer (1971) [20] synonymized this genus with *Livolia*. Samuelson (1973) [36] followed his opinion. Because of several reasons mentioned below, the authors would like to treat *Livolia* and *Micrepitrix* as independent genera, not as synonyms.

4. *Serraticollis*:

This genus was treated by Arnett (1963) [13] (following Wilcox's opinion) as a synonym of *Orthaltica*. The authors agree that White's (1942) [25] original description of this genus can be completely adopted into *Orthaltica*.

Genus vs. Subgenus/Lumping vs. Splitting.

Scherer (1971, 1974, 1982, 1988) [20, 6, 29, 37] synonymized *Livolia* and *Micrepitrix* with *Orthaltica*. The first two genera have a symmetrical aedeagus, whereas *Orthaltica* as an asymmetrical one, which is extremely rare in the Alticinae. Of course, Scherer recognized this fact and maintained that such differences should be regarded as the characters of a subgenus level. The basis of his assertion seems to be his special concept of a genus. In his 1973 paper [38], Scherer pointed out "how reliance on topological criteria and over-ranking of lesser units can destroy the phylogenetic image of a genus." He also regretted that many systematists are likely to treat closely related species groups as independent genera based only on morphological characters. According to Scherer, *Livolia* and *Micrepitrix* should not be separated from one another (the latter, which was established more recently than the former, is regarded as a junior synonym) and neither should be distinguished from *Orthaltica* at genus level. Thus, this *Livolia-Micrepitrix* complex is regarded as a synonym of *Orthaltica* and should be distinguished

from *Orthaltica* in the strict sense (*Orthaltica* (s. str.)) only at the subgeneric level as *Orthaltica* (*Livolia*). In the case of *Orthaltica*, if one makes a classification based on Scherer's broadened concept, he would be considered a "lumper" (i.e. joining groups together); in contrast to this, many systematists are "splitters" (i.e., dividing groups apart). Occasionally the distinction between the so-called "lumper" and "splitter" has been discussed in systematics; it is, of course, a somewhat relative and subjective matter.

The authors would like to point out the following two problems. First, Scherer (1973, 1982, 1988) [38, 29, 37] suggests that taxonomists use a broadened interpretation of the genus by "lumping" subunits which share common ecology and/or historic-zoogeography into subgenera rather than "splitting" them into several genera. Although Scherer agrees that the genus should include species of common ancestry (monophyletic), he considers that interpretation of the "gap" separating higher categories is a critical aspect of defining generic level ranks (i.e. genera or subgenera). However, even as Scherer partially admits, the information (e.g. ecology, historic-zoogeography, etc.) necessary to define a genus is not always available for many groups; on the contrary, it is often quite limited. Although the authors agree in principle with Scherer's (1973) [38] definition of the genus concept, we suggest that some of his examples of genera (especially *Orthaltica*) are too broadly defined ("lumped") and may be as difficult to interpret evolutionarily as with genera which he claims are over-split.

Secondly, several items that may lead to different systematic treatment should be considered. Synonymizing of genus A with genus B will result in automatic transfer of the species members of A to B. This also means automatic extension of category A. In the present case, if *Livolia* and *Micrepitrix* are synonymized with *Orthaltica*, this automatically extends *Orthaltica* into having a very wide geographical range. On the contrary, if we regard these three as independent genera, we understand their distribution as follows: *Orthaltica* from North America, *Livolia* from Africa, and *Micrepitrix* from Southwest Asia to Pacific. Of course, comprehension of such facts are important

for us and although some may consider that such a divided treatment of ranking in a taxon is essentially not important, this demonstrates a gross misunderstanding. For example, when we consider phylogenetic relationships at the genus level, from the lumpers' viewpoint (Scherer, 1974, 1988) [6, 37] the differences among these three groups (*Orthaltica*, *Livolia*, *Micrepitrix*) may be regarded as intra-generic variation, whereas for the splitters they may be viewed at the inter-generic level. This may be deduced by an ordinary comparative method. Suzuki (1984, 1989a) [39, 40] has pointed out that the ranking of any taxon must strongly influence the phylogenetic consideration of that group.

Lumping and splitting have both good and bad points. Actually, one should judge individual cases of taxon ranking according to the differences in the effect on the understanding of the groups in question. Our conclusion about this problem is that in a group for which there is a wealth of information, Scherer's (1973) [38] broadened treatment of the genus (using subgenera) may help the evolutionary understanding; however, in cases where there is not much information about the group in question, Scherer's lumping treatment can have a negative effect on the evolutionary understanding. Unlike some systematists the authors do not think that splitting is an improper systematic practice. Rather we recognize the nature of each of the groups which we study and prefer to enhance the knowledge of each group by finding and analyzing differences between/among them. Essential characteristics and relationships of a given group can be obscured by the lumping treatment.

Concerning the *Livolia-Micrepitrix-Orthaltica* problem discussed in this paper, unfortunately there is currently only limited information about them. A lumping treatment of these genera into *Orthaltica* would indicate their general similarity but the individual characteristics and differences of each of three groups would be hidden. Therefore, at this relatively initial stage, based on differences in the aedeagus and geography and in the interest of clarify of these entities for future evolutionary analysis, the authors prefer to treat *Livolia*, *Micrepitrix*, and *Orthaltica* as three independent genera.

In the phylogenetic sense of cladistics, it is important to establish that each genus has evolved from a single ancestral lineage or clade, i.e. monophyletic. The above examination of the problematic and complex situation of the genus *Orthaltica* has gradually unfolded to the authors and based on it we now begin to approach the core of GA Problem. Concerning the higher systematic position of *Orthaltica*, there is a difference of opinion among some chrysomelid systematists, i.e. even its subfamily placement (Furth, 1985, 1988 [41, 42]; Reid, 1990, 1992 [43, 44]).

Recognition of Higher Taxa in Chrysomeloidea.

Mainly based on extensive comparative morphological study of the internal reproductive systems of both sexes, Suzuki (1988) [45] pointed out that the family Chrysomelidae cannot be regarded as a monophyletic group in relation to the two other families Cerambycidae and Bruchidae of the superfamily Chrysomeloidea. Suzuki's first essential question about chrysomeloid phylogeny concerned the fact that, surprisingly, the Chrysomelidae (Leaf Beetles) cannot always be clearly distinguished from the Cerambycidae (Long-horned Beetles) and Bruchidae (Seed Beetles); he naturally assumed that there must be greater differences among higher categories than among lower ones. The classification at subfamilial level in these three families has been considerably well established and consistent, although there are still differing opinions. There are, however, relatively few obvious differences that separate these three families from each other.

The assignment of a given species to any of the three families is automatically determined by the fact that the species belongs to a particular subfamily within them; a kind of inverted funnel system. Suzuki (1984, 1989a) [39, 40] pointed out that this type of problem is one of essential weak points in the Linnaean hierarchical classification system and its concomitant hierarchic system of category names. In most entomology textbooks, one can find some characteristics to separate these three families, and actually one can classify most specimens/taxa into families, but there are several exceptions. In a recent popular book, White (1983) [46] mentioned that "(the family Chry-

somelidae) cannot be readily characterized; family members are very diverse and have no distinctive characters in common." This is a very basic statement, but if true, how should we answer the question "what is a Leaf Beetle or a Long-horned Beetle or a Seed Beetle?" Actually beetle workers have not really answered this question. For the phylogenetic relationships in this superfamily, the first author will give a general interpretation elsewhere (Suzuki, in press [47]). The present GA Problem is a smaller version of the same kind of problems mentioned above; that is, GA Problem involves the questions "what is Galerucinae?" or "what is Alticinae?" or "how can one separate the Galerucinae and Alticinae from each other?". There are probably similar situations in many groups; however, in this case our current system of recognition for these two subfamily groups is relatively advanced.

Relationship of the Galerucinae and Alticinae, and the MS Organ.

Howe have we separated the Galerucinae and Alticinae so far? Actually there is a diagnostic character, as indicated by the name "flea beetle," the members of the Alticinae can jump using a well developed hind leg. They have a special jumping organ, which has been known as Maulik's organ or metafemoral spring (MS) (Furth, 1982) [48] in their hind femora (Fig. 1, [49]). In fact, the scientific name of the type genus (*Altica* Fabricius) is derived from the Greek 'haltikos' which means good at jumping (Furth, 1988) [42]. Most chrysomelid systematists have regarded the presence of this MS organ as a diagnostic character by which they can separate the Alticinae from the Galerucinae. However, there are several potential exceptions to which this rule cannot be applied. The genus *Orthaltica* represents just such an exceptional group, because it lacks the MS organ in the hind femora. The authors confirmed this fact in the three North American species. If we follow the rule strictly, the genus *Orthaltica* should belong to the Galerucinae. Based on this fact Scherer (1974) [6] and J. A. Wilcox (personal communication) maintained that *Orthaltica* was an exceptional alticine genus lacking MS organ. But Furth opposes this point and has asserted that the genus belongs

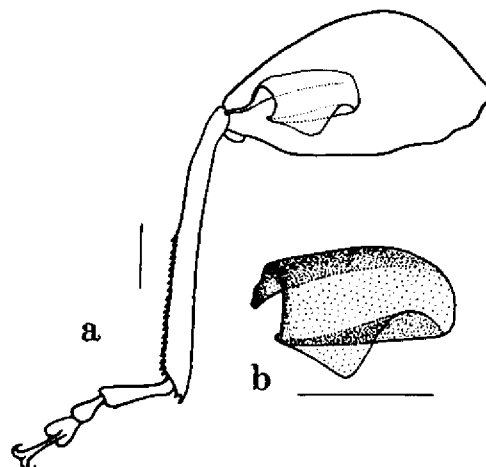


FIG. 1. The MS organ (Metafemoral Spring) of *Nonarthra postfasciatum* (Fairmaire, 1889) (Coleoptera, Chrysomelidae, Alticinae). (a) Posterior view of left leg including the MS organ. (b) Enlarged MS organ. Scale: 0.5 mm. Taken from Suzuki and Furth (1990b) [49].

to the Galerucinae (Furth, 1985, 1988, 1989) [41, 42, 50].

Before proceeding, the authors would like to point out the following facts:

1. Besides *Orthaltica*, both *Livolia* and *Micropitrix* also lack the MS organ (Furth & Suzuki, in preparation).
2. The genus *Eubaptus*, the only member of the subfamily Eubaptinae (Bruchidae), has the MS organ (Terán, 1964, 1967) [51, 52]; the authors have also confirmed this fact. The authors examined many other bruchids but could not find this organ in any other groups (Suzuki & Furth, 1990b [49]). In addition, the authors have examined some Sagrinae species (Chrysomelidae), which have been occasionally considered as close relatives of the Bruchidae, and the genus *Rhaebus* (Bruchidae, Rhaebinae), which has been treated as a group of the Sagrinae, but has been transferred to the Bruchidae (Crowson, 1946 [53]; Kingsolver & Pfaffenberger, 1980 [54]; Borowiec, 1987 [55]); the authors could not find the MS organ in either group.
3. There are species of the Rhynchaeninae (superfamily Curculionoidea, family Curculionidae) that have the MS organ. Maulik (1929) [56]

mentioned that the metafemoral organ existed in one species of the genus *Rhynchaenus* but that it differed from that in the Alticinae. Pomorski (1978) [57] first described this metafemoral organ for another species of *Rhynchaenus*. Furth has recognized a considerable intrasubfamilial (intergeneric) morphological variation and discovered seven different MS morpho-groups in the Alticinae genera (Furth, 1980, 1982, 1985, 1988) [58, 48, 41, 42]. The MS organ in the Rhynchaeninae is quite similar to that in the *Eubaptus* and to the most simple morpho-group in the Alticinae (Furth & Suzuki, 1992 [59]).

The above facts indicate that the MS organ has evolved independently in three phylogenetically separated groups. Furth and Suzuki (1992) [59] have discovered that it also exists in other coleopterous groups. This suggests that these groups may not have acquired this organ in their hind femora in the same way, i.e., evolution of this organ may have been regulated by the same developmental constraints but under different selective pressures. At the same time we must also contemplate the reason why the MS organ did not develop in other groups. In fact, there are various coleopterous groups which have a developed jumping ability in different ways (cf. Pomorski, 1983 [57], Furth & Suzuki, 1992 [59]). The MS organ evolved from the sclerotization of the metafemoral tibial extensor tendon (Furth & Suzuki, 1990b) [61]. There are several non-jumping beetle groups with well developed (swollen) hind femora (Furth & Suzuki, 1990b) [61]; therefore, the enlargement of hind femora is not always concerned with a jumping function. The authors have examined comparatively many insect orders as well as beetles with enlarged hind femora from the viewpoint of leg morphology (Furth & Suzuki, 1990a, 1990b) [60, 61].

The Galerucinae and Alticinae have long been treated as independent subfamilies. Suzuki (1988) [45] pointed out that there are few essential differences between them concerning much of their internal reproductive systems; however, there are some general differences between them in the aedeagus (male) and the spermathecae (female). For example, the aedeagus is usually asymmetrical in Galerucinae and almost always symmetrical in

Alticinae, the transverse spermathecal folds on the spermathecal capsule are quite consistent in the Galerucinae but variable in the Alticinae and the bending of the basal part of the spermathecal capsule (cf. Suzuki, 1988) [45] is distinctive in most of the alticine genera.

Wilcox (1965) [62] mentioned that: "the Alticinae can be distinguished from Galerucinae by the sclerotized extensor apodeme [=MS organ] in the posterior femora of the former. *Orthaltica* and *Leptotrichaltica* from the United States, *Micrepitrix* Laboissière from the Oriental Region, and *Micrantipha* Blackburn from Australia seem to be the only exceptions to the rule. They appear to be flea beetles which lack the extensor apodeme." Wilcox (1975) [63] also listed many genera, long treated as the members of the Galerucinae, which he claimed should be transferred to the Alticinae. He considered the MS as the only character to distinguish the Alticinae from the Galerucinae. It should be mentioned here that recently Reid (1990) [43] synonymized *Micrantipha* with *Orthaltica* as a subgenus of the latter. Reid included all species of *Livolia* into *Micrantipha* (*Micrantipha* was described in 1896 and, therefore, its name takes precedence over *Livolia* described in 1903). However, even more recently Reid (1992) [44] suggests that his 1990 *Micrantipha* subgenus (including the former *Livolia* and *Micrepitrix*) should be restored to generic status. This is consistent with the principles of the current paper as stated above and previously (Suzuki & Furth, 1990a, 1990b) [64, 49].

Suzuki (1988, 1989b) [45, 65] emphasized character correlation among the phylogenetically important morphological characters. If we adopt the MS organ as the only character to separate the Galerucinae and Alticinae, at least the following three assumptions should be valid:

1. The Galerucinae and Alticinae are each monophyletic groups, we use this term in a cladistic sense to show phylogenetic relationships.
2. The MS organ was acquired in the alticine lineage after they diverged from the common ancestor of the galerucine and alticine lineages.
3. In the alticine lineages species did not lose the MS organ secondarily and similarly in the galerucine lineages no species acquired the organ

secondarily. These assumptions mean that the MS organ is a completely derived (apomorphic) character of the Alticinae. In other words, the members of the Alticinae can be recognized by the shared derived (synapomorphic) existence of the MS organ. If these assumptions are valid, we should be able to trace logically the transformation process of the organ based on a comparison of the existing species or groups. However, does the MS organ guarantee us this ability? In other words, does the MS organ reflect a clade (single lineage) or a grade (group of lineages; cf. Huxley, 1957 [66])? If assumptions 2 and 3 are not valid, then we cannot determine definitely whether *Orthaltica* and the other two genera belong to the Alticinae, an alticine lineage that secondarily lost its MS organ, or the Galerucinae.

CONCLUSIONS

The diversity of Galerucinae (489 genera and about 6,000 species—Seeno & Wilcox, 1982 [26], Jolivet, 1987 [67]) and the Alticinae (more than 500 genera and approximately 8,000–10,000 species (Seeno and Wilcox, 1982 [26]; Scherer, 1988 [37]) is so great that our current knowledge of most aspects of relationships within each subfamily and between them is very primitive. The variation is extremely large in body size and form, color and pattern, external and internal morphological characters, as well as some important aspects of their biology. Although the MS organ is currently a useful taxonomic morphological character for separating the Galerucinae and Alticinae as well as for distinguishing and grouping Alticinae genera, its evolution within the Chrysomelidae needs much more study. Wilcox (1975) [63] listed 20 genera formerly considered to be Galerucinae which he transferred to other families or chrysomelid subfamilies. Most of these were transferred to the Alticinae based solely on the presence of the MS organ. This underlines the historical confusion of these two obviously closely related chrysomelid subfamilies.

The authors are beginning a long term study using morphological character correlation, including the MS organ, to elucidate the classification within the Alticinae and their relationship to the

Galerucinae. Only after such a study is well underway can we attempt to answer the questions posed above about the assumptions for the phylogenetic relationship between the Galerucinae and the Alticinae. Along with the questions raised by assumptions 2 and 3 mentioned above, is the question of assumption 1. In other words, can we be certain that the Galerucinae and Alticinae are monophyletic? If either or both subfamilies have evolved from different (several) lineages (clades), this would be considered paraphyletic (in a cladistic sense) and would not be a valid unit for considering a phylogenetic analysis. However, there may still be value in analyzing such a combination of clades (cluster of groups or grades). This idea of grades was discussed by Huxley (1957) [66] and some systematists maintain that such grades also reflect valid evolutionary processes (see Takagi, 1978) [68]. In fact, in many groups it is difficult to clearly define clades or to be certain of monophyly; in other words, whether a group is composed of a clade or several grades. This indicates one of the problems with premature cladistic analysis. However, as Huxley (1957) [66] pointed out, clade and grade agree in many cases.

The GA Problem reflects a situation where, based on our limited current state of knowledge, it is not possible to make definite statements about phylogeny or evolutionary relationships. Even though there is theoretically no way at this point in our knowledge of Galerucinae/Alticinae relationships to prove how the MS organ evolved or if it could be secondarily lost, we must rely somewhat on what is known from an increasingly large number of genera from both subfamilies. We must proceed to study as many aspects (e.g. morphology, ecology, genetics, etc.) of the relationship of these two groups as possible with the ultimate goal of confirming or negating the above three assumptions. However, the authors prefer to take a conservative approach without over-speculation, without lumping, and to consider the Galerucinae and Alticinae as valid and separate subfamilies.

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