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Metafemoral Spring Studies of Some Neotropical Genera of Alticinae

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ABSTRACT. — Examination of the metafemoral spring in a variety of Neotropical genera was undertaken in order to further the study of this internal generic level character and to relate some Neotropical genera to the previously established metafemoral spring morpho-groups of Palearctic and Nearctic genera. Although this study concerns only a portion (91) of the more than 220 genera of Neotropical Alticinae, it does elucidate relationships of certain genera and groups of genera. Study of other generic level morphological characters such as male and female reproductive structures increases the security of establishing generic group relationships. It is currently evident that most subfamily group names, especially tribes, used in the past have little foundation, and their use only adds confusion to research on systematics and phylogeny of Alticinae.

Although the large and unique biodiversity of the Neotropical Region has been known for a long time, it is only in recent years that we are beginning to realize the immensity of this diversity and that much of it may be lost before it (and its practical and theoretical applications) is known to science. One of the best indicators of the "new biodiversity awareness" is the diversity of the Chrysomelidae being discovered in the rainforest canopy (Farrell and Erwin, this symposium). The author has begun to examine differences and similarities of the metafemoral spring (jumping organ) in some Neotropical genera, partly because of his proximity to this area, but also because of the growing awareness of the importance and necessity for learning initially the generic level diversity of the Neotropical Alticinae fauna. Previous study of this chitinized organ inside the hind femora has revealed that genera can be separated using morphological characters of the spring (Furth, 1980). Further examination and comparison established anatomical terminology for the metafemoral spring (Furth, 1982) and a system of grouping genera according to simple morphological differences and similarities of this structure (Furth, 1985). The six "spring morpho-groups" were intended only as a convenient way of grouping the alticine genera of the Palearctic Region (Furth, 1982) and then for comparison with the Nearctic Region (Furth, 1985). These six morpho-groups are not in any way intended to imply phylogeny for the

genera treated, although certain relationships may appear evident. The zoogeographic regional approach to the study of the metafemoral spring was initially one of convenience and practicality. I first lived in the Palearctic Region and had access to generic material from that Region; subsequently, I lived in the Nearctic Region and studied the alticine fauna there (Furth, 1982 and 1985, respectively). The histological composition of the metafemoral spring was investigated (Fruth et al., 1983) and all aspects of this flea beetle jumping apparatus were recently reviewed (Furth, 1988).

This structure that enables most Alticinae to be such effective jumpers was first discovered by Maulik (1929), although he indicated its presence with a figure (no discussion) earlier (Maulik, 1926). Maulik referred to this structure as a chitinized tendon; subsequently, most workers referred to it as "Maulik's Organ" (Lever, 1930; Paulian, 1942; Costa Lima, 1955; Sherer, 1971; 1974), but it has also been called Costa Lima's Organ (Barth, 1954), and the extensor apodeme (Laboissière, 1932 [as apodeme]; Wilcox, 1965, in litt., and pers. comm.). Along with its associated musculature (primarily for tibial extension), this structure is the cause of the metafemur being greatly swollen. The enlarged metafemur (with spring) has been mentioned by several workers as the separating character between Galerucinae and Alticinae (Heikertinger, 1948; Mohr, 1960; Wiesner, 1970; Scherer, 1971; Furth, 1985; 1988). After careful consideration of the structure and function, I prefer to call the flea beetle jumping organ the metafemoral spring.

Because the metafemoral spring morphology is constant within each genus, the discrete monophyletic nature of alticine genera can be inferred. However, because the metafemoral spring is, at present, the only such generic level alticine character, considerably more study of genera from other geographic regions is necessary. In addition, it is becoming increasingly apparent that the generic group relationships and phylogeny of the Alticinae could be best realized if other characters (e.g., male aedeagus and female spermatheca) were examined together with the spring of each genus (Furth, 1985) in order to find character congruence that would increase the validity and confidence of proposing either a tribal or phylogenetic system for Alticinae.

METHODS

This study concerned 91 genera of Alticinae found in the Neotropical Region. A few of these genera are widely distributed (cosmopolitan); these and a few others have been treated in a previous project concerning the Nearctic Region (Furth, 1985). However, the vast majority of these Neotropical genera have never been examined for their metafemoral spring morphology. Specimens for this study were borrowed from various museum collections (see Acknowledgments). Preparation of the metafemoral spring involves removing the left hind leg, then soaking the leg in 10% KOH overnight in order to dissolve the muscle tissue that

is inside the metafemoral capsule. This process can be accomplished more quickly by placing the hind leg in hot KOH for several minutes. After the muscle tissue is dissolved the metafemoral capsule is dissected open on the ventral side at its apex, and the spring (attached to the tibia) is removed. The spring can then be separated from the tibia by severing the connecting ligament, then measured and illustrated. These dissections and illustrations were done using a Wild M5 dissecting microscope with a camera lucida attachment. Detailed measurements were made of the length and width of the metafemoral capsule and the width and length of the dorsal extended arm of the metafemoral spring. The figures were produced by enlarging the original figures with a photocopy machine, then tracing and inking the final figures.

RESULTS

In previous metafemoral spring studies of the Palearctic genera (Furth, 1980; 1982) and the Nearctic genera (Furth, 1985), it was apparent that the spring morphology usually reinforced previously established morphological similarities. However, there were several cases where differences from the standard catalogue arrangement were indicated. The Neotropical genera show the same phenomenon, which may indicate the reliability of more traditional morphological relationships as well as the necessity to question and further examine certain generic relationships. In this section I point out a number of cases of Neotropical genera for which such similarity or difference seems significant. A table of the Neotropical Alticinae metafemoral spring Morpho-Groups of the 91 genera examined thus far is provided (Table 1). This table will assist the reader in following the Results and Discussion sections. For more detailed explanation of the anatomy and morphological aspects of the spring morpho-groups see Furth (1982; 1985; and 1988).

Morpho-Group 1 (MG-1) includes the genus *Blepharida* (Chevrolat, which has a rather unusual distribution (Afro-tropical, Nearctic, Neotropical). Based on general external morphology, the genus *Notozona* Chevrolat has been considered a close relative of *Blepharida* (Heikertinger and Csiki, 1940; Seeno and Wilcox, 1982). The metafemoral spring of *Notozona* clearly belongs to MG-1 (Fig. 1). The spring of *Acrocycum* Jacoby studied previously (Furth, 1985) also corroborates its traditional placement near *Blepharida* and *Notozona* in MG-1. Furth (1985) incorrectly placed *Euplectroscelis* Crotch in MG-5; however, careful reexamination of this genus revealed that it belongs in MG-1, although its dorsal lobe is rather short. *Crimissa* Stål and *Elithia* Chapuis are quite apparently related based on external morphological characters, and their spring morphology is also similar in MG-1. These two genera are also placed near the beginning of the subfamily (like *Blepharida*) in the checklist/catalogue (Seeno and Wilcox, 1982). The

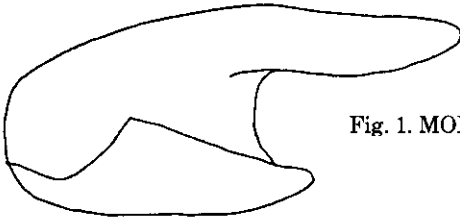


Fig. 1. MORPHO-GROUP 1: *Notozona histrionica* Baly (Ls=1.35 mm=length of spring).

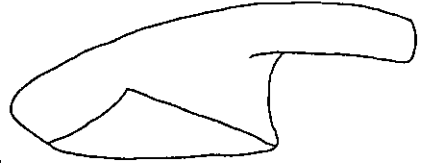


Fig. 2. MORPHO-GROUP 1: *Cacoscelis melanoptera* (Germar) (Ls=1.89 mm).

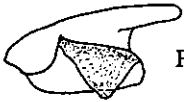


Fig. 3. MORPHO-GROUP 2: *Diphaltica nitida* (Jacoby) (Ls=0.57 mm).

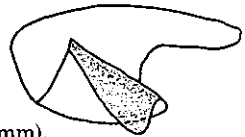


Fig. 4. MORPHO-GROUP 2: *Diphaulaca aulica* Olivier (Ls=0.70 mm).

presence of *Cacoscelis* Chevrolat (Fig. 2) and *Iphitroides* Jacoby in MG-1 is curious and has no apparent explanation at this time.

Morpho-Group 2 (MG-2) of the Neotropics contains more genera (i.e., true Neotropicals) than it did in either the Palearctic or Nearctic (Furth, 1985). As indicated in the table of spring morpho-groups, the enigmatic genus *Forsterita* Bechyné does have a spring which fits into MG-2. Virkki (1988), in an appended footnote, said that Furth (pers. comm. = in litt.) reported that there was no spring in *Forsterita*. Actually, this resulted from examination of a single specimen from Junín, Peru (sent to the author by Virkki) which, indeed, had no spring; I then wrote to Virkki stating that (because of the absence of a spring) in my opinion this specimen was a Galerucinae. Soon afterwards I was able to examine a paratype of *Forsterita boliviensis* Bechyné from Bolivia which did have a metafemoral spring. Therefore, the true *Forsterita* are Alticinae; however, this brings into question the conclusions in some of Virkki's papers (1969, 1970, 1988) in which he indicates that *Forsterita* is a genetically primitive Alticinae. The genera *Diphaltica* Barber and *Diphaulaca* Chevrolat are placed next to each other in catalogue arrangements (Seeno and Wilcox, 1982), and their springs are quite similar to each other (Figs. 3 and 4). Two other genera from MG-2 that are similar in form and have also been placed near each other in Seeno and Wilcox (1982) are *Chlamophora* Chevrolat and *Caeporis* Chevrolat (Figs. 5 and 6).

Table 1. Neotropical Alticinae — metafemoral spring morpho-groups.

| | | |
|----------------|-----------------|------------------|
| GROUP 1 | GROUP 3 | GROUP 5 |
| Acrocyum* | Agasicles | Alagoasa |
| Blepharida* | Apraea | Asphaera* |
| Cacoscelis | "Asiorestia" | Aspicela |
| Crimissa | Cornulactica | Capraita* |
| Elithia | Cyrsylus | Chaetocnema* |
| Iphitroides | Disonycha* | Glyptina* |
| Nitozona | Dysphenges* | Kuschelina* |
| GROUP 2 | Exoceras | Omophoita |
| Acanthonycha | Glenidion* | Paranaita |
| Altica* | Hemilactica | Walterianella |
| Aphanocera | Homoschema | GROUP 6 |
| Caeporis | Lactina | Aedmon |
| Calliphron | Lupraea* | Allochroma |
| Chlamophora | Monomacra* | Apalotrius |
| Diphaltica | Nasigona | Argopistes* |
| Diphaulaca | Nephrica | Atyphus |
| Epitrix* | Ocnoscelis | Cerichrestus |
| Forsterita | Pedilia | Dibolia* |
| Hemiglyptus* | Phenrica | Distigmoptera* |
| Leptophysa | Phydanis | Exartematopus |
| Lysathia* | Phyllotreta* | Heikertingerella |
| Macrohaltica | Platiprosopus | Homotyphus |
| Mesodera | Prasona | Hydmosyne |
| Phyrnocephala* | Propiasus | Megistops |
| Plectrotetra | Pseudodisonycha | Octogonotes |
| Pseudogona | Ptocadica | Omototus |
| Strabala* | Systema* | Orodes |
| Syphrea* | GROUP 4 | Phylacticus |
| Trichaltica* | Longitarsus* | Physimerus |
| | | Pseudodibolia |
| | | Pseudolampsis* |
| | | Psylliodes* |
| | | Rhinotmetus |
| | | Roicus |
| | | Sphaeronychus |
| | | Tetragonotes |

*also found in the Nearctic Region

Regarding the genus *Crepidodera* Chevrolat, there is some confusion and, based on recent reexamination, my previous paper (Furth, 1985) should be corrected as follows: the Palearctic members of the genus *Asiorestia* Jacobson should be placed in MG-1 (near *Blepharida*), as it was in Furth (1980), the Palearctic/Nearctic genus *Crepidodera* Chevrolat actually belongs to MG-3, and the Neotropical "*Asiorestia*" (? described as *Crepidodera*) (see Table 1) also belongs to MG-3 but is not

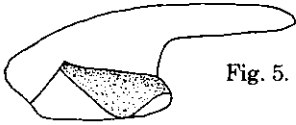


Fig. 5. MORPHO-GROUP 2: *Chlamophora costulata* Harold
(Ls=0.83 mm).

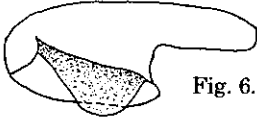


Fig. 6. MORPHO-GROUP 2: *Caeporis marginata* Clark (Ls=0.87 mm).

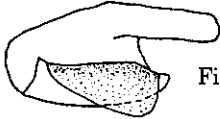


Fig. 7. MORPHO-GROUP 3: "*Asiorestia*" *brasiliensis* Baly
(Ls=0.54 mm).

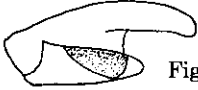


Fig. 8. MORPHO-GROUP 3: *Crepidodera aurea* (Geoffroy) (Ls=0.54 mm).

congeneric with either the Palearctic *Asiorestia* or with the actually Holarctic (Palearctic/Nearctic) *Crepidodera* but apparently requires a new generic name. The status of the Afro-tropical and Indo-australian *Asiorestia* is not known at this time. Besides the spring differences of a smaller recurve flange and less depressed apex of the dorsal lobe in Holarctic *Crepidodera* (Figs. 7 and 8), there are external differences. The Neotropical "*Asiorestia*" has: weak frontal tubercles, not bordered above by distinctly impressed sutural lines; elytral punctures fine, weakly impressed, and striae becoming obsolete in apical one quarter of elytra; male with first tarsal segment of the fore and middle tarsi greatly swollen — the Holarctic *Crepidodera* is the opposite in these characters. The Palearctic *Asiorestia* shares the above external characters with the Neotropical "*Asiorestia*" but differs in the following: pronotum dorsally very convex (appearing inflated), laterally sinuate with anterolateral angles prominent and thickened; pronotum with longitudinal, sublateral impressions long, straight, extending anterior of transverse subbasal impression. Some other external characters differ, and the genitalia have not yet been examined but will probably also show significant differences. However, to date the metafemoral spring seems to be the best evidence for this separation.

A distinctive aspect of the Neotropical genera is the large increase over the Palearctic and Nearctic in the number of members in Morpho-Group 3 (MG-3). In the majority of cases, genera share the same metafemoral spring morpho-group with genera traditionally placed near them in the catalogues. For example, *Systema* Chevrolat and *Prasona* Baly, placed next to each other in Seeno and Wilcox (1982), have a sim-

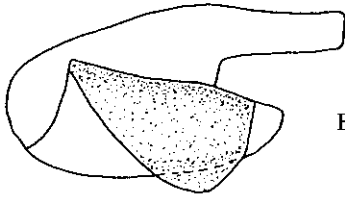


Fig. 9. MORPHO-GROUP 3: *Systema s-littera* (Linnaeus)
(Ls=0.46 mm).

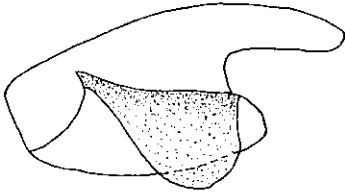


Fig. 10. MORPHO-GROUP 3: *Prasona viridis* Baly
(Ls=0.95 mm).

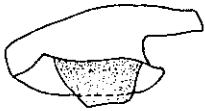


Fig. 11. MORPHO-GROUP 3: *Phenrica austriaca* (Schaufuss)
(Ls=0.87 mm).

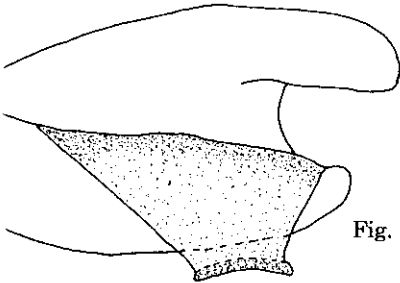


Fig. 12. MORPHO-GROUP 3: *Nephrica kirschi* Harold
(Ls=1.28 mm).

ilar spring morphology (Figs. 9 and 10). These two genera share MG-3 with *Sysphenges* Horn, *Cyrskylus* Jacoby, and *Agasicles* Jacoby — all placed close to them in catalogues. However, *Leptophysa* Baly, close to *Systema* and *Prasona* in catalogues, belongs to MG-2. Another similar pair of genera in MG-3 that are placed next to each other in catalogues is *Phenrica* Bechyné and *Nephrica* Harold (Figs. 11 and 12). They are similar in spring morphology to *Disonycha* Chevrolat (Fig. 13), *Pseudodisonycha* Blake, and *Pedilia* Clark. The morphology of *Ptocadica* Harold is similar to *Pedilia* and *Monomacra* Chevrolat — both quite distantly placed from *Ptocadica* in catalogue arrangements (Seeno and Wilcox, 1982). Probably the catalogue position of *Ptocadica* (near miscellaneous genera such as *Forsterita*, *Scelidopsis* Jacoby and not far from *Longitarsus* Berthold) should be reviewed. Furth (1985) incorrectly placed *Monomacra* in MG-2; it belongs to MG-3 (Fig. 14). *Ocnoscelis* Erichson is currently placed in MG-3 because of its dorsally convex shape, recurve flange, etc. (Fig. 15); however, it has certain morphological aspects (i.e., the narrow keel-shape of the dorsal lobe) which indicate

a possible unique placement. *Ocnoscelis* is currently placed in catalogues as a separate group (see Seeno and Wilcox, 1982) near *Platiprosopus* Chevrolat (MG-3), *Leptophysa* (MG-2), and *Systema/Prasona* (MG-3).

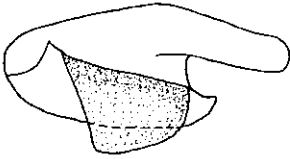


Fig. 13. MORPHO-GROUP 3: *Disonycha triangularis* (Say)
(Ls=0.83 mm).

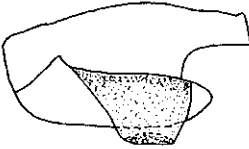


Fig. 14. MORPHO-GROUP 3: *Monomacra citrina* (Harold)
(Ls=0.57 mm).

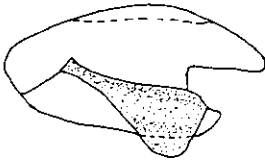


Fig. 15. MORPHO-GROUP 3: *Ocnoscelis viridipennis* (Clark)
(Ls=0.76 mm).

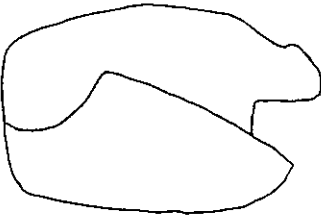


Fig. 16. MORPHO-GROUP 5: *Alagoasa decemguttatus* (Fabricius) (Ls=0.89 mm).



Fig. 17. MORPHO-GROUP 5: *Paranaita bilimbata* (Baly) (Ls=1.33 mm).

Morpho-Group 5 (MG-5), although currently represented by relatively few genera, contains several very diverse genera of the group ("subtribe") Oedionychina (see Virkki, this Symposium) that used to be lumped into *Oedionychus* Berthold. This formerly large single genus was split into several genera by Jan Bechyné (1955, 1956, 1959, etc.): *Alagoasa* Bechyné (Fig. 16), *Asphaera* Chevrolat, *Omophoita* Chevrolat, *Paranaita* Bechyné (Fig. 17), *Walterianella* Bechyné, etc. — all consistently belong to this spring morpho-group.

Morpho-Group 6 (MG-6) is one of the largest spring groups with 25 Neotropical genera. Most (18) of these belong to a group sometimes called the Monoplatini, with globosely swollen apical metatarsal segments and striate-punctate elytra. Even though this group of genera is somewhat confusing morphologically, all genera studied to date have a

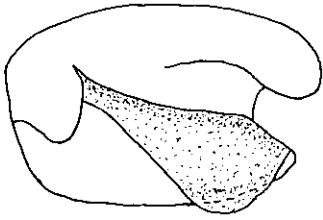


Fig. 18. MORPHO-GROUP 6: *Allochroma sexmaculata* Clark (Ls=0.98 mm).

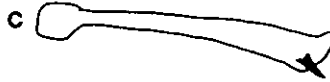
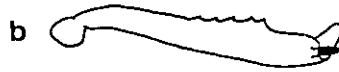
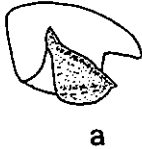


Fig. 19a. MORPHO-GROUP 6: "*Sphaeroderma*" *opima* LeConte (Ls=0.44 mm).
 Fig. 19b. Metatibia, lateral view. (Ltb=0.95 mm=length of metatibia). Fig. 19c. Metatibia, dorsal view.

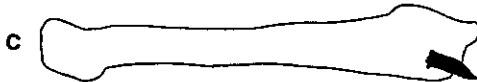
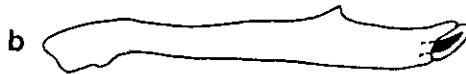
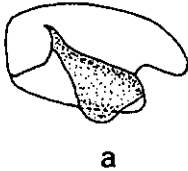


Fig. 20a. MORPHO-GROUP 6: *Heikertingerella adusta* Harold (Ls=0.61 mm). Fig. 20b.
 Metatibia, lateral view (Ltb=1.43 mm). Fig. 20c. Metatibia, dorsal view.

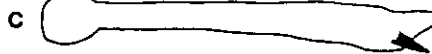
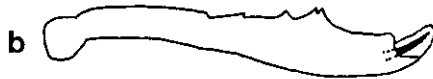
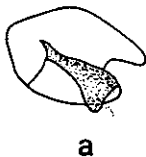


Fig. 21a. MORPHO-GROUP 6: *Pseudodibolia picea* Jacoby (Ls=0.46 mm). Fig. 21b. Meta-
 tibia, lateral view (Ltb=1.00 mm). Fig. 21c. Metatibia, dorsal view.

metafemoral spring belonging to MG-6 (Figs. 18, 19a, 20a, 21a). Also in MG-6 are the cosmopolitan *Dibolia* Latreille and the Neotropical *Megistops* Boheman which, in determination keys, are grouped together because of a wide, bifurcated, apical metatibial spur; presumably, for

this reason they are considered together as a separate group in Seeno and Wilcox (1982).

A curious case involves the Nearctic *Sphaeroderma* Stephens, the Neotropical *Pseudodibolia* Jacoby, and the Neotropical *Heikertingerella* Csiki. All are coccinelliform in body shape, have metatibial dorsal excavations subapically, and have similar MG-6 springs (Figs. 19, 20, 21). These three genera are placed quite distant from each other in Seeno and Wilcox (1982), especially *Sphaeroderma*. Upon close examination, the single Nearctic species *Sphaeroderma opima* LeConte is not congeneric with the Palearctic species of the genus (Furth, unpub.), although this has also been suspected by some other workers (E. Riley, pers. comm.). This Nearctic species (*S. opima*) shares detailed morphology of the metatibia with *Pseudodibolia* (Figs. 19b-c, 21b-c). However, *S. opima* has a very different female spermatheca than either *Pseudodibolia* or *Heikertingerella* (Furth, unpub.). In the list of Nearctic spring morpho-groups published previously (Furth, 1985), *Sphaeroderma* is listed as MG-5 — this is an error, it should be in MG-6. Furthermore, the Palearctic (and presumably in other Old World regions) *Sphaeroderma* definitely has a MG-5 spring; therefore, the Nearctic *Sphaeroderma* is not congeneric with the Palearctic (? Old World) members of that genus, but is closer to *Pseudodibolia*. Apparently, this Nearctic genus needs to be renamed; however, further comparative studies of the reproductive structures are necessary to positively establish this fact.

DISCUSSION

The results of the present study demonstrate corroboration of traditional close relationships that are implied in catalogues such as the following: *Blepharida*/*Notozona* and *Crimissa*/*Elithia* of MG-1; *Diphaltica*/*Diphaulaca* and *Chlamophora*/*Caeporis* of MG-2; *Systema*/*Prasona*, *Phenrica*/*Nephrica*, *Ptocadica*/*Pedilia* of MG-3; the many genera split from *Oedionychus* of MG-5; and *Dibolia*/*Megistops* and the many genera of "Monoplatini" of MG-6.

It seems apparent that Bechyné oversplit the genera of the former *Oedionychus* based on many weak and ambiguous characters (see Scherer, 1983). For example, the monotypic *Pyxidaltica* Bechyné differs from *Paranaita* Bechyné only by the swelling of the apical four segments of the antennae; many of the genera that Bechyné split from *Oedionychus* are monotypic. One important result of the present study is that *Disonycha* and relatives show a distinctly different spring morpho-group (MG-3) than the genera related to *Oedionychus*, i.e., the justification of *Disonychina* and *Oedionychina* subtribes of Virkki (this symposium).

Detailed examination of the spring morphology presented here reveals that the species of two New World genera, Neotropical *Crepid-*

odera and Nearctic *Sphaeroderma*, are not congeneric with the Old World members and need to be renamed.

This study is essentially the third geographical treatment of Alticinae genera according to the morphology of their metafemoral spring (Furth, 1982; 1985). As mentioned above, this geographical approach has been primarily one of convenience and availability to me of material from those areas. However, it is becoming increasingly apparent that further research on the metafemoral spring and its potential for study of Alticinae relationships may be better accomplished by examination of genera suspected of being "primitive/transitional" with the Galerucinae (e.g., the Decarthrocerini of Seeno and Wilcox, 1982), those that have been formerly included in the Galerucinae and recently transferred to the Alticinae (Wilcox, 1975), or other genera suspected of being unusual based on other morphological characters, e.g., internal reproductive structures or wing venation (Suzuki, pers. comm.) — "phylogenetic" approach. Metafemoral spring studies of these "problematic alticine genera," as well as of certain genera previously considered to be "related" based on their proximity in catalogues (e.g., Seeno and Wilcox, 1982), will certainly reveal even more information about relationships in the Alticinae than a geographical approach. The arrangement of genera in catalogues or "catalogue phylogeny" is usually based on similarities and/or differences of various traditional morphological characters that imply relationship or phylogeny; however, in many cases the basis of generic placement in such catalogues is quite superficial, and because there is no explanation of this arrangement, there is need for a more structured approach to the relationships of the genera of Alticinae. In fact, as mentioned by Seeno and Wilcox (1982) in their checklist/catalogue of the genera of Chrysomelidae, there is no satisfactory system of tribal distinction in the Alticinae. Seeno and Wilcox (1982) do give a list of the previously proposed tribal and family group (= subfamily) names, and they state that "Until these groups are better understood, we feel that the family-group names should be omitted from the checklist of generic names." However, Seeno and Wilcox *do segregate* the generic list into such groupings and even indicate the "nominate" genera of each group. Even though it was apparently their intent only to show historical grouping of genera into tribes or other subfamily-group names, in effect they have created (recreated) a tribal system for the Alticinae, not found in any other contemporary reference. This seems to contradict their above statement, and unfortunately, several authors have begun to use tribal names based on this system (e.g., Virkki, this Symposium).

Ideally, there needs to be a combined effort to correlate different aspects of Alticinae, such as: metafemoral spring; genetics (see papers by Segarra, Petitpierre, Virkki — this Symposium); defense glands (Pasteels, this Symposium); internal reproductive structures (Suzuki, 1988), etc., into a type of character congruence analysis of the alticinae

genera and eventually into a tribal system. The present and previous geographical studies of the metafemoral spring of Alticinae genera are only a contribution towards such a character congruent tribal system and are not meant to imply a phylogeny of these genera. Although previous studies have revealed only six morpho-groups (Furth, 1982; 1985), others will certainly be discovered using the above "phylogenetic" approach. Recently a new (seventh) spring morpho-group was discovered in *Chalaenosoma* Jacoby (Furth, 1988) which has an extremely simplified morphology; the genus *Gastrida* Chapuis (a member of the Decarthrocerini, mentioned above) also has a similar, simplified spring morphology (Furth, unpubl.). Both of these genera have very slender metafemora which is contrary to the traditional diagnostic character used to distinguish Alticinae from Galerucinae — a swollen/enlarged metafemur. Whether or not these two genera, by virtue of a slender metafemur and simplified metafemoral spring morphology, are to be considered primitive, remains to be decided. There are approximately 500 genera of Alticinae worldwide (Scherer, 1988); however, many more need to be examined and studied before significant phylogenetic implications (based on metaformal spring character phylogeny or other congruent characters) can be made or before anything approaching a tribal system for the Alticinae can be proposed.

The first study of metafemoral spring morphological differences among general of Alticinae (Furth, 1980) attempted to show that there are two basic forms of this jumping organ, based on its shape and other details of its anatomy, with several variations forming other morphological groups. The first basic spring form (MG-1) has a long, straight dorsal lobe, with the apical part (extended arm) not depressed and extending considerably beyond the apex of the ventral lobe and with no sclerotized recurve flange attached to the ventral lobe. The second basic spring form (MG-5) has relatively little extension of the dorsal lobe beyond the ventral lobe, and the dorsal edge (dorsal lobe) of the spring is strongly convexed (apically depressed), giving the spring a compact form; there is also no sclerotized recurve flange. A subsequent study of Palearctic genera (Furth, 1982) gave a detailed explanation of each of the six metafemoral spring morpho-groups and illustrations of spring anatomy. Morpho-groups 2 and 6 are simple variations of the two basic forms (MG-1 and MG-5, respectively), each possessing the addition of a well-developed sclerotized recurve flange attached to the ventral lobe. MG-3 has a shorter dorsal lobe (but noticeably longer than the ventral lobe), apically depressed, with a small recurve flange. MG-4 is similar to MG-3 but with the ventral lobe widest in the middle and without a recurve flange (*Longitarsus* only). As mentioned above, recently, a MG-7 was discovered with a very simplified, hook-shaped form (Furth, 1988, Fig. 9c). There is a temptation to say that this simplified MG-7 spring form is a "primitive" type and that the more elaborate MG-6 is more "advanced." However, it is premature to consider these seven spring

morpho-groups as representing the character phylogeny of this structure or as inferring the phylogeny of the Alticinae, because there remain many genera and groups of genera to be studied.

Based on certain morphological evidence such as the presence of the metafemoral spring and genitalic characters, the author has considered the Alticinae to be a monophyletic subfamily within the Chrysomelidae. Evidence of more simplified (possibly primitive) metafemoral spring types (e.g., MG-7), Alticinae with Galerucinae-type genitalia (e.g., *Chalaenosoma*), together with genetic evidence such as the single (fused) testes unique to both these subfamilies (Petitpierre, pers. comm.), and studies of wing venation and internal reproductive systems demonstrated by Suzuki (1988, and pers. comm.) indicate that the Galerucinae and Alticinae may be a single group sharing a common monophyletic lineage. However, considerably more research in these and related disciplines must be conducted in order to determine the evolutionary/phylogenetic relationships of Alticinae.

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