

CHARACTER CORRELATION STUDIES OF PROBLEMATIC GENERA OF ALTICINAE IN RELATION TO GALERUCINAE (COLEOPTERA: CHRYSOMELIDAE)

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INTRODUCTION

The closest relatives to the Alticinae are members of the Galerucinae which do not jump and do not have swollen metafemora. Although the Galerucinae have far fewer described species worldwide than the Alticinae they have almost as many described genera (489 compared to 500, respectively, cf. Sceno and Wilcox, 1982). However, the relationship and evolution of the Galerucinae and the Alticinae is not at all understood. Although Chapuis (1875) lumped these two subfamilies into the Galerucidae, most 20th century systems of chrysomelid classification separate them into distinct subfamilies (Seeno and Wilcox, 1982), some exceptions such as Böving and Craighead (1931), Crowson (1955), Lawrence and Britton (1991), and some others will be discussed below. Suzuki (1988) used a different classification system for the Chrysomelidae consisting of 9 subfamilies and 19 tribes in which the Galerucinae and the Alticinae were treated as "tribes". Even so Suzuki (1988) basically discussed the similarities and differences of Galerucinae and Alticinae as originating from a common ancestor but with no close relationship to any other existing chrysomelid group. Furth (1989) also recognized the close relationship of the Galerucinae and Alticinae with a possible common ancestry. The only "reliable" way to distinguish these two subfamilies has been the distinctly swollen metafemora of Alticinae and the possession of the internal hind leg organ or metafemoral spring (Maulik, 1929, Furth, 1980, 1985). Unexpectedly Furth (1980, 1982, 1985, 1988, 1989) discovered that this metafemoral spring organ was morphologically different among alticine genera (constant within each genus) and could be used to divide Alticinae into groups of genera based on spring morphology (i.e. spring morpho-groups). Currently all Palearctic, Nearctic, and about one quarter of the Neotropical alticine genera have fit into six distinct spring morpho-groups (Furth, 1980,

1982, 1985, 1988, 1989). In general the relationships of genera in these spring morpho-groups corroborates the traditional generic relationships found in older keys and catalogues; however, there are some interesting exceptions (Furth, 1985, 1989).

In the revision (supplement) of the Coleopterorum Catalogus for Galerucinae, Wilcox (1975) recognized that a number of genera needed to be transferred to the Alticinae because, although they had slender metafemora, they possessed an "extensor apodeme" (metafemoral spring). Therefore, the traditional external method for separation of Galerucinae from Alticinae had to be questioned. In addition, there are some Galerucinae with somewhat swollen metafemora and some other Alticinae with relatively slender hind legs. Furth (1985, 1988, 1989) stated that the only definitive character separating Alticinae from other chrysomelids was the presence of a metafemoral spring, whether or not they used it to jump. Even though the presence or absence of a metafemoral spring is quite definitive, the use of this single character to delineate these two largest Leaf Beetle subfamilies is somewhat controversial because it means that a few genera, traditionally Alticinae, would have to be transferred to Galerucinae, e.g. *Orthallica* Crotch (Furth, 1985, Suzuki and Furth, 1990a, 1990b, 1992).

In an attempt to clarify/resolve the position of the Galerucinae and Alticinae, in this study the authors have begun to examine the "problematic/transitional" genera, such as those transferred from the Galerucinae to the Alticinae by Wilcox (1975) as well as certain other apparently "problematic" genera. It quickly became obvious that these genera were indeed unusual in the morphology of their metafemoral spring, hind wing venation, female spermatheca and male aedeagus. The hind wing venation, especially the cubitus veins, has been shown to be useful in the higher classification of the Chrysomelidae (Jolivet, 1959a, 1959b, Suzuki, 1969, 1988, 1994). Although hind wing venation charac-

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ters are stable at the subfamily level they may be somewhat variable within the subfamily; yet still quite useful and revealing even at the generic level. The female spermatheca was shown to be useful for higher level (subfamilies and genera) studies (Spett and Lewitt, 1926, Suzuki, 1988), but it has been used only relatively recently to distinguish species and has often been found to be a much better specific character than the male aedeagus (Samuelson, 1966, Leonardi, 1970, 1972, 1973, Seeno and Andrews, 1972, Furth, 1979b, 1980, 1984, 1986, and others more recently). The male aedeagus has been used for at least 100 years to differentiate species including by Furth (1976, 1979b, 1980, 1981, 1984, 1986). Therefore, the authors began to compare this group of four independent internal and external characters in these "problematic" genera in an attempt to correlate these characters at the genus level and to formulate a character congruence study.

The Alticinae is the only chrysomelid subfamily for which no system of higher classification exists, i.e. a tribal system. In Seeno and Wilcox (1982) the accepted system of tribes, subtribes, and sections is given for all of the other major chrysomelid subfamilies, including Galerucinae. In fact Seeno and Wilcox (1982) state in their checklist that no satisfactory tribal system exists for the Alticinae. This is further indication that the Alticinae are poorly understood and that, together with consideration of the Galerucinae/Alticinae relationship, there needs to be a careful global study of the genera of Alticinae in order to formulate a higher (tribal) classification. Unfortunately, a few authors (e.g. Segarra and Petitpierre, 1985, Virkki, 1988, 1989, etc.) have begun to use the Alticinae tribal names, unintentionally implied in Seeno and Wilcox (1982) or taken from the complicated superficial system developed by J. Bechyné (Bechyné and Bechyné, 1966, 1975, etc.). Furth (1989) discussed the confusion and unfounded use of tribal system names in the Alticinae. The traditional unexplained arrangement of genera in catalogues ("catalogue phylogeny") is sometimes based on superficial characters and such "phylogeny" is often perpetuated through generations of literature then misinterpreted or used for convenience by some workers; however, this usually only serves to confuse the higher classification further.

For generations of taxonomic/systematic study biologists have usually examined organisms in detail and compiled lists of characters that helped them distinguish different species, genera, families, etc. In essence what they have been employing is a type of character congruence/correlation, albeit usually subjectively and unconsciously. There have been relatively few analytical/objective character congruence/correlation studies of insect groups and virtually none in the Chrysomelidae. Furth (1985) demonstrated a type of character correlation by examining the metafemoral spring, male aedeagus, and female spermatheca of all Palearctic and Nearctic genera of Alticinae in order to reveal relationships

among some of the genera. Suzuki (1989) discussed how evolutionary relationships can be revealed through study of "character correlation" of the internal male and female reproductive systems in Chrysomelidae. Furth (1989) suggested that a combination of a variety of characters may allow a character congruence analysis that could produce a reliable tribal system for the Alticinae. The current study demonstrates the usefulness of character correlation studies in higher classification/systematics in the Chrysomelidae.

METHODS

For the methodology of dissection, examination and study, and illustration of the metafemoral spring, male and female reproductive structures, and the hind wing venation, the authors followed Furth (1988), Suzuki (1988) and Suzuki (1969 and 1994), respectively.

The terminology used here for the metafemoral spring follows Furth (1988 and 1989) and Furth and Suzuki (1992). For the spermathecal characters (Fig. 3c) we refer to the main sclerotized part as the spermathecal capsule or chamber, including basal and apical parts (a sclerotized appendix is sometimes attached to the apex) which generally correspond to the receptacle and pump, respectively of the system used by Furth (1976 and subsequent papers on the Alticinae fauna of Israel). The spermathecal ductus originates (its base) from the bursa copulatrix (vagina) and extends to near the base of the spermathecal capsule (its apex), ending at the point where the spermathecal gland attaches (Fig. 2c). The apex of the ductus is often swollen, strongly sclerotized, or modified and appearing to be part of the capsule base. Some further details of terminology can be obtained from Suzuki (1988) (see also Figs. 2c and 3c). The scale bars used for some of the figures are of three types: solid lines = 1.0 mm; dotted lines = 0.1 mm; and dashed lines = 0.5 mm.

RESULTS

For practical reasons, previous studies of the metafemoral spring were conducted by examining genera from single biogeographic regions, i.e. Palearctic (Furth, 1980, 1982), Nearctic (Furth, 1985) and Neotropical (Furth, 1989). Those studies revealed only six spring morpho-groups; however, the present study is based on "apparent morphological relationships" ("catalogue phylogeny") using 19 "problematic" genera and it has revealed six new spring morpho-groups. This is a high percentage (32%) of new spring types and is, therefore, a good indicator that our morphological approach using "problematic" genera is a significant one. In previous spring studies (Furth, 1980, 1982, 1985, 1988, 1989) the spring morpho-groups were referred to by number; however, from this point on it is more practical to name the twelve morpho-groups after a

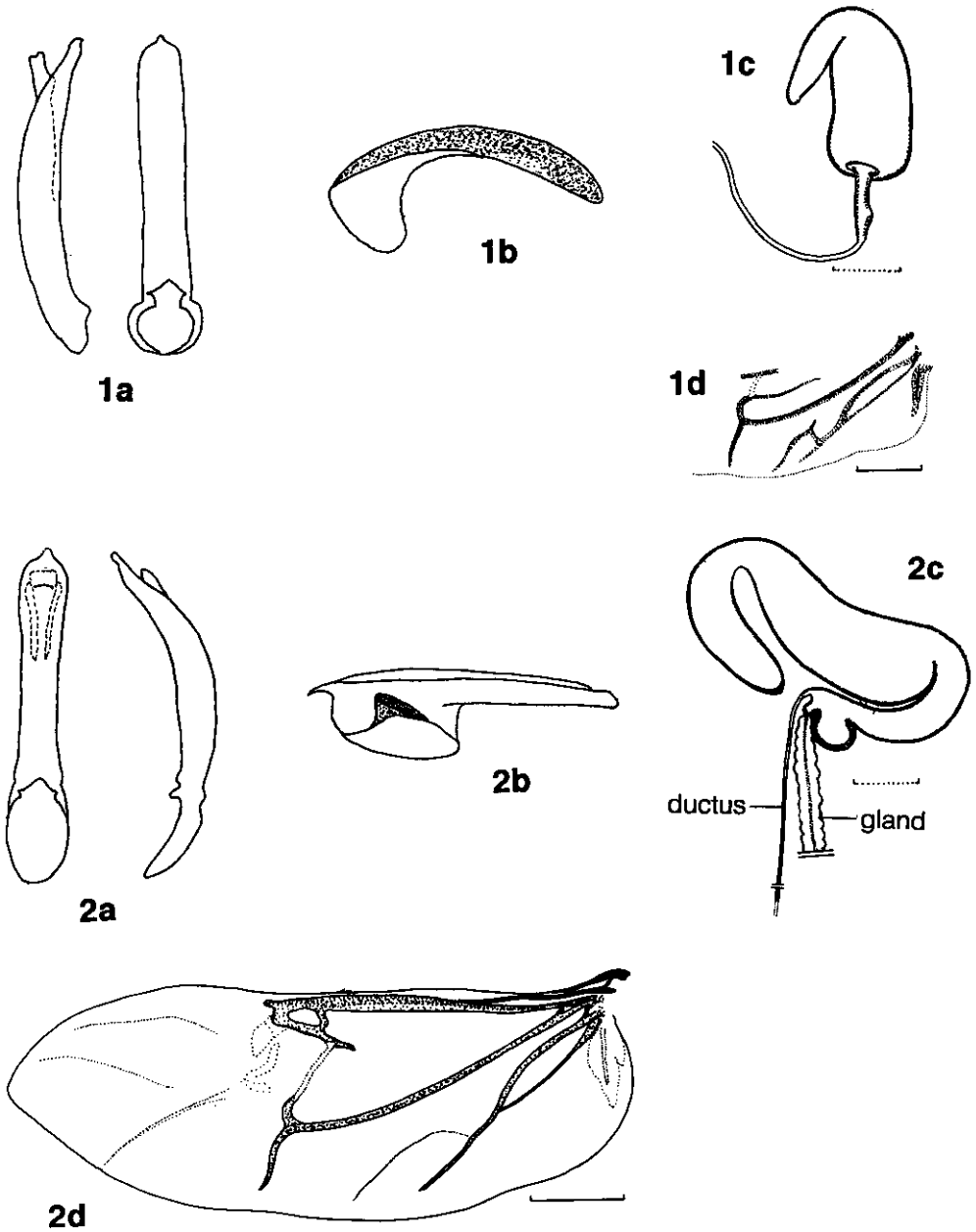


Figure 1. *Chaloenus latifrons* a) Aedeagus lateral and ventral views (Length [maximum] = $L_{aed} = 2.35\text{mm}$). b) Metafemoral Spring (Length [maximum] = $L_{spr} = 0.76\text{mm}$). c) Spermatheca (dotted scale bar = 0.1mm). d) Hind Wing (anal area) (solid scale bar = 1.0mm).

Figure 2. *Sangariola punctatostriata* a) Aedeagus lateral and ventral views ($L_{aed} = 2.8\text{mm}$). b) Metafemoral Spring ($L_{spr} = 0.99\text{mm}$). c) Spermatheca. d) Hind Wing.

representative genus. Therefore, from now the former: morpho-group #1 = *Blepharida*-group; morpho-group #2 = *Alica*-group; morpho-group #3 = *Phyllotreta*-group; morpho-group #4 = *Longitarsus*-group; morpho-group #5 = *Chaetocnema*-group; and morpho-group #6 = *Psyllodes*-group. The six new groups are named below.

The spermatheca and its associated parts are useful indicators of affinity to Galerucinae or Alticinae. Even though spermathecal characters are neither 100% Galerucinae nor 100% Alticinae, they do show significantly strong tendencies toward one of these two subfamilies. The spermathecae of Alticinae can be put into two groups: Type A - the most typical alticine type (no galerucines have this

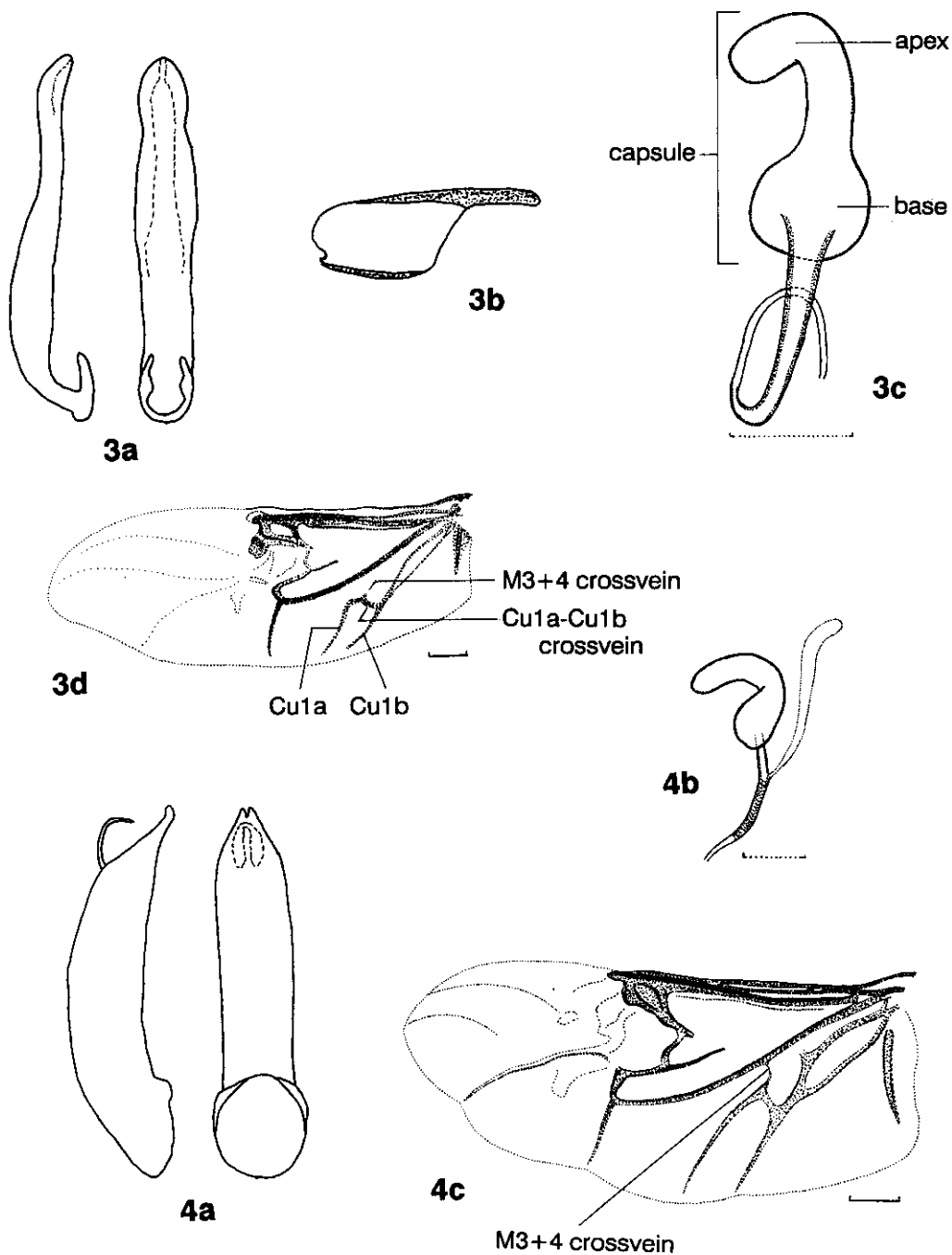


Figure 3. *Mandarella nagpurensis* a) Aedeagus lateral and ventral views (Laed = 1.5mm). b) Metafemoral Spring (Lspr = 0.69mm). c) Spermatheca. d) Hind Wing.

Figure 4. *Philocalis pulchra* a) Aedeagus lateral and ventral views (Laed = 3.55mm). b) Spermatheca. c) Hind Wing.

type) with the base extended or bent, the gland attached in a consistent way, a "C" or upside-down comma overall shape (Figs. 2c, 5c, 7c, 16c) and with the capsule surface apparently smooth (at lower magnifications) (Fig. 7c). Type B - the non-typical alticine type (common in galerucines) with the base

not bent, the gland attachment and capsule shape variable, the capsule walls thicker and its surface with horizontal folds (apparent at low magnification, see Fig. 13c) and with the apex of the ductus commonly invaginated into the base of the capsule (Figs. 3c, 4b, 9c, 11b, 12c, 13c, etc.). The ductus in

Galerucinae is usually much shorter than in Alticinae.

Examination of the characters of the male aedeagus has corroborated an established significant tendency that a large number of Galerucinae possess an asymmetrical shape (in ventral or dorsal view), whereas almost all Alticinae examined to date have a symmetrical aedeagus; only some of the species of *Chaloenosoma* Jacoby have an asymmetrical aedeagus (see also Scherer, 1969).

Study of the hind wing venation characters has revealed a number of tendencies of either Galerucinae or Alticinae affinity. The cu1b-cu1a crossvein is lacking in most (ca. 80%) Alticinae, especially those with Type A spermatheca; however, most of the "problematic" genera examined in this study do have it (e.g. Figs. 3d, 10c, 11c). There is a small spur vein (m-cu remnant crossvein) projecting from Cu1a which is a remnant of the connection to m-cu and is more common in Galerucinae than Alticinae; however, it is present in some of the "problematic" genera studied here (e.g. Figs. 4c, 12d). Also the reduction or loss of cu1a is more typical of Alticinae than of Galerucinae (e.g. Figs. 13d, 16d, 5d).

The original group of "problematic/transitional" genera was taken from the catalogue of Galerucinae (Wilcox, 1975), at the end of which was a list of 16 taxa (mostly generic names) that had been or were proposed to be transferred to the Alticinae. Although not stated by Wilcox (1975) these taxa were previously included in the Galerucinae primarily because they possess slender hind femora (unlike most Alticinae). Research in the present paper confirms this fact and that at least some Alticinae have a metafemoral spring inside a slender hind femur. Below we list these taxa, the reasons for considering them in this study or not, and the results/affinities of our study of the four character systems.

Borbaita Bechyné was described as a Galerucinae with the statement that it indeed had inflated metafemora but did not contain a Maulik's Organ (= metafemoral spring). However, upon examination of a paratype Wilcox (1975) transferred this genus from the Galerucinae to the Alticinae based on the presence of an extensor apodeme (= metafemoral spring). The types are deposited in the Museum G. Frey (Tutzing, Germany) which has been closed to the scientific community and, thus, these specimens were unavailable to the authors for study.

Chaloenus viridis Bryant was synonymized with *Terpnochlorus perrieri* Fairmaire by Bechyné (1955). We examined the true *Chaloenus* Westwood (i.e. *Chaloenus latifrons* Westwood) from SE Asia and decided to include it in our study because of its slightly swollen hind femora. *Chaloenus* has: a simplified *Buphonella* morpho-group metafemoral spring, hatchet-shaped with a short ventral lobe and with the dorsal lobe elongate and concave from below (Fig. 1b); a symmetrical aedeagus (Fig. 1a); a Type B spermatheca (Fig. 1c); and hind wing venation including the cubital crossvein as well as the remnant connection of m-cu (Fig. 1d).

Charidea Baly, *Lochmaeina* Medvedev, and

Lophallya Hincks are listed by Wilcox (1975) as synonyms of *Sangariola* Jacobson. Study of *Sangariola punctatostriata* Motschulsky from Asia revealed: a new spring group, the *Sangariola* morpho-group, with a slight recurved flange at the basal angle of the ventral lobe, a tapered base of the dorsal lobe and a laterally extended edge along the length of the dorsal lobe (Fig. 2b); a Type A spermatheca with a basally bent capsule (Fig. 2c); a symmetrical aedeagus (Fig. 2a); and hind wing venation with no apparent crossveins (or greatly reduced) and a reduction of the base of Cu1a (Fig. 2d).

Wilcox (1975) pointed out that *Luperodes antillarum* Blake and *L. semiflavus* Fall were synonyms of species in the alticine genera *Lysathia* Bechyné and *Luperaltica* Croich, respectively. For discussion on the spring and genitalia of these two genera see Furth (1985).

Mandarella Duvivier was examined using *M. nagpurensis* Duvivier which revealed: a new spring *Mandarella* morpho-group, simple and flattened with only a slight curvature (anteriorly) of both the dorsal and ventral lobes (Fig. 3b); a Type B spermatheca with the apex of the ductus attached to the side of the capsule base (Fig. 3c); a symmetrical aedeagus (Fig. 3a); hind wing venation with a strongly developed cula-culb crossvein and distinct evidence of an m-cu crossvein (Fig. 3d).

Micrantipha Blackburn contains: no metafemoral spring; a Type B spermatheca (Reid, 1992); and a symmetrical aedeagus (Reid, 1992). The hind wing venation is somewhat difficult to interpret because the greatly reduced body size affects the venation.

The authors agree with Wilcox (1975) that the original description and illustrations of *Neoclietena* Abdullah and Qureshi (1968) indicate a taxon similar to *Altica*, including swollen metafemora. We have not examined this genus, the only known specimens (types) are deposited at the University of Karachi, Pakistan.

Peltobothrus Enderlein (Tierra del Fuego, Argentina) was also not examined for the present study although Wilcox (1975) transferred this genus to the Alticinae based on the presence of a spring and indicated that it is closely related to *Caeporis* Chevrolat.

The present studies of *Philocalis pulchra* Boisduval from New Guinea illustrate that *Philocalis* Dejean is indeed a galerucine with: no metafemoral spring; a Type B spermatheca with an invaginated apex of the ductus (Fig. 4b); a symmetrical aedeagus (Fig. 4a); and hind wing venation displaying a strong cula-culb crossvein and a distinct strong m-cu crossvein (Fig. 4c).

Phyllotrupes Hope is now considered a synonym of *Platiprosopus* Chevrolat (Seeno and Wilcox, 1982). The present study of *P. acutangula* (Chevrolat) from South America illustrates that this genus has: a *Phyllotrreta* morpho-group metafemoral spring (Fig. 5b); a Type A spermatheca with a long ductus and a large gland (Fig. 5c); a symmetrical

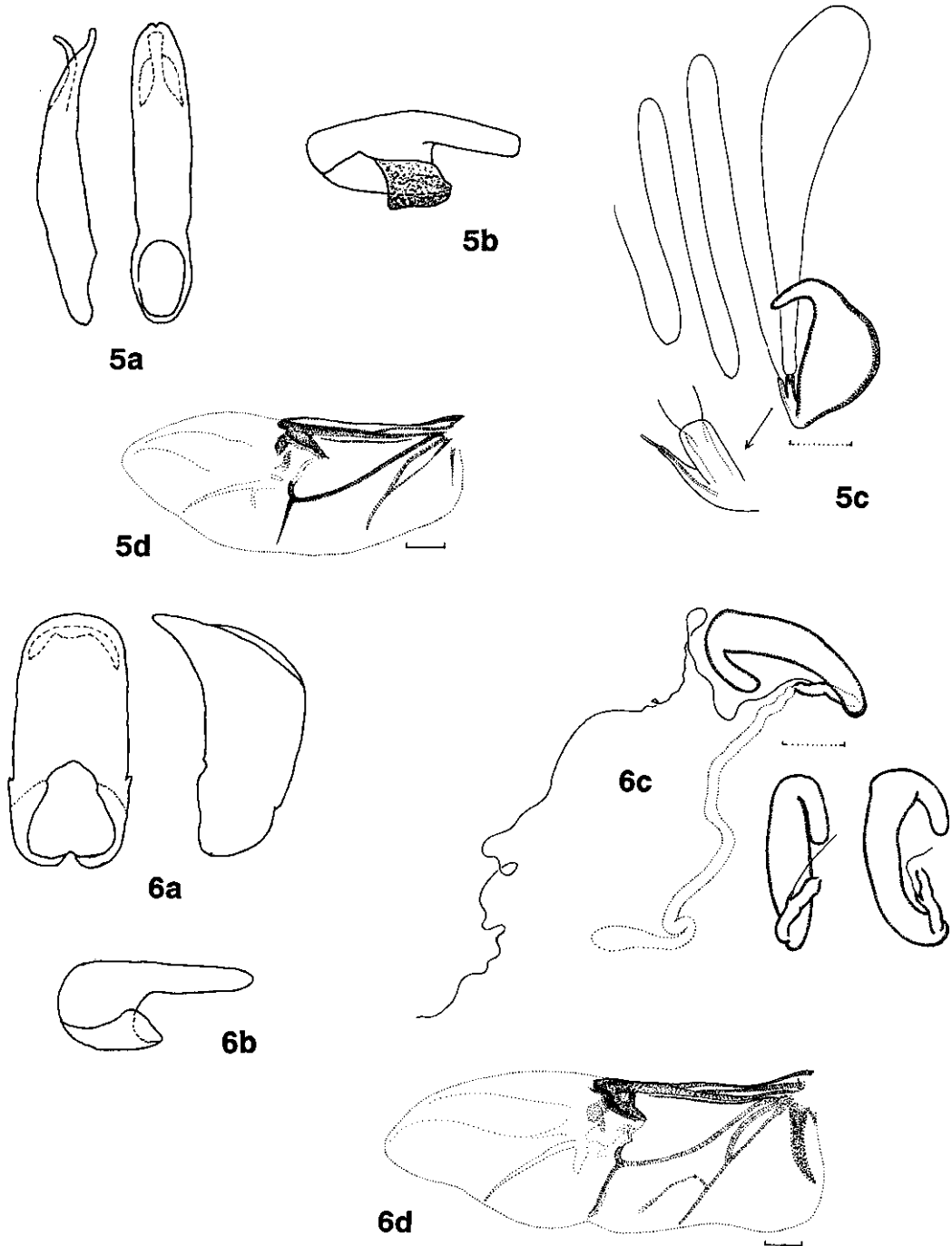


Figure 5. *Platiprosopus acutangula* a) Aedeagus lateral and ventral views (Laed = 2.5mm). b) Metafemoral Spring (Lspr = 0.88mm). c) Spermatheca. d) Hind Wing.

Figure 6. *Procalus mutans* a) Aedeagus lateral and ventral views (Laed = 2.0mm). b) Metafemoral Spring (Lspr = 0.81mm). c) Spermatheca. d) Hind Wing.

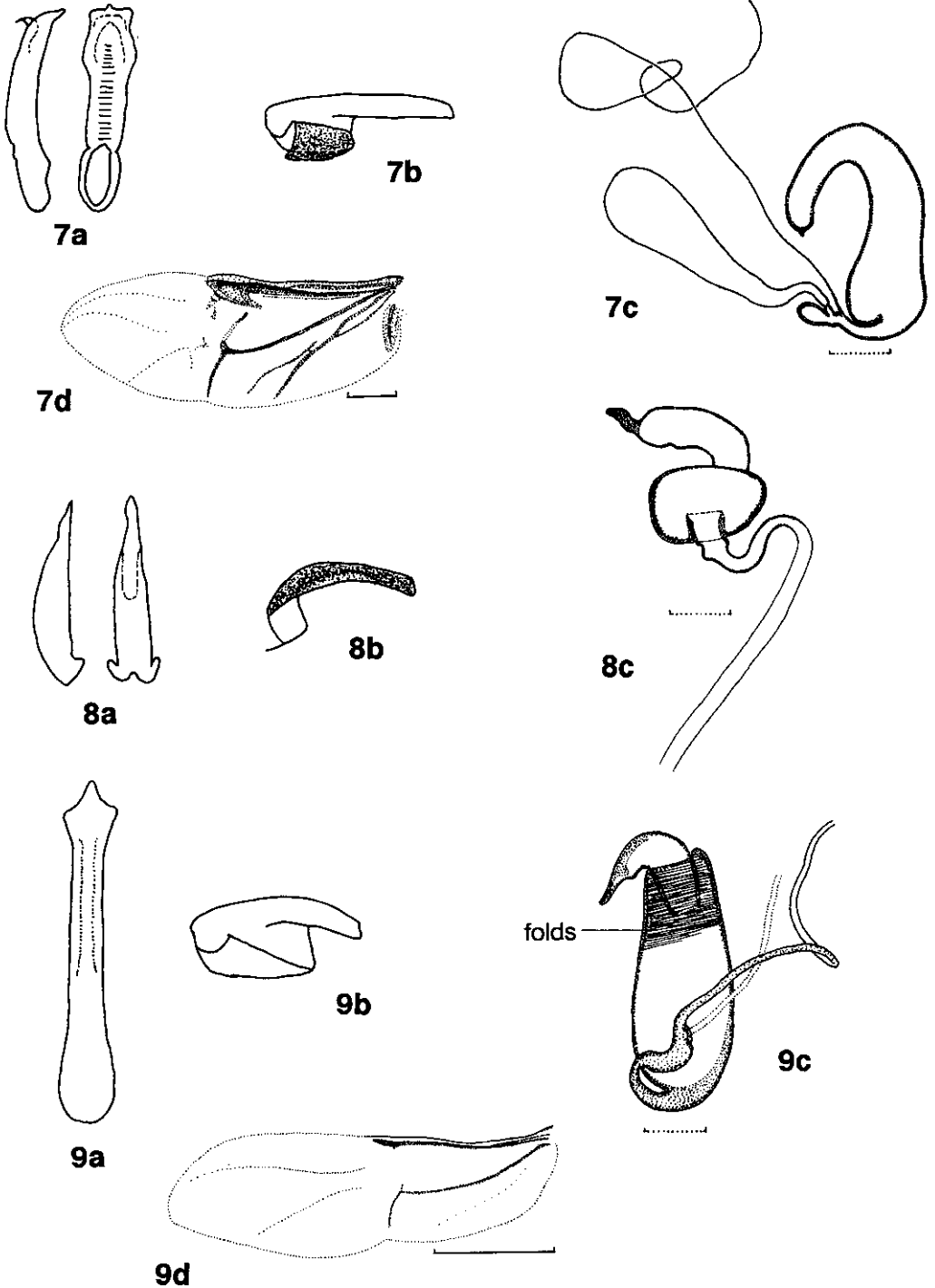


Figure 7. *Scelidopsis rufofemorata* a) Aedeagus lateral and ventral views (Laed = 1.65mm). b) Metafemoral Spring (Lspr = 0.61mm). c) Spermatheca. d) Hind Wing.

Figure 8. *Sjoestedtinia montivaga* a) Aedeagus lateral and ventral views (Laed = 0.98mm). b) Metafemoral Spring (Lspr = 0.30mm). c) Spermatheca.

Figure 9. *Terpnochlorus perrieri* a) Aedeagus ventral view (Laed = 1.1mm). b) Metafemoral Spring (Lspr = 0.35mm). c) Spermatheca (partial surface folds indicated). d) Hind Wing.

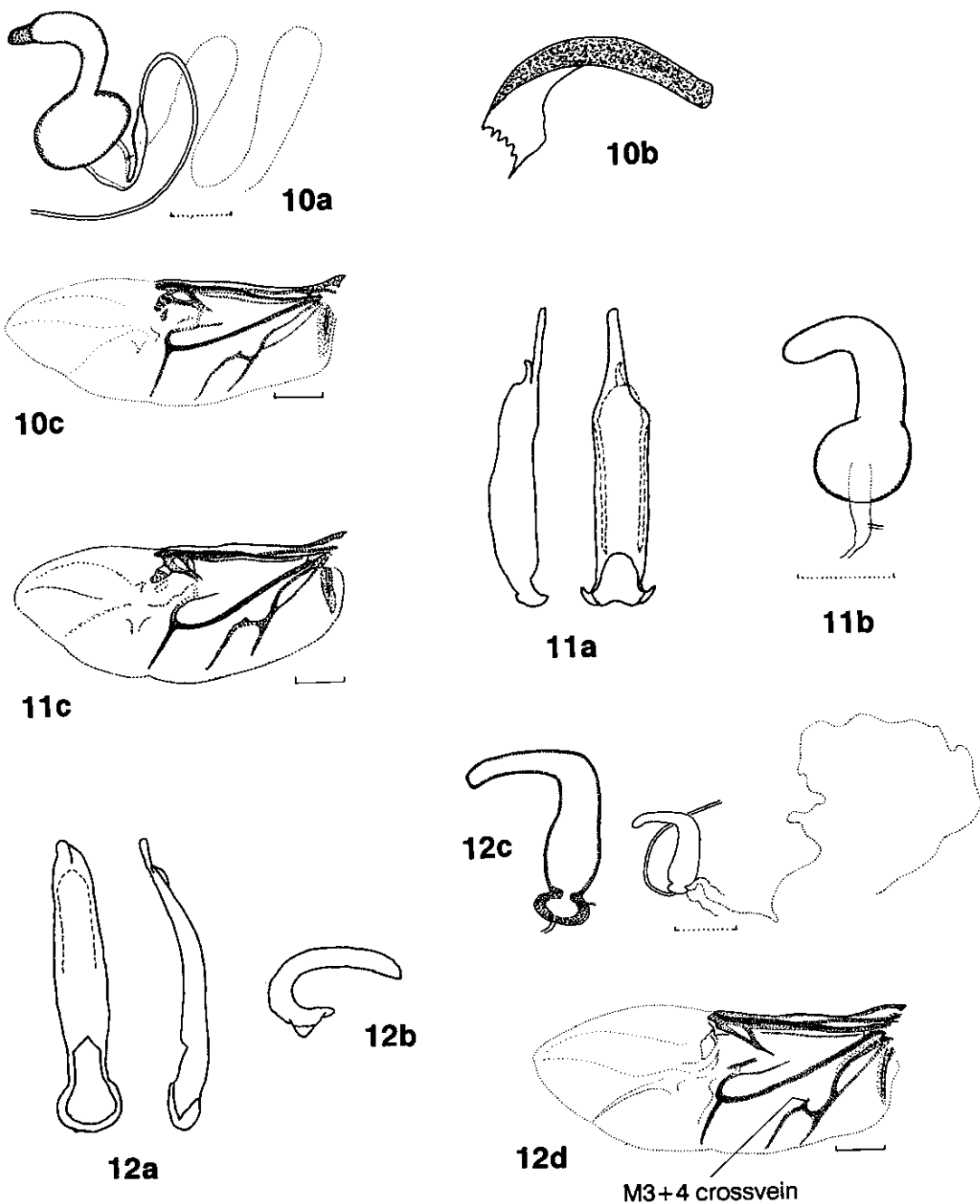


Figure 10. *Buphonella murina* a) Spermatheca (Scale Bar = 0.1mm). b) Metafemoral Spring (Lspr = 0.55mm). c) Hind Wing.

Figure 11. *Gastrida abdominalis* a) Aedeagus lateral and ventral views (Laed = 2.3mm). b) Spermatheca. c) Hind Wing.

Figure 12. *Chaloenosoma metallica* a) Aedeagus lateral and ventral views (Laed = 2.97mm). b) Metafemoral Spring (Lspr = 0.96mm). *Chaloenosoma* sp.: c) Spermatheca. d) Hind Wing.

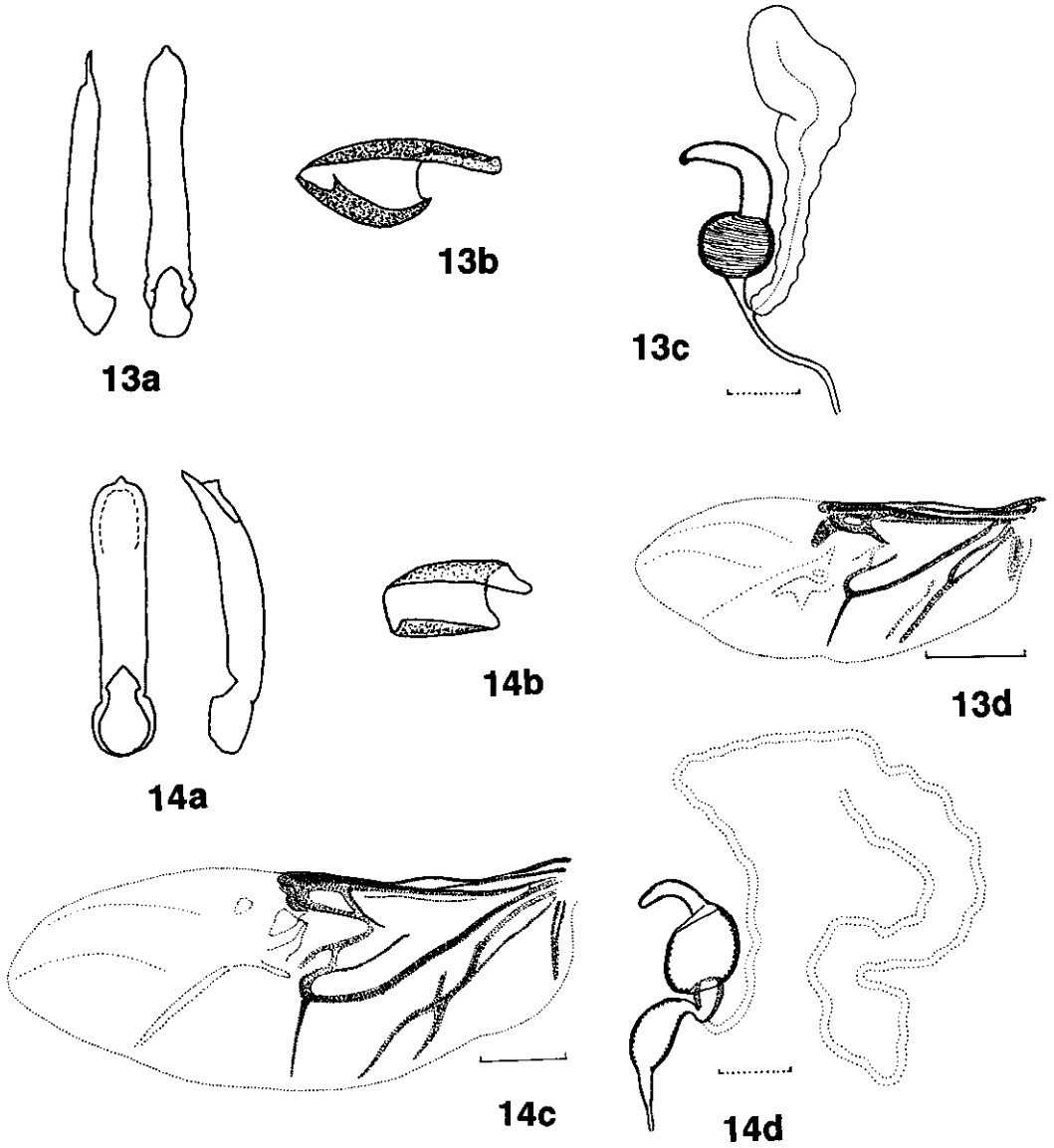
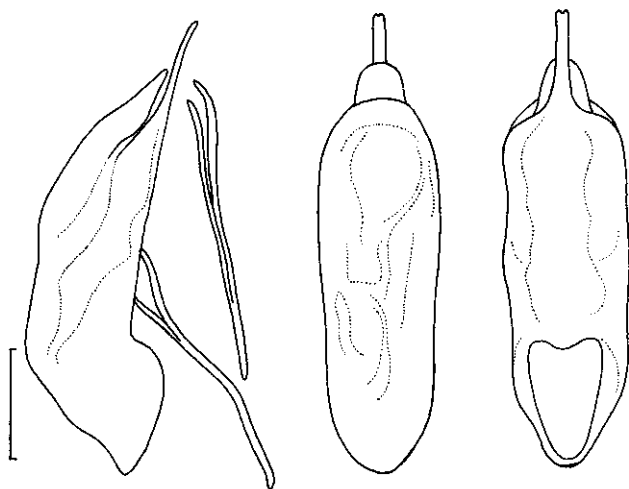
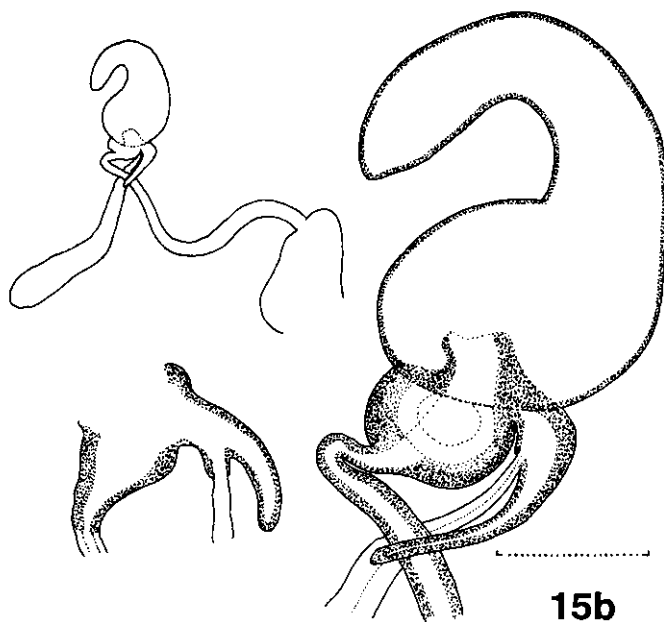


Figure 13. *Luperomorpha birmanica* a) Aedeagus lateral and ventral views (Laed = 1.35mm). b) Metafemoral Spring (Lspr = 0.55mm). c) Spermatheca. d) Hind Wing.

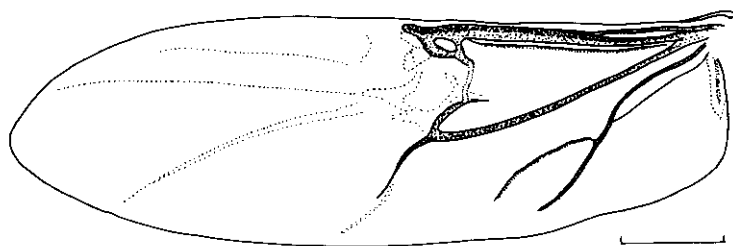
Figure 14. *Nonarthra cyaneum*: a) Aedeagus lateral and ventral views (Laed = 1.05mm). b) Metafemoral Spring (Lspr = 0.60mm). *Nonarthra bifasciatum*: c) Spermatheca. d) Hind Wing.



15a



15b



15c

Figure 15. *Microdonacia pilosa* a) Aedeagus lateral, dorsal and ventral views. b) Spermatheca. c) Hind Wing.

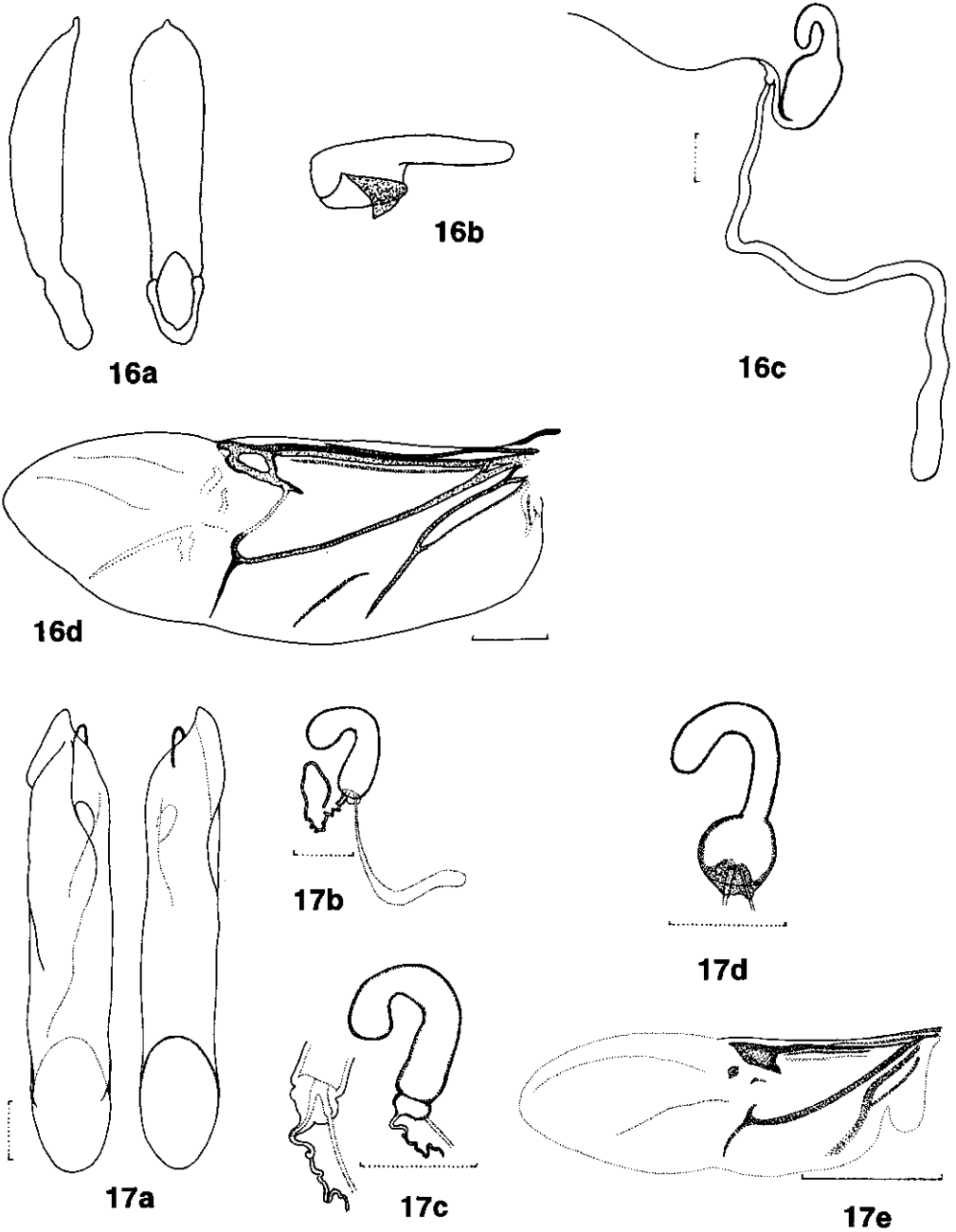


Figure 16. *Phygasia flavipennis* a) Aedeagus lateral and ventral views (Laed = 2.3mm). b) Metafemoral Spring (Lspr = 0.65mm). c) Spermatheca. d) Hind Wing.

Figure 17. *Orthalica copalina*: a) Aedeagus dorsal and ventral views. b) Spermatheca. c) *O. melina*: Spermatheca. d) *O. recticollis*: Spermatheca. e) *O. copalina*: Hind Wing.

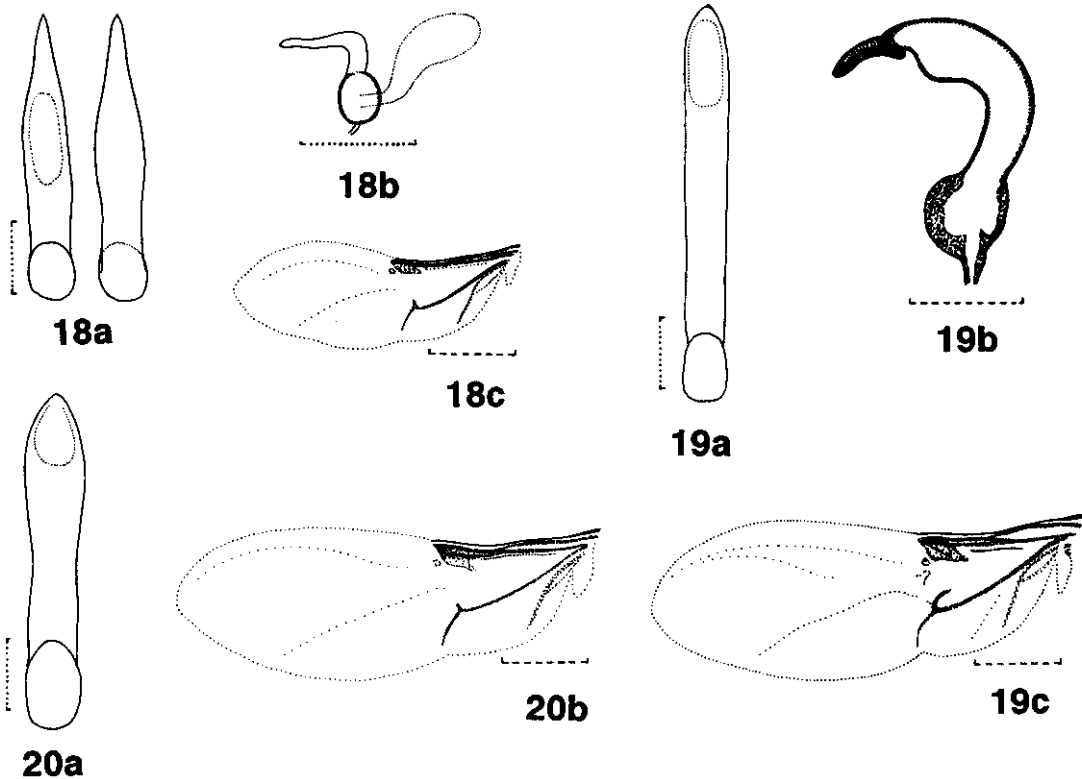


Figure 18. *Livolia carolina*: a) Aedeagus ventral (left) and dorsal views. b) Spermatheca (dashed scale bar = 0.5 mm). c) Hind Wing.

Figure 19. *Micrepitrix picea*: a) Aedeagus ventral view. b) *M. laboissièrei* Spermatheca. c) Hind Wing.

Figure 20. *Micrepitrix serraticollis*: a) Aedeagus ventral view. b) Hind Wing.

aedeagus (Fig. 5a); and hind wing venation with no crossveins and with the complete loss of *cu1a* (Fig. 5d).

The present study of *Procalus* Clark, using *P. mutans* (Blanchard) from Chile, demonstrates that: the spring is clearly from the *Blepharida* morpho-group (Fig. 6b); the spermatheca is Type A with both long ductus and gland (Fig. 6c); the aedeagus is short, broad and symmetrical (Fig. 6a); and the hind wing venation shows evidence of only the *cu1a-cu1b* crossvein (Fig. 6d).

The present study of *Scelidopsis* Jacoby is based on *S. rufofemorata* Jacoby which reveals: an *Altica* morpho-group spring (Fig. 7b); a Type A spermatheca with a long ductus and gland (Fig. 7c); a symmetrical aedeagus with median horizontal ribbing on its venter (Fig. 7a); and hind wing venation with a cubital crossvein and a spur (remnant crossvein) toward the median vein (*m-cu*) (Fig. 7d).

Wilcox (1975) lists *Serraticollis* B. White as an *Alticinae* following its synonymy with *Leptotrichalica* Heikertinger. The latter genus was subsequently synonymized under *Orthaltica* Crotch (Scherer, 1974) (see Suzuki and Furth, 1992 and the discussion of *Orthaltica* below).

Wilcox (1975) follows Laboissière (1932) by treating *Sjoestedinia* Weise as an *Alticinae*. Exami-

nation of *S. montivaga* Weise from Mt. Kilimanjaro (Tanzania) reveals: a *Buphonella* spring morpho-group, hatchet-shaped with the dorsal lobe concave from underneath (Fig. 8b); a Type B spermatheca with the apex of the ductus invaginated into the base of the capsule, thick capsule walls, and an appendix (Fig. 8c); a slightly asymmetrical aedeagus (Fig. 8a); and an atrophied hind wing, thus apterous, under the distinctly shortened clytra.

The current study of *Terpnochlorus* Fairmaire examined *T. perrieri* Fairmaire which possesses: a *Blepharida* morpho-group spring (Fig. 9b); a Type A spermatheca with some unusual apical characteristics and horizontal surface folds (Fig. 9c); a symmetrical aedeagus (Fig. 9a); and the hind wing venation so greatly reduced that it is of little use in evaluating its affinity (Fig. 9d).

Buphonella Jacoby was studied using *B. murina* (Gerstaecker) from South Africa which disclosed: a new *Buphonella* spring morpho-group which is simple with little differentiation into a ventral lobe and with the dorsal lobe concave from beneath (Fig. 10b); a Type B spermatheca (Fig. 10a); and the hind wing venation with a *cu1a-cu1b* crossvein as well as an apparent *m-cu* crossvein remnant (Fig. 10c). No males were available for study of the aedeagus.

Examination of *Gastrida* Chapuis through *G.*

abdominalis Chapuis from East Africa revealed: no metafemoral spring (Furth, 1989 mistakenly reported the presence of a simplified spring in *Gastrida*); a Type B spermatheca, its ductus with an apex invaginated into the capsular base (Fig. 11b); an asymmetrical aedeagus (Fig. 11a); and hind wing venation with distinct evidence of the cula-culb and the remnant of m-cu crossveins (Fig. 11c).

Chaloenosoma Jacoby, represented by *C. metallica* Jacoby from India, has a new *Chaloenosoma* spring morpho-group (see also Furth, 1989) which is somewhat hook-shaped with a kind of flange extending ventrally from the ventral lobe (Fig. 12b). This species also has: a Type B spermatheca with an unusual base which apparently consists of a fusion of the base of the capsule and the ductus (Fig. 12c); an asymmetrical aedeagus (Fig. 12a); and hind wing venation with strong cula-culb and a remnant of m-cu crossveins (Fig. 12d).

Luperomorpha Weise was studied using *L. birmanica* Jacoby from Taiwan and revealed: a new *Luperomorpha* spring morpho-group with the base of the dorsal and ventral lobes forming an acute angle (Fig. 13b); a Type B spermatheca with thick capsular walls and distinct horizontal folds on its base and apparently with the apex of the ductus invaginated into the base of the capsule (Fig. 13c); a symmetrical aedeagus (Fig. 13a); and hind wing venation without any indications/remnants of crossveins and with cula somewhat atrophied (not connected to culb) (Fig. 13d).

Nonarthra Baly represented by *N. cyaneum* Baly from Japan demonstrated a new *Nonarthra* spring morpho-group (Fig. 14b) and a symmetrical aedeagus (Fig. 14a). The study of *N. bifasciatum* Jacoby from Philippines illustrated a Type B spermatheca with an apparently greatly modified ductus whose apex is invaginated into the base of the capsule (Fig. 14c) and hind wing venation with no apparent cula-culb crossvein but with a remnant m-cu connection (Fig. 14d).

Examination of *Microdonacia* Blackburn using *M. pilosa* Reid revealed: no metafemoral spring; a Type B spermatheca with a highly modified apex to the ductus which is invaginated into the capsule's base and an unusual appendix to the ductus at its base (Fig. 15b); a symmetrical aedeagus (but see Reid, 1992 - most species have asymmetrical aedeagus (Fig. 15a); and hind wing venation without any apparent crossveins (Fig. 15c).

Phygasia Dejean, represented by *P. fulvipennis* Baly from Japan, has: an *Altica* morpho-group spring (Fig. 16b); a Type A spermatheca (Fig. 16c); a symmetrical aedeagus (Fig. 16a); and hind wing venation with no cubital or median crossveins and with only a partial remnant of Cula (Fig. 16d).

Orthaltica Crotch (*sensu stricto*) contains three Nearctic species (*copalina* (Fabricius), *melina* Horn and *recticollis* LeConte) all of which were examined for this study. *Orthaltica* species have no metafemoral spring. They have a Type B spermatheca with the apex of the ductus strongly

invaginated into the base of the capsule (Figs. 17b, 17c, 17d); a strongly asymmetrical aedeagus (Fig. 17a); and reduced hind wing venation, including the presence of an anal lobe, with no cubital or m-cu crossveins and no apparent Cula (Fig. 17e).

Livolia Jacoby, represented here by *L. carolina* Chûjô from Palau, has no metafemoral spring. It has an unusual Type B spermatheca with the spermathecal gland attached laterally in the middle of the base of the capsule (Fig. 18b), a symmetrical aedeagus (Fig. 17a), and reduced hind wing venation (probably at least in part caused by a small body size) with no cubital or median crossveins, no cula, but with a small anal lobe (Fig. 18c).

Microreptirix laboissierei Chen was studied here using *M. laboissierei* Chen from Taiwan and *M. picea* Samuelson from New Guinea. This genus also has no metafemoral spring, but has a Type B spermatheca with a thick walled base of the capsule (Fig. 19b). The aedeagus is symmetrical (Fig. 19a, 20a) and the hind wing venation is reduced with no cubital or m-cu crossveins, no apparent Cula, and an anal lobe (Fig. 19c, 20c).

DISCUSSION

This study concentrates on 19 genera of Chrysomelidae which, for a variety of reasons, are considered "problematic" or "transitional" in the interpretation of the relationship between the Galerucinae and the Alticinae. It has long been recognized that these two subfamilies are closely related. Chapuis (1875) lumped them together as "Galerucides" apparently based on external adult characters. More recently Lawrence and Britton (1991) lumped them apparently based on larval characters. However, these and other studies have not comprehensively studied either subfamily, partially because of their enormous diversity even at the generic level.

The Galerucinae do have an accepted higher classification system (tribal) (cf. Seeno and Wilcox, 1982). On the other hand the Alticinae do not have an accepted system of higher classification, even though there were some very superficial groupings ("catalogue phylogenies") proposed for all or parts of this subfamily, e.g. Chapuis (1875), Horn (1889), Leng (1920), Bechyné (1968), Bechyné and Bechyné (1973, 1975), Seeno and Wilcox (1982) (unintentional higher grouping system).

Essentially the sole reliable character (used in keys, etc.) to distinguish the Galerucinae from the Alticinae has been the swollen metafemora, with its internal spring mechanism. However, this basis has created many problems when considering genera/species of Galerucinae with somewhat swollen hind femora or Alticinae with slender hind femora, especially without confirmation of the presence or absence of the metafemoral spring. Most of the genera considered in this study have been confused as to their subfamily placement for this reason. We assume that there are other genera currently placed in

the Galerucinae that are actually in the Alticinae (e.g. *Stenoluperus* Ogloblin, cf. Medvedev, 1992) and, perhaps, vice versa.

The current study is actually the beginning of a much larger, long-term project to survey a large percentage (a majority) of the genera of Alticinae with the eventual goal of composing some type of higher classification system for the Alticinae. The procedure for this involves detailed morphological examination of four independent character systems in the adults (metafemoral spring, female spermatheca, male aedeagus, and hind wing venation) and the correlation of these characters. Because of the necessity to examine a large number of genera, we feel that these four independent character systems are adequate to achieve our goals. In addition, we plan to survey the major groupings of Galerucinae using these same character systems.

Based on our current and previous research of the metafemoral spring, we believe that the Alticinae represent a monophyletic lineage distinct from the Galerucinae but certainly closely related (i.e. sister group). However, correlation of other independent morphological characters, even if only by affinity towards Galerucinae or Alticinae, is useful information. Proper phylogenetic studies within and between these two large chrysomelid subfamilies are still premature because only a small percentage of the genera have been amply studied. In the current study we begin to study this problem; however, first we must make a basic survey of these four character systems in a large percentage of the Alticinae before we can reliably even consider formulating a higher classification (tribal) system in this subfamily.

The metafemoral spring serves as the primary character for separating Galerucinae from Alticinae (Furth, 1985, 1988, 1989), but it also serves as a generic level character (Furth, 1980). Like other such characters it presumably can be used to evaluate relationships between genera or groups of genera; however, final analysis of the extent of its application can only be made when it has been studied in a large number of alticine genera. By naming each spring morpho-group after the representative genus first found to have that type, we intend no implication of relationship.

The recent discovery of the independent evolution of the metafemoral spring in four families of Coleoptera (Furth and Suzuki, 1992) is actually consistent with the application of the metafemoral spring in the current study. Like in the Alticinae, the spring of the other beetle families has a constant morphology within a genus but differs between genera; however, of special note is the fact that in all of these other families the spring morphology is simplified/reduced relative to most Alticinae. We interpret this simplified morphology to be less developed (see also Furth and Suzuki, 1990b). In the Alticinae, especially among the genera studied here, several spring morpho-groups have a simplified or less developed form. This simplification could be interpreted as being more primitive; however, be-

cause the spring morphology of too few genera has been examined, it is too early to make such judgments.

In fact four of the six new spring morpho-groups established here have a simplified morphology and almost all of the genera have slender hind femora. These two levels of development (spring and metafemur) indicate less developed tibial extensor musculature (see Furth and Suzuki, 1990b) which probably also means less jumping ability. However, there is no good correlated observational data available for most of these genera. Several (6) of the "problematic" genera studied here were found to lack a metafemoral spring and, therefore, by our definition are not considered Alticinae; these presumably also cannot jump well.

In the present study the metafemoral spring is used in correlation with the other character systems in order to show affinity towards Galerucinae or Alticinae. Other than the presence or absence of the metafemoral spring, probably the next most informative character system for determining subfamily affinity is the female spermatheca. As explained above in the Results, there are basically two types (A and B) which are more typically Alticinae or Galerucinae, respectively. The venation of the hind wing can also be a quite informative character system with the reduction of venation, i.e. loss of *cu1a-cu1b* crossvein, loss of *m-cu* crossvein remnant, and loss or reduction of *Cu1a* being more typical of Alticinae. In a few cases (e.g. *Livolia*, *Micrepitrix*, and *Micranthpha*) the tiny body size causes the wing venation to be so greatly reduced as to obscure any informative interpretation of the venation.

The male aedeagus has proven to be informative only relative to whether it is symmetrical (Alticinae affinity) or asymmetrical (Galerucinae affinity) and this has been used in combination with other independent characters as evidence for placing *Orthaltica* Crotch in the Galerucinae (Furth, 1985, Suzuki and Furth, 1992). Other characters of the aedeagus (e.g. shape of apex or base) have not yet proven useful for associating genera with either subfamily; however, future study of other aedeagal characters such as the internal sac shape and vestiture may prove to have generic or subfamilial value.

Many of the results and conclusions correlating these four character systems are based on the authors' experience and study of these character systems in other genera of Galerucinae and Alticinae. Based on the correlative results of the above-mentioned four character systems, we indicate below our opinion of the subfamily affinities in each of the 19 "problematic" genera studied here.

Chaloenus is currently considered to be a Galerucinae (Seeno and Wilcox, 1982); however, because of the presence of a metafemoral spring (*Buphonella* morpho-group) we consider this genus to be a member of the Alticinae. Nevertheless, the spermatheca and hind wing venation do show distinct Galerucinae tendencies.

Several synonyms of *Sangariola* were placed in the Galerucinae because of general body form and slender hind legs. Although Wilcox (1975) did not state that any of the *Sangariola* synonyms have a spring, there is one. The *Sangariola* morpho-group metafemoral spring is in fact quite elongate, but it is not reduced/simplified as in some others discussed in this paper. Actually *Sangariola* was recognized as an alticine by Jacobson (1922), as a problematic galerucine by Laboissière (1932), but subsequently described again as a galerucine (Hincks, 1949, Medvedev, 1956). The Type A spermatheca of *Sangariola* is quite typical of Alticinae as is the hind wing venation; therefore, all four character systems indicate a strong Alticine correlation.

Mandarella was transferred to the Alticinae by Wilcox (1975) based on the presence of a spring in the hind femora. However, Seeno and Wilcox (1982) considered this genus as *incertae sedis* in the Alticinae. Medvedev (1992) also transferred this genus from Galerucinae to Alticinae claiming that it was near to *Luperomorpha*. Although *Mandarella* displays some galerucine tendencies in the spermatheca and hind wing venation, the presence of a symmetrical aedeagus and a metafemoral spring (a new *Mandarella* morpho-group) certainly make it an alticine.

Micrantipha Blackburn, with one species *M. paradoxa* Blackburn, was originally placed in the Galerucinae but transferred by Wilcox (1975) to the Alticinae despite its lack of a metafemoral spring. Wilcox stated only that "most other characters indicate its closer affinity to Alticinae". Seeno and Wilcox (1982) placed this genus in Alticinae near *Orthaltica* and Reid (1990) synonymized *Micrantipha* with *Orthaltica* as a subgenus. Reid (1990) also synonymized *Livolia* Jacoby under *Micrantipha* and *M. paradoxa* as a synonym of *Crepidodera vestita* Baly; therefore, this taxon became *Orthaltica vestita* (Baly). However, consistent with our previous research on this group (Furth, 1985, 1988, Furth and Suzuki, 1990a, 1990b, Suzuki and Furth, 1992) as well as the present study, we consider *Micrantipha* to be a valid and distinct galerucine genus from *Orthaltica* based on the absence of a metafemoral spring and the presence of a Type B spermatheca (Reid, 1992). Reid (1992) has recently reversed his previous (1990) synonymy and now believes *Micrantipha* should be restored to generic status.

Wilcox (1971) included *Philocalis* in the Galerucinae (Galerucini); however, Wilcox (1975) follows Heikertinger and Csiki (1939) by placing this genus in the Alticinae, but without offering any particular justification. Based on the absence of a metafemoral spring, the strongly galerucine hind wing venation, especially m-cu crossvein, and the galerucine-like spermatheca, the authors transfer *Philocalis* back to the Galerucinae.

Wilcox (1975) states only that *Phyllotrupes* Hope has been used by Bechyne for Neotropical Alticinae; now considered a synonym of *Platiprosopus*

Chevolat (Seeno and Wilcox, 1982). As indicated in the Results and figures, all four character systems correlate well with the Alticinae.

Procalus Clark was placed in the Galerucinae by Weise (1924), into the Alticinae by Laboissière (1932), but it was removed from Heikertinger and Csiki's 1939 catalogue of the Alticinae. Wilcox (1975) notes the presence of a metafemoral spring and considers *Procalus* to be an alticine. Basically all of the four character systems considered here correlate with the Alticinae although the wing venation is not completely typical of Alticinae. Other morphological affinities of this genus have been discussed elsewhere (Furth, 1992).

Based on the discovery of a metafemoral spring in several species of *Scelidopsis* Jacoby, Wilcox (1975) transferred it to the Alticinae near *Lupraea* Jacoby. Although externally galerucine-like, including slender hind legs, the characters examined in this study indicate its affinity to the Alticinae, except the wing venation.

Scherer (1973, 1982, 1988) in discussing the origins and zoogeography of Alticinae mentions "two wingless [also with short elytra], very closely related genera at elevations above 3000m" and that it is "almost impossible to separate *Forsterita* from *Sjoestedtinia* on morphological characters"; *Forsterita* Bechyne is found in the high South American Andes and *Sjoestedtinia* Weise is found in the high mountains of East Africa. Scherer asks whether these are relicts from the time when South America separated from Africa or the result of ecological convergence. Scherer (1973) seems to imply a close relationship and also that these two genera are primitive. Furth (1989) demonstrated that the metafemoral spring of *Forsterita* is in the *Altica* morpho-group. In the present paper we clearly show that *Sjoestedtinia* has a reduced type (*Buphonella* morpho-group) metafemoral spring (Fig. 8b). This is clear morphological evidence that *Forsterita* and *Sjoestedtinia* are in fact quite different and that the wingless, short-elytra, and other characters are only convergent; these characters are found in other insect groups isolated geographically, especially on mountain tops. Besides *Buphonella*, the genus *Chaloenus* also has the type of simplified metafemoral spring found in *Sjoestedtinia*. There is indication of a galerucine tendency through a slight asymmetry of the aedeagus (Fig. 8a) together with the Type B spermatheca.

Scherer (1980, 1988) also wonders if the unusual disjunct distribution of species of *Terpnochlorus* (Central Africa, Madagascar, Venezuela and Mexico) may be a relictual Gondwanian pattern. *Terpnochlorus* was transferred by Wilcox (1975) from the Galerucinae to the Alticinae without stating his specific reasons. The spring is a typical *Blepharida* type and the spermatheca (though somewhat unusual) and aedeagus have typical Alticine characters. The hind wing has unusual, greatly reduced venation which is difficult to assign subfamily affinity.

"With considerable hesitation" Wilcox (1975) created a Galerucinae tribe Decarthrocerini for three genera from Africa (*Decarthrocera* Laboissière, *Buphonella* Jacoby, and *Gastrida* Chapuis) which he said "do not seem to be closely related nor similar in form to any other species of Galerucinae". Wilcox (1975) noted that *Buphonella* and *Gastrida* have a less developed extensor apodeme (spring). Seeno and Wilcox (1982) transferred this group of genera (tribe) to the beginning of the Alticinae. Furth (1989) and the present study show (as indicated by Wilcox, 1975) a simplified or reduced spring morphology in this new morpho-group. The spermatheca and wing venation of *Buphonella* indicate a galerucine tendency.

As indicated above, Furth (1989) mistakenly reported a spring in *Gastrida*; however, examination of several specimens in the present study distinctly showed the absence of the metafemoral spring in this genus. In addition the aedeagus is distinctly asymmetrical and the spermatheca and wing venation are galerucine-like. Therefore, all four character systems correlate well and demonstrate that *Gastrida* (unlike *Buphonella*) is a Galerucinae genus.

Furth (1989) actually first reported a new simplified spring morphology in *Chaloenosoma* even though no description or comparative studies were given. Therefore, in the present study we still consider this *Chaloenosoma* type spring as a new morpho-group which is significantly simplified or reduced. However, the asymmetrical aedeagus (in the majority of species), the strongly Type B spermatheca and wing venation all suggest a strong galerucine tendency.

Luperomorpha has been placed in the beginning of the Alticinae "catalogue phylogeny" by Heikertinger and Csiki (1939) and by Seeno and Wilcox (1982). As the genus name implies, it is galerucine in its general appearance; however, its distinctive (new morpho-group) spring, symmetrical aedeagus, and hind wing venation are indicative of typical Alticinae. Only its spermatheca with distinctive horizontal folds on the thick-walled capsule base and with apparent invagination of the apex of the ductus into the base of the capsule show galerucine tendencies. *Luperomorpha* contains over 30 species almost all of which are distributed from China and Japan into SE Asia and India (Heikertinger and Csiki, 1939, Gressitt and Kimoto, 1963, Scherer, 1969) with the type species from E. Siberia and with apparently some extension to Australia and the Solomon Islands (Samuelson, 1973). A number of species were originally described as *Phyllotreta* Chevrolat and as *Aphthona* Chevrolat. In fact they are superficially quite similar to *Phyllotreta*, including some with light and dark longitudinal elytral pattern. This genus is in need of careful revision to determine the true extent of its components, distribution and relationships.

Nonarthra has been considered as different from most alticine genera because of its 9 segmented

antennae, its pollen feeding adult biology (Samuelson, 1989) and indications that its larvae feed on mosses (Takenaka, 1971). It has usually been placed at the end of the Alticinae in various "catalogue phylogenies" (Seeno and Wilcox, 1982). Although its new and well-developed metafemoral spring type and symmetrical aedeagus fix association with the Alticinae, its spermathecal morphology and hind wing venation show Galerucinae tendencies.

Microdonacia has recently been studied by Reid (1992) who described as new 7 of the 10 species and places this genus as *incertae sedis* near *Orthaltica* in the Galerucinae (*sensu lato*) (see discussion below). *Microdonacia* was originally placed in Donaciinae by Blackburn (1893), into Eumolpinae by Monrós (1958), then into Alticinae by Jolivet (1968) and also considered as Alticinae *incertae sedis* (Seeno and Wilcox, 1982). The current study together with Reid's (1992) revision indicates through character correlation that this genus belongs in the Galerucinae (*sensu stricto*) because of its lack of a metafemoral spring, unusual spermathecal morphology, majority of species with an asymmetrical aedeagus (unlike Fig. 15a, see Reid, 1992 figs. 48-55) and hind wing venation which is not unusual for Galerucinae. The exact placement of *Microdonacia* within the Galerucinae is not within the scope of this study. However, such placement is premature because relatively few genera or even tribes within the Galerucinae have been studied in adequate detail.

Phygasia was chosen because of its galerucine body form and relatively slender hind femora. However, all four character systems studied are very typical Alticinae.

The last three genera *Orthaltica*, *Livolia*, and *Micreptirix* have been the subject of some recent controversy relative to their synonymy and subfamily placement (Scherer, 1974; Furth, 1985, Reid, 1980, Furth and Suzuki, 1992, Reid, 1992), see also the above discussion of *Micrantipha*. None of these genera possess a metafemoral spring and all have greatly reduced venation apparently due to their small body size. *Orthaltica* (*sensu stricto*) includes three Nearctic species with asymmetrical aedeagus and Type B spermatheca, characters which are common in Galerucinae. *Livolia* which contains species from Africa, W. Australia, Sri Lanka, SE and S. Asia, Borneo and the Caroline Islands was synonymized with *Orthaltica* by Scherer (1974). Scherer (1959, 1971, 1982b) noted the close similarity/relationship of *Livolia*, especially the African species, with *Djallonia* Bechyné - a typical Alticinae with obviously swollen metafemora. *Micreptirix* originally included five species from Vietnam, S. and E. China and New Guinea and was synonymized by Scherer (1971) with *Livolia*. *Livolia* was synonymized with *Micrantipha* by Reid (1990) who also claimed *Micrantipha* to be a synonym of *Orthaltica*; however, Reid (1992) has changed his 1990 opinion to consider *Micrantipha* (still including *Livolia*) as a separate valid genus again. This

complicated synonymy is explained in Suzuki and Furth (1992) who, based on several reasons, prefer not to lump all these but to keep them as separate genera.

We acknowledge the similarity of *Micrantipha*, *Livolia*, and *Micreplitrix* revealed here (see also Reid, 1992) through character correlation of symmetrical aedeagus and hind wing venation; however, spermathecal and zoogeographical differences still indicate distinctiveness. The authors have not been able to completely examine the characters of the African *Livolia* or the remaining *Micreplitrix* species. Any potential synonymy pertaining to these three genera must include a detailed study of several character systems and must consider most of the taxa involved. Based on the current research we continue to follow our opinion as stated in Suzuki and Furth (1992) that *Orthaltica*, *Micrantipha*, *Livolia* and *Micreplitrix* are all separate genera in the Galerucinae.

Reid (1992) lumps the current, more commonly accepted, system of the separate subfamilies Galerucinae and Alticinae into tribes of the Galerucinae (*sensu lato*) (about 1000 genera). This lumped version of the Galerucinae was first proposed by Chapuis (1875), with no special explanation, as part of a general list for all Coleoptera. Böving (1927) and Böving and Craighead (1931) also followed this broad view of Galerucinae based, however, on relatively few genera and species and only using larval characters. Crowson (1955) follows Jacoby (1908) stating only that "the difficulty of clearly separating the Galerucines and the Halticinae [Alticinae] has long been recognised, particularly in relation to the larvae" (presumably referring to Böving and Craighead's work). The Crowson (1967) which Reid (1992) refers to is only a reprint of Crowson (1955). As indicated by Reid (1992), Crowson later reversed his opinion of lumping Galerucinae and Alticinae (Crowson, 1981, Mann and Crowson, 1981, 1983a, 1983b). Lawrence and Britton (1991) also lump these two largest chrysomelid subfamilies, again, only mentioning the lack of larval differences and that "transitional forms occur among the adults as well".

The problem with all of the above systems is that they only mention superficial reasons for their ideas without any detailed discussion of characters or character systems. Böving (1927) mentioned twelve "tribes" of "Halticinae" based on one Australian genus and several Holarctic and Neotropical genera. Except for a few of these studied by others, it is not evident what is the source of Böving's (1927) data; he states that, because the larvae of the "Blepharidini" are "a type so distinctly different", that they "should be excluded from the Halticinae". Most authors currently recognize *Blepharida*-related genera as quite typical Alticinae. Using larval characters only Böving and Craighead (1931) examined a few (13) Nearctic genera of "Halticinae" (=Alticinae (*sensu stricto*)) and considered them as a subfamily of Galerucidae which also contained

Galerucinae (6 Nearctic genera examined) and Diabroticinae (3 Nearctic genera examined). They also stated that their "Halticinae" genera were "remotely related" and that "when better studied, the classification of the entire family Galcrucidae will unquestionably be changed".

The authors believe that without careful and relatively comprehensive study of the Alticinae and Galerucinae, it is premature to form an accurate classification of either or the relationship between them. The current study is the beginning of just such a comprehensive study even though character systems of only adults are considered. Nevertheless we find it more justified even if based on few characters, i.e. metafemoral spring and the tendencies of several others, to consider the Alticinae as distinctly separate from the Galerucinae and not to lump the two.

SUMMARY

Examination of internal and external morphological characters (including male and female reproductive organs, metafemoral spring and hind wing venation), particularly of "problematic" or "transitional" genera between the Alticinae and Galerucinae, demonstrated that these genera possess correlated groups of characters revealing both how unusual they are as well as the closeness of these two chrysomelid subfamilies. Several new metafemoral spring morpho-groups were discovered in alticine genera. This study provides the basis for analyzing these characters in many genera of Alticinae and Galerucinae in order to attempt to devise a higher classification of them, especially for the Alticinae.

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