

## 17. The jumping apparatus of flea beetles (Alticinae) – The metafemoral spring

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### 1. INTRODUCTION

Flea Beetles (Alticinae) is the largest subfamily of the Chrysomelidae with approximately 560 genera and 8000 species described. The scientific name of the type genus, *Altica* Fabricius 1775, is derived from the Greek 'haltikos' which means good at jumping. Although the Latinization of the original Greek name by Fabricius (1775) may not be entirely correct, following the rules of the International Code of Zoological Nomenclature the correct spelling for the type genus is *Altica* not *Haltica* (thus, Alticinae not Halticinae) (see detailed discussion in Furth 1981). The common name, Flea Beetle, is also basically derived (in several languages) from their ability to jump in an analagous fashion to the true fleas (Siphonaptera). Flea Beetles include, with the possible exception of some species of fleas (Rothschild et al 1975), the best jumpers among all insects and, indeed, among all living creatures. Most Alticinae use this jumping ability voluntarily in a very effective manner to avoid potential predators or entomologists. Lindroth (1971) observed that birds are not able to catch Flea Beetles that are on foliage because of the beetle's effective escape by jumping. Jumping also serves as an efficient method of locomotion, especially for flightless populations. Flea Beetles can leap long distances relative to their body size (length). For example, a 7 mm long *Blepharida sacra* (Weise) has been measured to jump up to 70 cm or about 100 times its body length! Also five European genera were tested in more detail and found to be excellent jumpers, at least one *Longitarsus* species jumped considerably more than 100 times its body length (M. Schmitt, in litt.). After leaping Flea Beetles might take off in flight, fall to the ground (often cryptically) and feign death, or alight in a normal way on a plant, possibly a foodplant, ready to feed, mate, or jump again.

Alticinae are easily distinguished from other Chrysomelidae, and most other Coleoptera, by greatly enlarged hind femora. Maulik (1929a) first discovered that the swollen Flea Beetle metafemora contained a special internal structure which he referred to as a 'chitinized endoskeletal tendon'. Maulik

also observed that this structure had a constant orientation and form with only slight variations. Maulik studied 12 genera by clearing the hind femora (he did not excise this structure from the metafemoral capsule); thus, morphological details were probably not apparent. Maulik speculated that this chitinized tendon acquired its form by constant use in a particular way. He believed that any chrysomelid possessing this 'tendon' was an alticine and that any Flea Beetle that could not jump demonstrated degeneration of this structure. This chitinized tendon has since often been referred to as Maulik's Organ (Scherer 1971), but also sometimes called Costa Lima's Organ (Barth 1954), extensor apodeme (Wilcox 1965), or metafemoral apodeme (Furth 1980). Because this structure is not an apodeme in the strict sense (see discussion below), and it is clearly the functional structure of the Flea Beetle jumping ability, it is currently referred to as the metafemoral spring (Furth 1982, 1983, 1985). The Sagrinae also have greatly swollen hind femora but are much larger than alticines, do not jump, and have no homologue to the metafemoral spring (Paulian 1942). The metafemoral spring has been referred to by previous workers as the distinguishing character between Alticinae and the nearest subfamily, the Galerucinae (Heikertinger 1948, Mohr 1960, Wiesner 1970, Scherer 1971). Some galerucines that have somewhat swollen hind femora may be difficult to distinguish from alticines unless a hind femur is examined (by clearing or dissection) for the presence or absence of the metafemoral spring. Recently, quite unexpectedly, it was discovered that there are differences in the metafemoral spring morphology among Flea Beetle genera (Furth 1976, 1979, 1980, 1982, 1983, 1985). Thus, the metafemoral spring may be an important factor in evaluating the phylogenetic relationships between the Galerucinae and Alticinae as well as among alticine genera.

## 2. SPRING ANATOMY

Figure 1 illustrates the position and orientation of the metafemoral spring in the hind femoral capsule and its attachment to the metatibia, it also shows the musculature associated with the spring. Figure 2 illustrates the anatomy of the spring with the associated terminology. The large primary tibial extensor muscle inserts onto the dorsal edge of the ventral lobe of the spring via an irregular layer of connective tissue – the cuticular sheet (Figure 4). In those genera that have the ventral lobe of the spring extended into a recurve flange, the primary tibial extensor is inserted onto it by the cuticular sheet. The significance of the recurve flange is not known; however, it increases the area of the spring body which stores the energy (Ker 1977). The secondary tibial extensor muscle inserts onto the dorsal lobe from behind (i.e., mostly in the dorsal furrow). The three furrows (Figure 2) are named for their position in the anatomy of the metafemoral spring and not for the direction that they face. The ventral furrow only occurs in genera with a recurve flange. Ker (in litt.)

has divided the dorsal lobe into basal and apical (Figure 2, extended arm) parts based on functional aspects of the jumping mechanism. The dorsal view of the metafemoral spring (Figure 8) shows its spring-like form, the central and dorsal furrows, the relationship of the ventral and dorsal lobes, and the parts of the dorsal lobe. Details of dissection and preparation of the metafemoral spring are given in Furth (1980, 1982, 1983).

### 3. SPRING FUNCTION

Other insects can jump a great distance relative to their body size, e.g., fleas, grasshoppers, leafhoppers. For this they require special energy storage mechanisms that are generally constructed either from rubbery or strong fibrous materials (Bennet-Clark 1976). Maulik (1929a), Lever (1930), and other assumed that this metafemoral 'organ' and Lever's triangular plate were made of chitin or a 'chitinized tendon'. Furth (1980b) suggested that the apodeme may be a type of modified sclerotized tendon possibly containing the elastic protein resilin, and possibly not chitin. However, various tests for resilin in the metafemoral spring have been negative (M. Rothschild in litt., R. Ker in litt., Furth et al. 1983). Furth et al. (1983) determined that the metafemoral spring is made of fibers of the polysaccharide alpha-chitin, together with protein. The orientation of these thick fibers and their chitinous composition are well-suited to a spring-like function of this organ. In addition, the different textures of the inner and outer surfaces of the spring seem to be consistent with a deflective distortion and recoil of this structure (Furth et al. 1983). Contraction of the spring muscles cause its dilation, with a build up and storage of tension energy, which probably causes a deformation of the chitinous tissue through an elastic bending of its rigid rod-like molecular structure. With the sudden release of the tension the tissue snaps back into shape. Even though the metafemoral spring has been referred to as an apodeme (Wilcox 1965, Furth 1980), this is not actually accurate. The classical definition of apodeme implies a usual rigid invagination of the exoskeletal wall (Snodgrass 1935, Leftwich 1976), which this structure is not (Furth 1980, 1982). The spring is floating in the metafemoral capsule attached to the exoskeleton by muscles and by a ligament to the base of the tibia. It is possible that during development chitin is deposited in the spring through the tibial ligament, but this remains to be proven.

Maulik (1929a) thought that the modifications of the metatibiae of the Alticinae which he examined (Maulik 1929b) were probably related to the development of the metafemoral spring. Expanding on Maulik's studies Lever (1930) discovered a triangular 'chitinized tendon' ventral to the apex of the spring. Lever's triangle is attached to the base of the tibia by a short tendon or ligament and to the ventral edge of the metafemur by a long tibial flexor muscle (Figure 1). Barth (1954) was the first one to give an explanation of the

morphology and function of the metafemoral spring as the jumping mechanism of Flea Beetles. Barth's theory states that the small Lever's triangle enters the femoral capsule, upon contraction of the tibial flexor, and is caught in a cavity on the inner wall of the femur. Simultaneously the spring becomes partially dilated by the some of the tibial extensor muscles and pushes against Lever's triangle; catching it and preventing tibial extension. The remaining tibial extensor muscles then contract to the point that Lever's triangle is dislodged releasing the stored tension, extending the tibia suddenly, thus catapulting the beetle into the air. Although Barth's explanation seems apparently reasonable, it is morphologically and functionally incorrect (Furth 1980, 1985; Ker 1977, in litt.). The muscular tension energy can apparently be voluntarily quickly created, held, and then quickly released. The two tibial extensor muscles (Figure 1) are definitely responsible for the quick and powerful jump, but the exact catch and release mechanism for this energy is not yet known. The primary tibial extensor muscle pulls on the cuticular sheet (Figure 4) which greatly distorts (dilates) the ventral lobe and stores most of the energy; whereas, the dorsal lobe distorts relatively little and stores little energy (Ker 1977, Furth 1982). The tension energy from the tibial extensors is focused through the spring onto the base of the metatibia by a tough ligament. Lever's triangle does enter the metafemoral capsule only when the tibia is flexed. Although it is ostensibly impressive that some Flea Beetles can jump more than 100 times their body length, from an energetics standpoint the important thing is the percent of the body weight that is used for jumping (H. Bennet-Clark in litt.).

#### 4. SPRING MORPHO-GROUPS

Examination of approximately 75 genera of Alticinae (primarily Palearctic and Nearctic, see Table 1) confirms the initial discovery (Furth 1980) that within each genus the morphology of the metafemoral spring is constant but with inter-generic differences of varying degrees. No variation of the metafemoral spring within or between species of a genus has been found due to sex, jumping ability, ecology, or distribution; only differences in spring size exist relative to different body size. Thus far, the springs of almost all genera can be classified into six morphological groups. The morphological differences among these spring groups are primarily based on: the overall spring shape; the relative length of the dorsal to the ventral lobe; the angle of the dorsal edge of the lobes relative to the perpendicular axis of the spring body; and the development of the recurve flange. For detailed descriptions of the morphological characteristics of each of the six spring morpho-groups see previous studies (Furth 1980, 1982). Figures 2-7 are representative of each of the six morpho-groups.

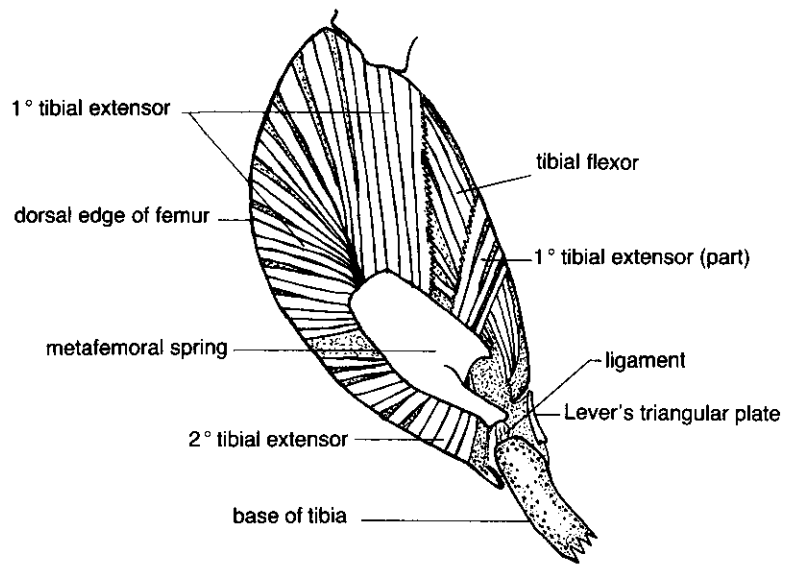


Figure 1. General anatomy of the metafemur, posterior view (after Barth 1954 and Furth 1982).

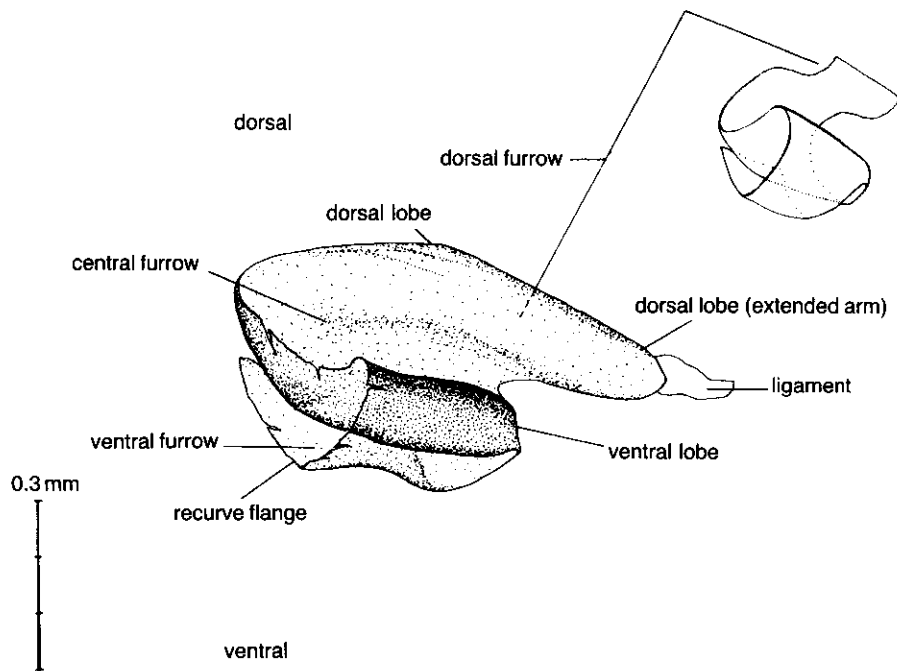


Figure 2. Morphology of the metafemoral spring, anterior view; with schematic drawing. *Alicia oleracea* (Linn.) – Morpho-group 2. (after Furth 1982).

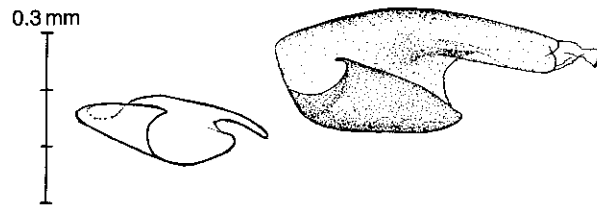


Figure 3. Metafemoral spring of *Hermaeophaga ruficollis* (Lucas) – Morpho-group 1. (after Furth 1982).

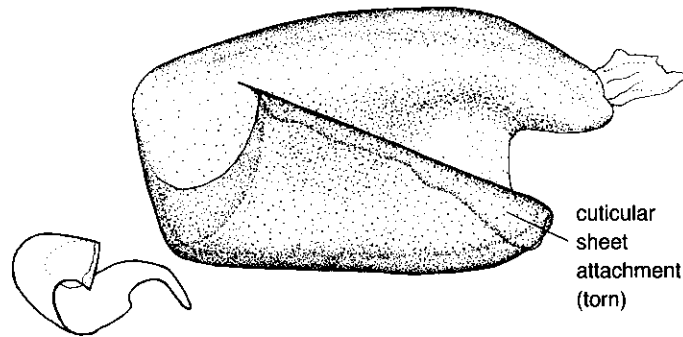


Figure 4. Metafemoral spring of *Chaetocnema coyei* (Allard) – Morpho-group 5. (after Furth 1982).

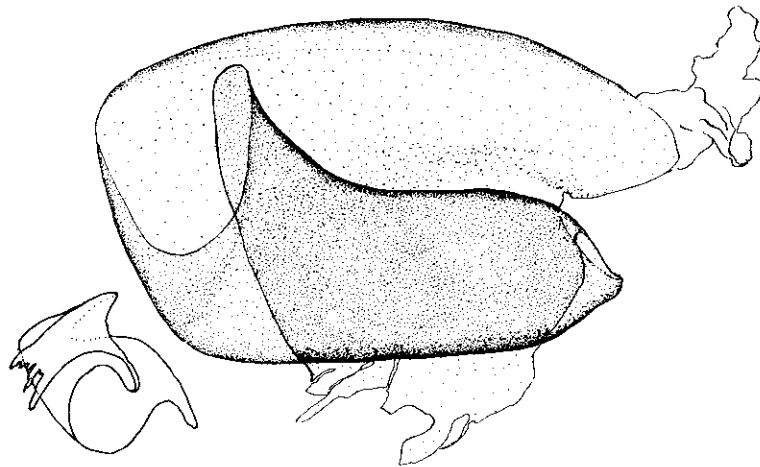
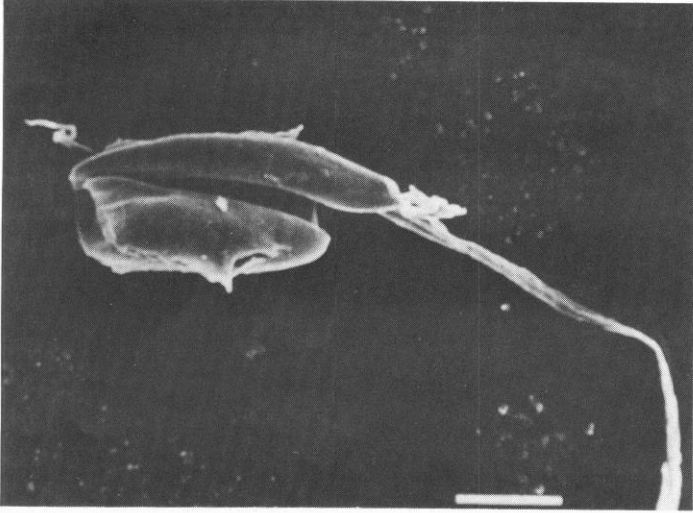
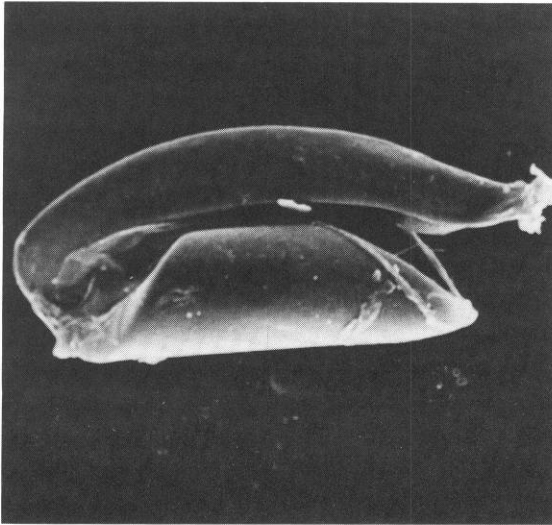


Figure 5. Metafemoral spring of *Psylliodes hyoscyami* (Linn.) – Morpho-group 6. (after Furth 1982).



*Figure 6.* Metafemoral spring of *Phyllotreta judea* Pic – Morpho-group 3. Scanning Electron Micrograph, white line (lower right) is scale of 100 microns (= 0.1 mm). (after Furth 1982).



*Figure 7.* Metafemoral spring of *Longitarsus nigrofasciatus* (Goeze) – Morpho-group 4. (after Furth 1982).

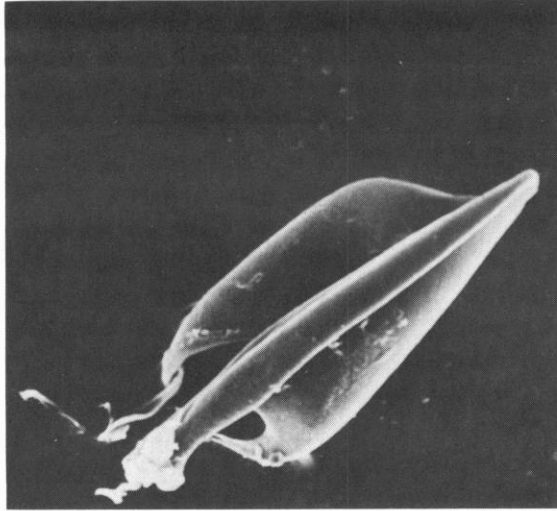


Figure 8. Metafemoral spring (dorsal view) of *Longitarsus nigrofasciatus*.

## 5. APPLICATION

Inter-generic morphological differences of the metafemoral spring are useful tools for systematic studies of Alticinae. These differences suggest that Flea Beetle genera are discrete monophyletic entities; this is not so apparent in some other chrysomelid subfamilies. Spring characteristics may be used for: correlation with other generic differences and study of inter-generic relationships; separation of similar genera (e.g. *Longitarsus* and *Aphthona*); and determination of genera in cases where legs have become detached from the remainder of the body (e.g. ecological surveys or paleo-coleopterology) – use of determined Coleoptera species to extrapolate paleoecology (Furth 1979). Studies of the metafemoral spring have demonstrated interesting correlation or non-correlation of classical ideas of generic relationships, often merely relationships indicated by placement in catalogues. For example, one of the smallest alticine genera *Anthobiodes* Weise (two species) has been thought to be synonymous with the largest genus *Longitarsus* Berthold; however, their springs are significantly different (Furth 1980). Also, the spring of *Chaetocnema* Stephens (morpho-group 5) is quite different from *Blepharida* Chevrolat (morpho-group 1) near which it is usually placed in catalogues, etc. Within the subtribe Oedionychina *sensu* Virkki (1985) two very closely related North American genera, *Kuschelina* Bechyné and *Capraitia* Bechyné (formerly *Oedionychus* Berthold), and the true *Oedionychus* from North Africa have very similar spring morphology. However, these previous three genera have a different spring from two other Oedionychina (*Asphaera* Chevrolat and *Omphoita* Chevrolat) whose spring morphology is quite similar to each other.



Although the metafemoral spring corroborates the relatedness of these five genera (spring morpho-group 5) and their separation into two subgroups, it is still premature to divide these into two tribes as in Seeno and Wilcox (1982) (Furth 1985). In fact, with the present state of knowledge, there is little justification for burdening alticine classification with tribal names. Eventually the metafemoral spring may help provide a foundation for a tribal system in the Alticinae. As indicated by spring morpho-group 2 (Table 1) several genera traditionally placed near *Altica* in catalogues also have a similar spring morphology (e.g. *Macrohaltica* Bechyné, *Lysathia* Bechyné, *Strabala* Chevrolat). Similarly within morpho-group 5 (Table 1) several genera usually catalogue-listed together show spring similarity (e.g. *Psylliodes* Latreille, *Dibolia* Berthold, and *Apteropeda* Stephens). In one instance, thus far, a generic synonymy was discovered through metafemoral spring studies: Nearctic *Or-*

Table 1. Metafemoral spring morpho-groups.

<b>Group 1</b>	<b>Group 2</b>	<b>Group 4</b>
Acrocycum	Altica	Longitarsus
Arrhenocoela	Asiorestia	
Blepharida	Crepidodera	<b>Group 5</b>
Hermaeophaga	Derocrepis	Anthobiodes
Mantura	Disonycha	Aphthona
Orestia	Epitrix	Argopus
Podagrica	Hemiglyptus	Asphaera
Pseudorthygia	Hippuriphila	Capraita
	Hornaltica	Chaetocnema
	Luperaltica	Euplectroscelis
	Lysathia	Glyptina
	Lythraria	Heyrovskya
	Macrohaltica	Kuschelina
	Minota (Cardax)	Oedionychus
	Mniophila	Pachyonychis
	Monomacra	Sphaeroderma
	Ochrosis	
	Phrynocephala	<b>Group 6</b>
	Strabala	Apteropeda
	Syphrea	Argopistes
	Trichaltica	Batophila
		Dibolia
	<b>Group 3</b>	Distigmoptera
	Dysphenges	Psylliodes
	Glenidion	
	Lupraea	
	Pachyonychus	
	Phydanis	
	Phyllotreta	
	Pseudolampsis	
	Systema	

*estioides* Hatch has been synonymized with the Palearctic *Orestia* Germar (Furth 1985). In the case of the Neotropical genus *Macrohaltica*, there were several strictly Nearctic species (Wilcox 1975) that had been placed in this genus; however, close examination of their spring morphology revealed that they actually belonged to *Altica* (Furth 1985).

It is reassuring to note that Virrki (this book, Chapter 11) has independently reconfirmed several of the metafemoral spring relationships using chromosomal cytotaxonomy.

## 6. ALTICINE RELATIONSHIPS

At first it may seem surprising that the structure enabling Flea Beetles to jump, the metafemoral spring, should be morphologically different from one genus to the next. One would expect the morphology of the functional aspects of the jumping mechanism to be the same for all Alticinae. Actually, it appears that the functional morphology of this internal chitinized organ is basically the same throughout Alticinae; however, inter-generic differences exist in apparently nonfunctional parts of the spring. It seems even more surprising that these inter-generic differences have not been noticed since the description of this structure by Maulik (1929a). Evidently early workers (e.g. Maulik, Lever, Barth, and others) did not dissect the metafemoral spring out of the hind leg capsule, or they only did so with a very few closely related genera; they were apparently only concerned with the presence or absence of this structure in conjunction with swollen hind femora to confirm the subfamily status. The inter-generic morphological differences are not correlated to geography, ecology, or behavior of the beetles.

Flea Beetles have always been known for their ability to jump, as the Greek root of their scientific name implies, even though some jump better than others. The relatively greatly enlarged hind femora have traditionally been the character that distinguishes them from the Galerucinae. There is some potential confusion and overlap because some galerucines do have rather swollen metafemora and in some alticines hind femora are not greatly enlarged. Since its discovery an important aspect of the metafemoral spring of Flea Beetles has been that its presence or absence indicated whether the taxon belonged to this largest chrysomelid subfamily, Alticinae. In fact many workers have mentioned this as the distinguishing characteristic between the Galerucinae and the Alticinae (Heikertinger 1948, Barth 1954, Mohr 1960, Wilcox 1965, Weisner 1970, Scherer 1971, Furth 1980, 1982, 1985). Therefore, a very basic question is – What constitutes a Flea Beetle? A case in point is the genus *Orthaltica* Crotch (*sensu* Scherer 1974), considered to be congeneric with *Livolia* Jacoby, *Leptotrihaltica* Heikertinger, *Micrepitrix* Laboissiere, etc., placed by Scherer (1982) in the middle of the Alticinae together with genera having similar pronotal impressions. *Orthaltica* has no metafemoral spring.

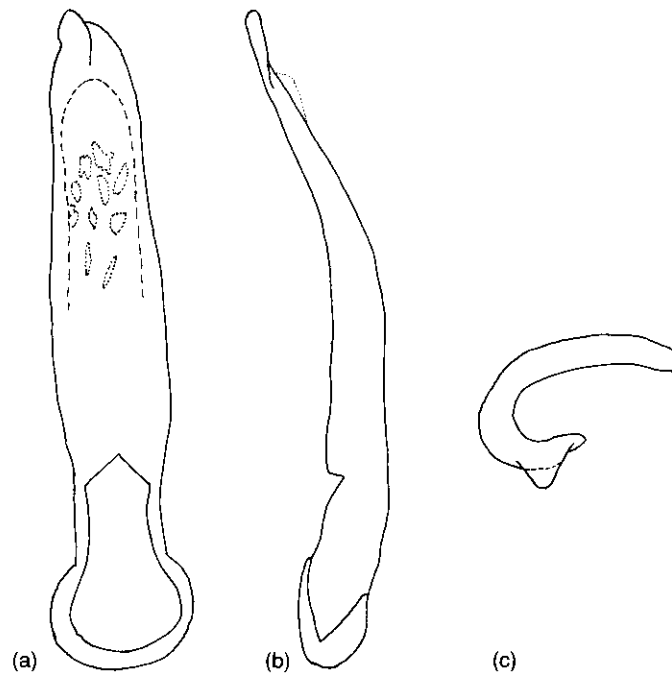


Figure 9. Aedeagus (a) ventral view, (b) lateral view and metafemoral spring (c) of *Chaloenosoma metallica* Jacoby.

Also, certain groups (subgenera *sensu* Scherer 1982) within *Orthaltica* have an asymmetrical aedeagus. Asymmetry of the aedeagus is quite common amongst galerucine genera but very rare in the Alticinae. Because of the absence of the metafemoral spring in *Orthaltica*, the galerucine-like aedeagus (Scherer 1982, Furth 1985) of some *Orthaltica*, and other non-alticine characteristics of *Orthaltica* (Furth 1985), the author does not consider *Orthaltica* to belong in the Alticinae but rather in the Galerucinae. The genus *Micrantipha* Blackburn, placed near *Orthaltica* (Seeno and Wilcox 1982), apparently also lacks a metafemoral spring (Wilcox 1965) and, therefore, is a galerucine.

The phylogenetic sequence and relationship of the Galerucinae and Alticinae have not been satisfactorily studied. Suzuki (personal communication and 1985) has indicated that the Galerucinae and the Alticinae have arisen from a common ancestral line. However, there still is great need for studying a variety of characteristics of many other alticine genera that may offer clues to their primitive relationships. For example, the Indian genus *Chaloenosoma* Jacoby has an asymmetrical aedeagus and a greatly simplified ('primitive') metafemoral spring (Figure 9). The African tribe Decarthrocerini (*Decarthrocera* Laboissiere, *Buphonella* Jacoby, and *Gastrida* Chapuis) was originally considered as Galerucinae but is currently placed at the beginning of the Alticinae (Seeno and Wilcox 1982). Wilcox (personal communication) considers this

tribe as transitional between the Galerucinae and the Alticinae. *Gastrida* has a metafemoral spring, *Buphonella* does not have a spring, and *Decarthrocera* has not been examined (Wilcox personal communication). Closer and more comprehensive examination of these and other such potentially transitional ('primitive') genera will probably lead to an understanding of the phylogenetic relationship between these two large chrysomelid subfamilies.

The metafemoral spring provides a new method for studying systematics and eventually phylogenetic relationships of Flea Beetle genera. The spring is not the only or most important character for study of Alticinae; however, even though subjectivity is not considered by some as important in systematics, the metafemoral spring is so critical to the locomotion and defense of Flea Beetles that it must be considered to be an important character – similar to genitalia. Ideally it is optimum to correlate such morphological systematic studies with research on the larvae and genetics (see Virkki Chapter 00) and other biological and morphological characters. Presence of the metafemoral spring, with the jumping ability that it provides, together with the fact that Alticinae are by far the most diverse chrysomelids (number of genera and species), as well as other aspects of Flea Beetle evolution (e.g. restricted foodplant relationships), indicate that the Alticinae are monophyletic and probably the most advanced subfamily of the Chrysomelidae.

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