

SPIXIANA	Supplement 7	11-27	München 1. Mai 1982	ISSN 0343-5512
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The Metafemoral Spring of Flea Beetles

(Chrysomelidae: Alticinae)

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Abstract

The metafemoral spring (= metafemoral apodeme) and its associated musculature extend the metatibia forming the mechanism by which Flea Beetles are able to jump so effectively. Although the exact function of this mechanism is not yet understood, morphological differences are consistent at the genus level. This spring offers a potential tool for studying the systematic and phylogenetic relationships among the genera of Alticinae from all faunal regions. In this study 118 mostly Palearctic species from all but one (29) of the Palearctic genera of Alticinae were examined.

The Palearctic genera separate into 6 groups of similarity based on morphology of the spring. The metafemoral spring morphology of these groups is described and illustrated by schematic drawings or Scanning Electron Microscope photographs, and the relationships of the Palearctic genera are discussed. A somewhat revised morphological terminology from the author's initial treatment of this structure is explained based on this more extensive study.

Introduction

Introducing this Symposium Dr. Gerhard SCHERER (1981 a) pointed out some of the interesting chorological statistics of the genera of Alticinae, the largest of the Leaf Beetle (Chrysomelidae) subfamilies, as well as the possible historical zoogeography of the origins of Alticinae. He mentioned that of the approximately 560 genera of Flea Beetles in the world, 210 are from the Neotropical Region and about 100 from the Oriental Region; these two alticine faunas are the oldest and most unique (endemic). SCHERER (1973) has previously emphasized the concept of the genus as a biological entity in evolutionary and geological time. It is indeed useful to study the phylogeny and historical zoogeography of a large group such as the Alticinae at the generic level. Therefore, I believe that the new methodology presented here for generic level study of the Alticinae, using the consistent inter-generic differences of the metafemoral spring, has great potential for getting at the phylogenetic and historic-zoogeographical origins ("roots") of Alticinae.

In the recent introduction to the inter-generic differences in the metafemoral spring (= apodeme) of Flea Beetles (FURTH, 1980 b), the basic orientation, anatomy and morphology, and preliminary generic-group relationships were given relative to this jumping mechanism of the Flea Beetles. Flea Beetles get their name from the fact that they are good

at leaping (haltikos in Greek) for locomotion and escape; thus, the original valid name of the type genus *Altica* Müller, 1764 (see FURTH, 1981). Many Flea Beetles are among the most effective jumpers in the animal kingdom, sometimes better than their namesakes the true Fleas (Siphonaptera). However, despite some intensive study of the anatomy and function of the metafemoral spring (BARTH, 1954; KER, 1977) the true function of this jumping mechanism remains a mystery. It probably is some sort of voluntary catch, involving build-up of tension from the large muscles that insert on the metafemoral spring (Fig. 1), and then a quick release of this energy. Of course some Flea Beetles jump better than others, but basically all have this internal metafemoral spring floating by attachment from large muscles in the relatively enlarged hind femoral capsule (see Fig. 1). In fact Flea Beetles can usually be easily separated from other beetles, including chrysomelid subfamilies, by their greatly swollen hind femora.

There are a few genera of Alticinae that have a metafemoral spring and yet do not jump. Actually there are a few genera that are considered to be Alticinae that lack the metafemoral spring, e. g. *Orthaltica* (SCHERER, 1974, 1981 b – as discussed in this Symposium). Also the tribe Decarthrocerini contains three genera from Africa that WILCOX (1965) considered as Galerucinae, but now thinks to be intermediate between Galerucinae and Alticinae; at least one of these genera does have a metafemoral spring (WILCOX, personal communication, and FURTH, unpublished data).

The metafemoral spring was first discovered by MAULIK (1929), but he only noted its existence within the hind femur as a “chitinized endoskeletal tendon”; he did not find any significant differences between genera. Since MAULIK this structure has been referred to as Maulik’s Organ by several authors and usually as representing the major difference between true Flea Beetles (Alticinae) and the closest subfamily Galerucinae. It has also been called Costa Lima’s Organ (BARTH, 1954), extensor apodeme (WILCOX, 1965), and metafemoral apodeme (FURTH, 1980b). In this paper the name of the structure has been changed (metafemoral spring) as well as some of its morphological terminology, for reasons explained below.

In the present study I have examined three additional Palearctic genera (only one very rare Palearctic genus was not seen) and 66 additional species; a few exotic genera were also examined. New morphological terminologies are presented with the additional taxa and some re-grouping of the generic morpho-groups as well as further discussion of evolutionary significance of the metafemoral spring.

Methods and Materials

MAULIK (1929) and various other workers since have observed the metafemoral spring through the wall of the metafemur by clearing the entire hind leg in potassium hydroxide or some other clearing agent, and without making any dissection. Most of these workers were only interested in its presence or absence, especially in cases where there was a question of whether a species was an alticine or a galerucine. However, for examination of the metafemoral spring the hind leg should be left overnight in 10% potassium hydroxide or some other clearing agent. For more rapid examination it can be placed in hot or boiling potassium hydroxide for approximately 30 seconds. Subsequently the spring can easily be removed from the metafemoral capsule for study and the mounted on a slide or on a cardboard triangle, submerged in a drop of a mounting medium such as Euparal and then placed on the pin with the specimen. It is also useful to dry mount (not submerged in a medium) some of these

structures in order to see the thin connective tissue layer (cuticular sheet, Fig. 6 – partially torn) and by which muscles are inserted onto the spring or the ligament by which the spring is attached to the base of the tibia (Figs. 2, 6). If it is desirable to study the gross musculature and their insertions onto the spring, then the hind leg should be boiled in water for 30–60 seconds and dissected under a binocular scope using micro-dissecting tools or even minuten pins inserted into the end of an applicator stick and bent in various ways for suitable dissection. It is most effective to begin such a dissection by breaking open the proximal posterior surface of the hind femur and proceed apically until the desired muscles are exposed. These muscles can carefully be teased away from the spring or all muscles can be removed in this fashion; however, with this method there is more of a danger of damaging the body of the spring or the connective tissues attached to it. The tough ligament attaching the apex of

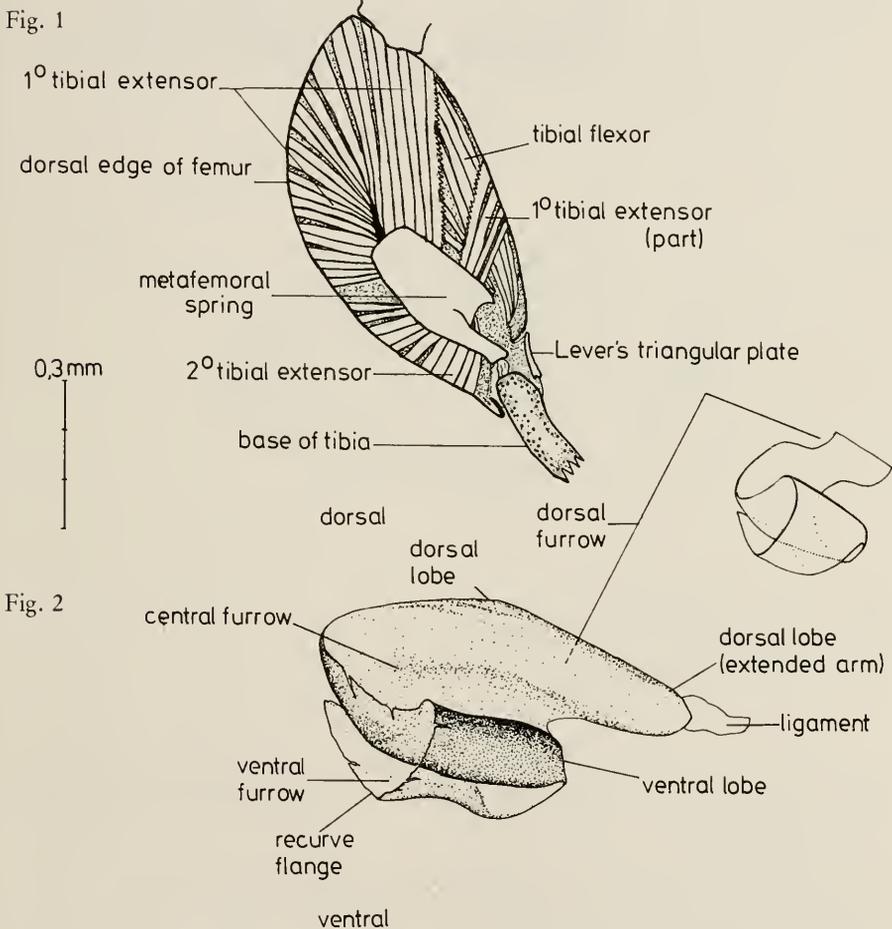


Fig. 1. General anatomy of metafemur, posterior view (after BARTH, 1954 and FURTH, 1980b).

Fig. 2. Morphology of metafemoral spring, anterior view; with schematic drawing; *Altica oleracea* (L.) (after FURTH, 1980b).

Fig. 3

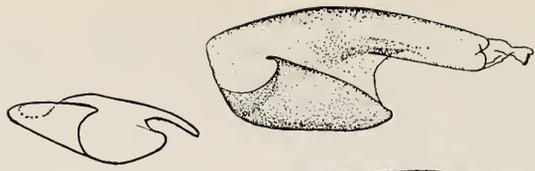


Fig. 4

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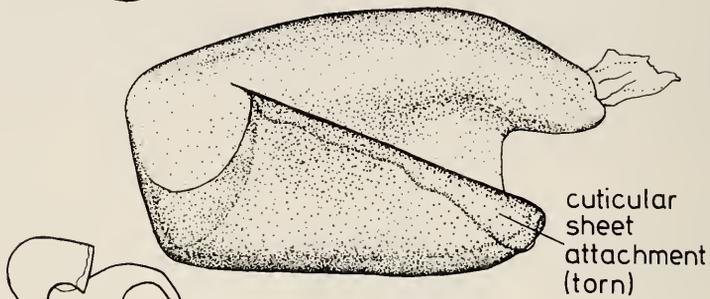
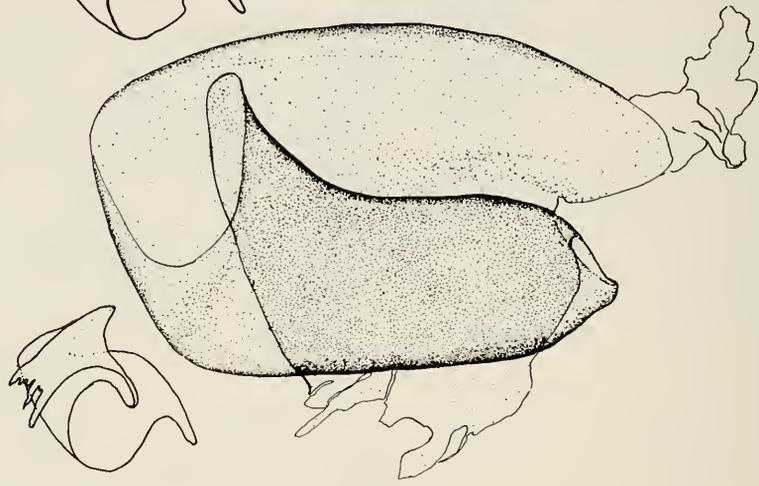


Fig. 5



- Fig. 3. *Hermaeophaga ruficollis* (Lucas).
- Fig. 4. *Chaetocnema coyei* (Allard) (after FURTH, 1980b).
- Fig. 5. *Psylliodes byoscyami* (L.) (after FURTH, 1980b).

the metafemoral spring to the base of the tibia must also be cut with care. The spring with or without any of its attached musculature can also be stored in glycerine in small neoprene vials on the pin with the specimen.

The figures (Fig. 2-5) were drawn by tracing the outline of the glycerine-preserved metafemoral spring projected with a micro-projector and then filling in details free-hand. The spring could not easily be cleared using conventional clearing agents, only 3% hydrogen peroxide overnight worked effectively. A three-dimensional sketch is provided with the drawings to help the reader understand this complex spring-like structure. The three-dimensional aspect of the metafemoral spring may create a problem for portraying it accurately in a figure (Fig. 10). It should be figured from an anterior view (Fig. 2) resting as flat as possible on its posterior side and/or with the dorsal lobe also rest-

TABLE 1. Groups of genera of the Palearctic Alticinae, based on the morphology of the metafemoral spring.

Group 1	Group 2	Group 3	Group 6
Blepharida	Asiolestia	Phyllotreta	Psylliodes
Podagrica	(= Crepidodera)		Dibolia
Mantura	Derocrepis	Group 4	Batophila
Hermaeophaga	Altica	Longitarsus	Apteropeda
Arrhenocoela	Ochrosis		
Orestia	Lythraria	Group 5	
	Crepidodera	Chaetocnema	
	(= Chalcoides)	Oedionychis	
	Minota	Heyrovskya	
	Epitrix	Argopus	
	Hippuriphila	Sphaeroderma	
	Mniophila	Aphthona	
		Anthobiodes	

TABLE 2. List of all the species examined in this study of the metafemoral spring of the 29 Palearctic genera (listed alphabetically).

<i>Altica ampelophaga</i> (Guerin-Men.)	<i>Asiolestia impressa</i> (Fabricius)
<i>Altica bicarinata</i> Kutschera	<i>Asiolestia peirolerii</i> (Kutschera)
<i>Altica brevicollis</i> Foudras	<i>Asiolestia transversa</i> (Marshall)
<i>Altica carduorum</i> Guer.-Men.	<i>Asiolestia</i> sp. (Spain)
<i>Altica impressicollis</i> (Reiche)	<i>Batophila aerata</i> (Marshall)
<i>Altica lythri</i> Aube	<i>Batophila rubi</i> (Paykull)
<i>Altica oleracea</i> (Linnaeus)	<i>Blepharida gedyei</i> Bryant
<i>Altica quercetorum</i> Foudras	<i>Blepharida marginalis</i> Weise
<i>Altica tamaricis</i> Schrank	<i>Blepharida sacra</i> (Weise)
<i>Altica</i> sp. (USSR: Transcaspija)	<i>Blepharida</i> sp. (South Africa)
<i>Anthobiodes angusta</i> (Weise)	<i>Chaetocnema aerea</i> (Letzner)
<i>Aphthona bonvouloiri</i> Allard	<i>Chaetocnema aridula</i> (Gyllenhal)
<i>Aphthona euphorbiae</i> (Schrank)	<i>Chaetocnema chlorophana</i> (Duftschmid)
<i>Aphthona gracilis</i> Falderman	<i>Chaetocnema concinna</i> (Marshall)
<i>Aphthona herbigrada</i> (Curtis)	<i>Chaetocnema conducta</i> (Motschulsky)
<i>Aphthona jacobsoni</i> Ogloblin	<i>Chaetocnema coyei</i> (Allard)
<i>Aphthona kuntzei</i> Roubal	<i>Chaetocnema hortensis</i> (Geoffroy)
<i>Aphthona lutescens</i> Gyllenhal	<i>Chaetocnema major</i> (Bauduer)
<i>Aphthona maculata</i> Allard	<i>Chaetocnema orientalis</i> (Bauduer)
<i>Aphthona pygmaea</i> Kutschera	<i>Chaetocnema procerula</i> (Rosenhauer)
<i>Aphthona semicyanea</i> Allard	<i>Chaetocnema tibialis</i> (Illiger)
<i>Apteropeda orbiculata</i> (Marshall)	<i>Crepidodera aurata</i> (Marshall)
<i>Apteropeda ovulum</i> (Illiger)	<i>Crepidodera aurea</i> (Geoffroy)
<i>Argopus brevis</i> Allard	<i>Crepidodera chloris</i> (Fabricius)
<i>Argopus nigritarsis</i> Gebl.	<i>Crepidodera</i> sp. (Spain)
<i>Arrhenocoela lineata</i> (Rossi)	<i>Derocrepis rufipes</i> (Linnaeus)
<i>Asiolestia ferrugineus</i> (Scopoli)	<i>Derocrepis sodalis</i> (Kutschera)

<i>Dibolia femoralis</i> Redtenbacher	<i>Oedionychis limbata</i> (Fabricius)
<i>Dibolia occultans</i> (Koch)	<i>Orestia bruleriei</i> Allard
<i>Dibolia phoenicia</i> Allard	<i>Orestia calabra</i> Heikertinger
<i>Dibolia schillingi</i> Letzner	<i>Orestia delagrangi</i> Pic
<i>Epitrix abeillei</i> (Bauduer)	<i>Orestia kraatzi</i> Allard
<i>Epitrix atropae</i> Foudras	<i>Phyllotreta corrugata</i> Reiche
<i>Epitrix dieckmanni</i> Mohr	<i>Phyllotreta cruciferae</i> (Goeze)
<i>Hermaeophaga</i> (<i>Hermaeophaga</i>) <i>cicatrix</i> (Illiger)	<i>Phyllotreta erysimi</i> Weise
<i>Hermaeophaga</i> (<i>Orthocrepis</i>) <i>ruficollis</i> (Lucas)	<i>Phyllotreta hebraea</i> Heikertinger
<i>Heyrovskya heyrovskii</i> Gruève & Petitpierre	<i>Phyllotreta judea</i> Pic
<i>Hippuriphila modeeri</i> (Linnaeus)	<i>Phyllotreta latevittata</i> Kutschera
<i>Longitarsus aeneus</i> Kutschera	<i>Phyllotreta nigripes</i> (Fabricius)
<i>Longitarsus anchusae</i> (Paykull)	<i>Phyllotreta peyerimhoffi</i> Heikertinger
<i>Longitarsus candidulus</i> (Foudras)	<i>Phyllotreta talassicola</i> Heikertinger
<i>Longitarsus dorsalis</i> (Fabricius)	<i>Phyllotreta</i> sp. (Kenya)
<i>Longitarsus emarginatus</i> Weise	<i>Podagrica fuscicornis</i> (Linnaeus)
<i>Longitarsus jacobaeae</i> (Waterhouse)	<i>Podagrica malvae</i> (Illiger)
<i>Longitarsus linnaei</i> (Duftschmid)	<i>Podagrica menetriesi</i> Falderman
<i>Longitarsus lycopi</i> (Foudras)	<i>Podagrica pallidicolor</i> Pic
<i>Longitarsus nigrofasciatus</i> (Goeze)	<i>Podagrica</i> sp. (Kenya)
<i>Longitarsus obliteratus</i> (Rosenhauer)	<i>Psylliodes chrysocephala</i> (Linnaeus)
<i>Longitarsus pratensis</i> (Panzer)	<i>Psylliodes circumdata</i> (W.Redtenbacher)
<i>Longitarsus rutilus</i> (Illiger)	<i>Psylliodes cuprea</i> (Koch)
<i>Lythraria salicariae</i> (Paykull)	<i>Psylliodes gibbosa</i> Allard
<i>Mantura chrysanthemi</i> (Koch)	<i>Psylliodes hospes</i> Wollaston
<i>Mantura judaea</i> Heikertinger	<i>Psylliodes hyoscyami</i> (Linnaeus)
<i>Mantura lutea</i> (Allard)	<i>Psylliodes inflata</i> Reiche
<i>Minota obesa</i> (Waltl)	<i>Psylliodes marcida</i> (Illiger)
<i>Mniophila muscorum</i> (Koch)	<i>Psylliodes saulcyi</i> Allard
<i>Ochrosis pisana</i> (Allard)	<i>Psylliodes sophiae</i> Koch
<i>Ochrosis ventralis</i> (Illiger)	<i>Sphaeroderma rubidum</i> (Graells)
<i>Oedionychis cincta</i> (Fabricius)	<i>Sphaeroderma testaceum</i> Weise

ing on the substrate from behind or at least parallel with the substrate. Figure 2 is tilted towards the apex of the spring in order to show the extent of the recurve flange. The Scanning Electron Microscope photographs were taken with a JEOL (JSM 35C) at the Faculty of Agriculture of the Hebrew University of Jerusalem (Rehovot), the scale and magnification are indicated at the bottom of each photograph. The white line under each SEM picture is 100 microns (0,1 mm) in length.

All truly Palearctic genera of Alticinae were examined in this study, except *Cardax* Weise which was unobtainable. In most cases at least two species in each genus were studied to check possible inter-specific variability, and two to several specimens (males and females) of each species were dissected as a check against intra-specific variability. Table 1 lists the 29 genera grouped according to the morphological differences and similarities of the metafemoral spring; within each group the genera are arranged in a decreasing order of similarity of the spring. Table 2 lists alphabetically the genera and species that were examined for this study.

The terminology of the metafemoral spring has been somewhat revised, with assistance from Dr. R. F. KER (in litt.), since the previous paper (FURTH, 1980 b) in an attempt to standardize a set of simple yet unambiguous terms that fit a logical orientation in three dimensions as well as the potential functional aspects of this structure. It is hoped that figures 1 and 2, with the accompanying explanations in the text, will serve this purpose.

Results

Even though the investigation of the inter-generic differences and similarities of the metafemoral spring is still at an early stage, it is useful to group the genera according to the morphology of this new character without necessarily making definite associations to the phylogenetic links of these groups. In this study 29 of 30 Palearctic genera of Alticinae were examined and 118 species, including four from tropical Africa. This is a significant addition to the previous study of 26 genera and 53 species (FURTH, 1980 b). In Table 1 all the genera are listed and divided into 6 groups based on morphological similarity; changes from the previous list are evident in this new one.

Before describing the various aspects of these generic morpho-groups of the metafemoral spring, it is useful to examine the orientation and anatomy of the spring with its terminology. The terminology has been altered somewhat from the previous paper (FURTH, 1980) partially in conjunction with the enlightening functional studies of this spring mechanism by KER (1977). However, the actual method of function of the Flea Beetle jump, which focuses on the metafemoral spring, is still not understood. The theory conceived by BARTH (1954) for the Flea Beetle jump is morphologically and functionally incorrect in several respects (FURTH, 1980 b and KER, in litt.). KER (1977) has also offered a theory of the jump mechanism.

Figure 1 illustrates the position and orientation of the metafemoral spring in the hind femoral capsule and its attachment to the metatibia as well as a generalized diagram of the musculature associated with the spring. Figure 2 shows the anatomy of the metafemoral spring itself, this terminology will be used below in describing the morphology of the groups of genera. The more functional term of metafemoral spring has replaced metafemoral apodeme (FURTH, 1980 b) because it is not an apodeme in the strict sense (SNODGRASS, 1935); there are other true apodemes in the metafemur also (KER, in litt.). The most functional name would be metatibial extensor spring (KER, in litt.) because this describes the action of the spring and its associated muscles; however, for the purposes of this more morphological/evolutionary study metafemoral spring is thought to be more appropriate.

The large complex primary tibial extensor muscle is inserted onto the dorsal edge of the ventral lobe of the spring by the "cuticular sheet" an irregular layer (sheet) of connective tissue; shown torn in the drawing (Fig. 4) and in the SEM picture (Fig. 6, the white tissue attached to the apex of the ventral lobe). In those genera that have the ventral lobe of the spring extended into a recurve flange, the primary tibial extensor is inserted onto it via the cuticular sheet. The secondary tibial extensor muscle inserts onto the dorsal lobe from behind, i. e. mostly in the dorsal furrow. It should be pointed out that the three furrows (dorsal, central, and ventral – see Fig. 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 those genera with a recurve flange. KER (in litt.) has divided the dorsal lobe into a basal part and an apical part (Fig. 2, extended arm) based on functional aspects of the jumping mechanism. A dorsal view of this structure (Fig. 10) reveals its spring-like form as well as the central and dorsal furrows, the relationship of the ventral and dorsal lobes, and the parts of the dorsal lobe.

The two extensor muscles are certainly responsible for the quick and powerful jump of Flea Beetles, through tibial extension; but the exact catch and release mechanism is not yet



Fig. 6. *Blepharida sacra* (Weise) metafemoral spring attached to metatibia, anterior view. Note part (torn) of cuticular sheet on the apex (right) of ventral lobe. White line, lower right, is scale of 100 microns (= 0.1 mm).



Fig. 7. *Lythbraria salicariae* (Paykull)



Fig. 8. *Phyllotreta judea* Pic



Fig. 9. *Longitarsus nigrofasciatus* (Goeze)

known. The primary tibial extensor muscle pulls on the cuticular sheet which distorts (dilates) the ventral lobe of the spring greatly and stores most of the energy (for the jump); whereas, the dorsal lobe distorts relatively little and stores little energy (KER, 1977). The tension energy from the extensor muscles is focused through the spring onto the base of the metatibia by a tough, ligament-like, connective tissue (tibial extensor ligament) (Figs. 2, 6). The focus and insertion of the smaller tibial flexor muscle is onto Lever's triangular plate, another sclerotized apodeme-like structure also firmly attached to the hind tibia; but this plate is actually located outside the metafemoral capsule and apparently enters the capsule upon flexing of the tibia.

MAULIK (1929), LEVER (1930), and others assumed that the spring and Lever's plate were made of chitin or a "chitinized tendon". FURTH (1980b) suggested that the spring may be some 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. and tests for chitin were positive (R. KER, in litt., D. FURTH, unpublished data). KER (1977 and in litt.) has probably correctly assumed the spring to be composed of chitin-containing cuticle. However it appears that chitin is only one of the histological components of the metafemoral spring of Alticinae and that it contains a substantial amount of other substances, possibly various proteins (FURTH, unpublished data).

The more extensive examination of species of the Palearctic genera of Alticinae verifies 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 difference in sex, jumping ability, ecology, or distribution; only differences in spring size exist relative to different body sizes. Because of the present study several modifications (explained below) have been made to the previous figures and the Table of generic groups (FURTH, 1980b).

The first of the metafemoral spring generic morpho-groups contains 6 of 29 genera and is one of the two basic forms of the spring (based on the relative extension and horizontal axis of the dorsal lobe); groups 2 to 4 also have similar basic form. Group 1 is typified by the fact that the apex (extended arm) of the dorsal lobe extends much beyond the apex of the ventral lobe and projects from its base on a relatively horizontal axis and, thus, the extended apex of the dorsal lobe (extended arm) appears only slightly depressed (Figs. 3, 6). Also the dorsal edge of the ventral lobe is usually at an angle to the dorso-ventral axis of the spring and is slightly thickened for the reception of the cuticular sheet insertion of the primary tibial extensor. The figure of *Blepharida* (FURTH, 1980b, Fig. 3) should be depicted with the dorsal edge of the ventral lobe thickened with its base coming to a sharper point and the apical extended arm of the dorsal lobe more flattened (not so trough-like); but see also Fig. 6, herein. The basic metafemoral spring form for group 1 has the general appearance of a hand closed with the forefinger pointed out.

Group 2 (= group 4, FURTH, 1980b) is very similar to group 1 with one major difference; the presence of the recurve flange as an extension of the ventral lobe. Sometimes the recurve flange is highly developed as in *Altica* (Fig. 2) yet in others such as *Asiolestia* the recurve flange is only slightly developed. In fact four genera (*Lythraria*, *Hippuriphila*, *Asiolestia*, and *Epitrix*) were formerly (FURTH, 1980b) placed in group 1 but have herein been placed in group 2 because it was discovered that they have some development of the recurve flange (Fig. 7). The genus *Minota*, one of three newly studied Palearctic genera,



Fig. 10. *Longitarsus nigrofasciatus* (Goeze), dorsal view.



Fig. 11. *Oedionychis cincta* (Fabricius)

also belongs in this group. Thus, this becomes the largest group containing 10 of the 29 Palearctic genera.

Group 3, containing only *Phyllotreta*, has a relatively short extended arm of the dorsal lobe which is significantly depressed apically and out-of-line from the horizontal axis of the dorsal lobe; but more gradually and less sigmoid than indicated in the figure of *Phyllotreta* of the previous study (FURTH, 1980b, Fig. 10) (see Fig. 8 herein). Also the ventral lobe is extended into a recurve flange, though not well developed; this was also overlooked in the previous study.

Group 4 (= group 2, FURTH, 1980b) contains only *Longitarsus* (Figs. 9, 10) is somewhat similar to group 1 but its dorsal lobe extension is not as long and is slightly depressed or even sigmoid at the extreme apex; the horizontal axis of the dorsal lobe is evidently quite strongly curved, almost semi-circular, moreso than in the first three groups. The dorsal edge of the ventral lobe is not gradually tapered apically as in the previous groups,



Fig. 12. *Batophila rubi* (Paykull)

but rather irregular by having a flat horizontal basal one third and then a gradual apical tapering or even slightly concaved edge for the apical two thirds.

Group 5 contains 7 of the 29 genera, including the additions of *Oedionychis* (Palearctic) (Fig. 11) and *Heyrovskya*; this is the main group with the second basic form. This basic form has a relatively short apical extension of the dorsal lobe (beyond the ventral lobe) and with a distinct-depression, or deflection downwards, from the horizontal axis of the base of the dorsal lobe (Figs. 4, 11). This gives the metafemoral spring a more rounded and humped appearance, especially dorsally, compared with groups 1–4. The upper edge of the ventral lobe is usually straight and tapered apically at a strong angle to the dorso-ventral axis of the spring.

Group 6 (=groups 6 and 7, FURTH, 1980b) contains 4 genera, including *Batophila* (Fig. 12) formerly considered as a separate group. This group is quite similar to group 5 with the addition of a significant recurve flange and a narrowly pointed and curved basal angle on the ventral lobe (Figs. 5, 12). The relationship of group 6 to group 5 is similar to that of group 3 to group 1.

These are the metafemoral spring morphological groups of the Palearctic genera; however, as other genera in different faunal regions are examined some very different groups will be added. For example, the author has also examined a few tropical genera such as *Physodactyla* Chapuis and *Philopona* Weise from tropical Africa, both of these fit rather well into group 5; however, *Chalaenosoma* Jacoby from India has a radically different metafemoral spring morphology from any of the above 6 groups.

Discussion

It may initially seem rather surprising that the metafemoral spring, the crux of the jumping mechanism in the Flea Beetles, would differ morphologically between and among genera, because one would expect at least the morphology related to the functional aspects of the jump to be the same for all Alticinae. Indeed, it appears that the functional anatomy of this internal sclerotized structure is the same throughout this largest subfamily of the Leaf Beetles; however, constant and distinct morphological differences and similarities are present inter-generically in the evidently nonfunctional parts of it. It is perhaps even stranger that this fact has gone undiscovered since the original description of this structure (MAULIK, 1929). However, apparently MAULIK as well as subsequent workers such as LEVER (1930), BARTH (1954), and others did not actually completely dissect the metafemoral spring from the hind leg capsule, or they only dissected one or two closely related genera; but rather they only noted the presence or absence of the spring in conjunction with the swollen hind femora as verification of subfamily status. The inter-generic differences in the morphology of the spring do not seem to be related to the geography, ecology, or behavior of the genera.

B. BECHYNÉ, this symposium) has made a general statement that there are South American species of Alticinae (no genus or species names given) in which the males have the metafemoral spring and the females do not. Such a phenomenon is quite contradictory to the present study of the metafemoral spring and may, in fact, be based on some taxonomic confusion. In fact, for several reasons this seems illogical because the jumping ability afforded by the metafemoral spring is too important of an aspect of Flea Beetle existence,

especially for flightless species. Wing reduction (flightlessness) would certainly occur before loss of the metafemoral spring and even then it would not be sexually dimorphic (FURTH, 1980a, SHUTE, 1980). The enlarged musculature associated with the spring for jumping would be reduced or lost long before the spring itself. Females would have little to gain in fecundity or other aspects important to their life cycle and reproduction, and much to lose, by loss of the spring. The present study suggests that loss or reduction of jumping ability in Alticinae at the genus level is correlated with the relative size reduction (volume or mass) of the metafemoral spring within the hind leg and without any differences between the sexes. Thus, sexual dimorphism in the metafemoral spring of Alticinae would have no apparent selective advantages.

This study of the genera and many species of Palearctic Alticinae establishes a reliable constancy to the morphology of the metafemoral spring in each genus and, in fact, the constancy of the alticine genera as distinct entities. Thus, it appears that this structure may prove to be a valuable tool for deciphering the systematics, zoogeography, evolution, and phylogeny of the Alticinae. This is not to imply that the metafemoral spring is the only or most important character or aspect of Flea Beetles; however, even though subjective or empirical science is sometimes frowned upon, a character like the metafemoral spring, that is crucial to the locomotion and defense (escape) of Alticinae, must be ranked as an important one – similar to genitalia. Of course, ideally it would be best to correlate these studies with research on larvae and genetics (as discussed by W. STEINHAUSEN and E. PETITPIERRE, respectively in this Symposium) as well as other biological and morphological characters.

Table 1 indicates relationships of the Palearctic genera of Alticinae based on the morphology of the metafemoral spring. This grouping is not necessarily intended to be phylogenetic; however, certain aspects of relatedness between and among genera are evident. Much of the arrangement of Alticinae in catalogues has evidently been perpetuated through time with little change (HEIKERTINGER, 1930; HEIKERTINGER & CSIKI, 1940; WILCOX, 1975). The basis of such arrangements of taxa is not often obvious, but apparently based on various morphological characters and relationships. The present studies of the metafemoral spring show some interesting relationships among genera, some of which substantiate the classical catalogue arrangement and others which show distinct differences. To my knowledge there is no comprehensive treatment of the phylogeny and/or evolution of the Alticinae. VIRKKI (1970) considered some genera of Neotropical Alticinae based on the cytology of their chromosomes and he constructed a phylogeny of those genera, including grouping the genera into tribes. Ideally a phylogenetic arrangement should consider a variety of aspects, such as morphological characters, ecology, genetics and biochemistry, biogeography, of genera from all zoogeographic regions. For much the same reasons, there seems to be little cause now for burdening the taxonomy of Alticinae with tribe names based on isolated selected aspects. Even though Table 1 contains a grouping of the Palearctic genera, it is still a system based on one, possibly very significant, morphological character and it certainly would be premature to consider these as tribes.

In the following discussion are some of the similarities and differences revealed by this study from the “classical” catalogue arrangement, i. e. HEIKERTINGER and CSIKI, 1940 (see also Table 1). The four large genera usually listed in the beginning of Alticinae catalogues (*Phyllotreta* Chevrolat, Fig. 8; *Aphthona* Chevrolat; *Longitarsus* Berthold, Fig. 9; *Al-*

tica Fabricius, Fig. 2) maintain distinct differences in their metafemoral spring morphology. The little-known genus *Anthobiodes* Weise is catalogued next to the largest alticine genus *Longitarsus* and, in fact, they are thought to be synonymous by some workers. However, the spring of these two genera is different enough to put them into two different groups. *Hermaeophaga* Foudras is usually placed near *Altica* but the recurve flange of *Altica* places it in another group. *Arrhenocoela* Foudras, *Lythraria* Bedel, and *Ochrosis* Foudras are close together in the catalogues but *Lythraria* and *Ochrosis* are in group 2 because they possess a recurve flange. The relationship of *Asiorestia* Jacobson (= *Crepidodera* Chevrolat sensu BECHYNÉ, 1956) and *Orestia* Germar is not upheld by the metafemoral spring morphology; *Orestia* lacks the recurve flange of *Asiorestia* and *Derocrepis* Weise, also considered to be closely related in catalogues probably due to similar pronotal impressions. The close relationship of *Hippuriphila* Foudras, *Crepidodera* (= *Chalcoides* Foudras sensu BECHYNÉ, 1956), *Epitrix* Foudras, and *Minota* Kutschera is apparent in both systems.

The genera mentioned in the above paragraph belong to groups 1–4 (see Table 1) and even though differences in the fine points of their spring morphology are evident, most have many features in common. The same can be said about groups 5 and 6, with the major difference again being the possession of a recurve flange. *Chaetocnema* Stephens (Fig. 4) has been considered as close to *Mantura* Stephens and also *Blepharida* Chevrolat (Fig. 6) of group 1, presumably because of similar tibial excavations; however, the metafemoral spring morphology indicates that *Mantura* and *Blepharida* are similar, but distant from *Chaetocnema*. Two newly examined Palearctic genera from the western Mediterranean, *Oedionychis* Berthold and *Heyrovskya* Madar and Madar, are more closely allied to *Chaetocnema* by the spring morphology. Based on the spring, *Sphaeroderma* Stephens and *Argopus* Fischer maintain the formerly assumed relationship in keys and catalogues. *Apteropeda* Stephens (also catalogued near *Cardax* Weise) and *Mniophila* Stephens (group 1) do not show the connection indicated in catalogues. *Dibolia* Latreille and *Psylliodes* Latreille (Fig. 5) have quite similar metafemoral springs, also similar to *Apteropeda*, but different from *Sphaeroderma*, *Argopus*, and *Mniophila* with which they are placed in catalogues. Re-examination of *Batophila* Foudras shows that it belongs to group 6, certainly not at all near *Longitarsus* as in catalogues.

It is still premature to analyze the phylogeny of Alticinae or even the Palearctic alticines based on the above studies only. Some of the six metafemoral spring groups are quite similar to others, e. g. groups 2, 3 and 4 are similar to group 1 and groups 5 and 6 are close. Thus, it may be misleading to stress the separation of *Hermaeophaga* and *Altica*, for example, if the evolution of the recurve flange is a rather simple genetic mechanism. The significance of the recurve flange is unknown; however, it does increase the area of the body of the spring which is the energy storage part of the spring (KER, 1977). It would, therefore, be interesting to compare the jumping efficiency of genera in groups with the recurve flange (groups 2 and 6) to those without it (groups 1 and 5) to see if its presence increases jumping ability. These six morpho-groups of the metafemoral spring for the Palearctic genera of Alticinae are similar to each other in several respects and it is possible to imagine the gradual transition that would link the different groups. Although some Palearctic genera exist in other zoogeographic regions, many other endemic genera exist in other regions. Therefore, the relative similarity in the metafemoral spring of Palearctic genera may be due to common phylogenetic lineages and historical zoogeography. If this

were a monograph on all of the Palearctic species of Alticinae a phylogenetic analysis, based on primitive and advanced (pleisiomorphic and apomorphic, respectively), may be expected; but this would be misleading and purely speculative because it is only a small portion of the total world alticine genera. Also there is not yet a basis, from such a small portion, for classifying the morpho-groups or parts of this structure as primitive or advanced. It can only be assumed that the presence of the metafemoral spring, with the jumping ability that it affords, indicates that Alticinae are the most advanced of the chrysomelid subfamilies. This statement is even more valid when correlated with other specialized aspects of Flea Beetle evolution, e. g. restricted host plant relationships.

As far as the exact evolutionary transition from Galerucinae to Alticinae, there is still need for extensive study of a variety of genera from different faunal regions. Study of the metafemoral spring may provide a key to solving this question. Some Alticinae reportedly lack the metafemoral spring, e. g. *Orthaltica* (sensu SCHERER, 1974, 1981 b – this Symposium), but it is always absent in Galerucinae. The Nearctic *Orthaltica* have an asymmetrical aedeagus unlike the African *Orthaltica* (= *Livolia* Jacoby) and the Oriental *Orthaltica* (= *Micrepitrix* Laboissiere) (SCHERER, 1974, 1981 b – this Symposium). JACOBY and LABOISSIERE considered *Orthaltica* to be primitive and transitional between Galerucinae and Alticinae, but SCHERER (1971, 1981 b) places *Orthaltica* in the middle of the Alticinae. Since the Galerucinae have an asymmetrical aedeagus, it would seem probable that alticine possession of such an important character may indicate a link with the galerucines (transitory or a primitive alticine). Another genus of Alticinae, *Chalaenosoma* from southern India, has an asymmetrical aedeagus (SCHERER, 1974). However, this genus does have a metafemoral spring that is extremely different from all Palearctic genera; it may prove to be a link between Galerucinae and Alticinae. WILCOX (1965 and personal communication) mentions three related African genera (*Decarthrocera* Laboissiere, *Buphonella* Jacoby and *Gastrida* Chapuis) which he considers as transitory between galerucines and alticines. *Gastrida* has a metafemoral spring (WILCOX, personal communication and FURTH, unpublished data), but *Buphonella* apparently does not and *Decarthrocera* has not been examined (WILCOX, personal communication). A closer and more comprehensive study of these potential transitory genera as well as their supposed relatives will probably lead to an understanding of the phylogenetic connection between these two most advanced chrysomelid subfamilies.

The metafemoral spring provides a new methodology for studying the systematics and phylogenetic or evolutionary relationships between and among genera of Alticinae. It can be used to: verify other morphological differences between genera; separate close genera (e. g. *Aphthona* and *Longitarsus*); establish new genera; and determine genera in cases where legs are separated from the remainder of the specimen (e. g. ecological or paleo-ecological surveys (FURTH, 1979)).

Acknowledgements

I would like to thank Dr. Gerhard Scherer (Zoologische Staatssammlung, München) for useful discussions, information, and some specimens of exotic genera. I am also very grateful to Dr. Robert Ker (University of Leeds) for assistance and information regarding terminology and function of the metafemoral spring.

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Angenommen am 1. 10. 1981

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Spixiana, Zeitschrift für Zoologie, Supplement](#)

Jahr/Year: 1982

Band/Volume: [007](#)

Autor(en)/Author(s): Furth David G.

Artikel/Article: [The Metafemoral Spring of Flea Beetles \(Chrysomelidae: Alticinae\) 11-27](#)