

The independent evolution of the metafemoral spring in Coleoptera

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Abstract. The metafemoral spring (jumping organ) was known previously only from all Alticinae (Chrysomelidae), one genus of Bruchidae, and two species of Rhynchaeninae (Curculionidae). Here this spring is reported from three subfamilies, seven tribes and twenty-two genera of Curculionidae (three Rhynchaeninae, one Eriirhininae (Derelomini), and eighteen Ceutorhynchinae) and also from five genera of Buprestidae (four Agrilinae and one Trachyinae). Jumping in Hexapoda is discussed, specifically in the other jumping Coleopteran families that were examined for the presence of the spring (e.g. Melandryidae, Mordellidae, Scaptiidae, Eucinetidae, Limnichidae, Scirtidae and Anthribidae). The phylogenetic value of the metafemoral spring is still unclear; however, there are indications that it is useful in assessing relationships among weevil tribes. As in Alticinae, Curculionidae and Buprestidae have constant intra-generic spring morphology and inter-generic differences. The spring in Bruchidae, Curculionidae and Buprestidae has a simpler morphology than in the Alticinae, but still possesses the features necessary for jumping (metatibial extension). The metafemoral spring has apparently evolved independently in Alticinae, Bruchidae, Curculionidae and Buprestidae, and is an example of convergent evolution.

Introduction

The ability to jump is widespread in Hexapoda, but reflects many different evolutionary events. The mechanisms used, and the morphological adaptations associated with jumping, are potentially valuable systematic tools, not only between orders, but also at lower levels. The purpose of this paper is primarily to discuss jumping structures, especially the metafemoral spring in various Coleoptera.

In most hexapods jumping is presumed to be used as a defensive behaviour to escape predation or any threatening situation. In some cases jumping may also be a useful means of locomotion and in still others it may be advantageous to take-off, i.e. to enable an insect to get off the substrate before the first wing beats and, therefore, avoid wing damage (Crowson, 1981).

In the majority of Hexapoda tibial extension, generally of the hind leg, is the basis for the jumping mechanism, such as in the metatibiae of some Orthoptera, Hemiptera, Psocoptera, Mecoptera (*Boreus*), Diptera (*Meromyza*

saltatrix L., Chloropidae and *Chionea* spp., Tipulidae) (Rothschild *et al.*, 1975; Byers, 1983). The Siphonaptera jump effectively using the metatibial extensor muscles; however, this action is greatly augmented by energy storage in resilin in the pleural arch – the homologue of wing hinge ligaments in flying insects (Rothschild *et al.*, 1975). There are some exceptions to metatibial jumping, such as Collembola, which use hydrostatic pressure to release a forked abdominal furcula (Manton, 1972) and Microcoryphia (jumping bristletails) which use a combination of abdominal muscles (Manton, 1972; Evans, 1975). In the micro-Hymenoptera many (e.g. Eulophidae, Encyrtidae) use modified mesothoracic or metathoracic muscles in combination with large tibial spurs (Riek, 1970) and Eupelmidae have a special mechanism involving retraction of mesotrochanters into the mesocoxae and resilin pads (Gibson, 1986).

Jumping in the Coleoptera has evolved independently in a variety of families and several different mechanisms are present in the order. One type of mechanism that has arisen independently in a variety of beetle families, e.g. Mordellidae, Melandryidae, Eucinetidae, and probably in Limnichidae (Thaumastodinae) and Staphylinidae

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(Trichopseniini), uses enlarged metacoxae with the depressor trochanteris muscles and allows the beetle to depress the hind legs quickly and strongly against the substrate causing a jump; most of these groups also have elongate metatibial spurs which assist this type of jumping (Crowson, 1981). The unique mechanism of the well-known 'click' of the Elateridae, Throscidae and Eucnemidae, used for escape as well as for correcting the body position from an inverted state, involves a pro/mesothoracic modification combined with resilin (Evans, 1972; Rothschild *et al.*, 1975; Crowson, 1981). Crowson (1981) also mentions several groups that jump using their front legs, e.g. certain species of Cryptophilidae (*Propalticus* Sharp), cryptocephaline and eumolpine Chrysomelidae, and Anthribidae. These groups have enlarged prothoraces including lengthened or thickened profemora.

Enlarged metafemora actually provide two different jumping mechanisms in Coleoptera. The Scirtidae (Helodidae) jump by means of greatly enlarged metatibial extensor muscles and tendons (Furth & Suzuki, 1990b) similar to Orthoptera. The second metafemoral mechanism in Coleoptera involves a metafemoral spring (Furth, 1980, 1982, 1988) homologous, at least in Alticinae (Chrysomelidae), to a sclerotized extension of the metatibial extensor tendon (Furth & Suzuki, 1990b). This spring consists of a hook-like shape with a longer dorsal lobe that is apically attached to the metatibial base and a shorter ventral lobe attached to most of the tibial extensor muscle; the protein and chitin mixture comprising the spring functions as the energy storage mechanism in the flea beetle jump (Furth *et al.*, 1983).

The metafemoral spring was originally found in Alticinae (Maulik, 1929). Maulik (1929) also examined and discussed jumping in Thysanura, Collembola, Orthoptera, Hymenoptera, Diptera, Hemiptera, Siphonaptera and Coleoptera (Elateridae, Eucnemidae, Helodidae and Curculionidae (one species of Rhynchaeninae)); he concluded that only Rhynchaeninae had an internal hind leg organ. This was confirmed by Furth (unpublished), and subsequently found in another species of Rhynchaeninae (Pomorski, 1978). Terán (1964, 1967) discovered the metafemoral spring and flexor sclerite in *Eubaptus* (Bruchidae).

Furth (1980) discovered inter-generic morphological differences in the metafemoral spring of Alticinae (Furth, 1980). Furth (1982, 1985, 1988, 1989) examined more than 125 genera from the Palearctic, Nearctic, Neotropical Regions and demonstrated that the genera from these regions could be placed in seven morphologically distinct spring groupings. There is evidence that many other spring morpho-groups exist (Furth, 1988; Furth & Suzuki, unpublished) and that future character analysis of the spring may reveal phylogenetic relationships.

A second sclerite is found in the leg of Alticinae (Lever, 1930) as well as other chrysomelid subfamilies, certain other Coleoptera, Megaloptera, Neuroptera, Hymenoptera and Hemiptera (Furth & Suzuki, 1990a), and known as Lever's Plate or the tibial flexor sclerite. However, this flexor sclerite probably functions in strengthening leg

flexion and apparently has no major function in jumping.

Furth & Suzuki (1990b) examined a variety of Coleoptera with enlarged metafemora with special reference to the relative sizes of the metatibial extensor and flexor tendons. They found that those groups whose hind legs functioned in grasping had enlarged metatibial flexor tendons and those groups whose hind legs functioned in jumping had enlarged metatibial extensor tendons. The current study examines Coleoptera that have been observed or are reputed to jump whether or not their metafemora are evidently enlarged.

Methods

The procedures used in this study were essentially the same as those in Furth & Suzuki (1990a, b).

Drawings were made in some cases of the posterior and in others of the anterior view of the metafemoral spring because of author preference at the time and because of the subsequent need for more figures. Posterior views were made by the second author, anterior views by the first author with shading by an artist. Fig. 8 shows both posterior and anterior views in order to give the reader a complete dimensional perspective. Fig. 1 shows the general location of the spring in the metafemoral capsule. Fig. 2 shows the spring attachment to the base of the metatibia and tibial flexor sclerite.

We consulted the literature and many coleopterists for information about which groups of beetles may jump and/or have enlarged femora. In describing the metafemoral spring morphology, the authors follow the terminology used in Furth (1982, 1988). For the classification of the Curculionidae O'Brien & Wibmer (1982, 1986) and Wibmer & O'Brien (1989) are generally followed, except as noted. For the Buprestidae classification the authors follow Bellamy (1985).

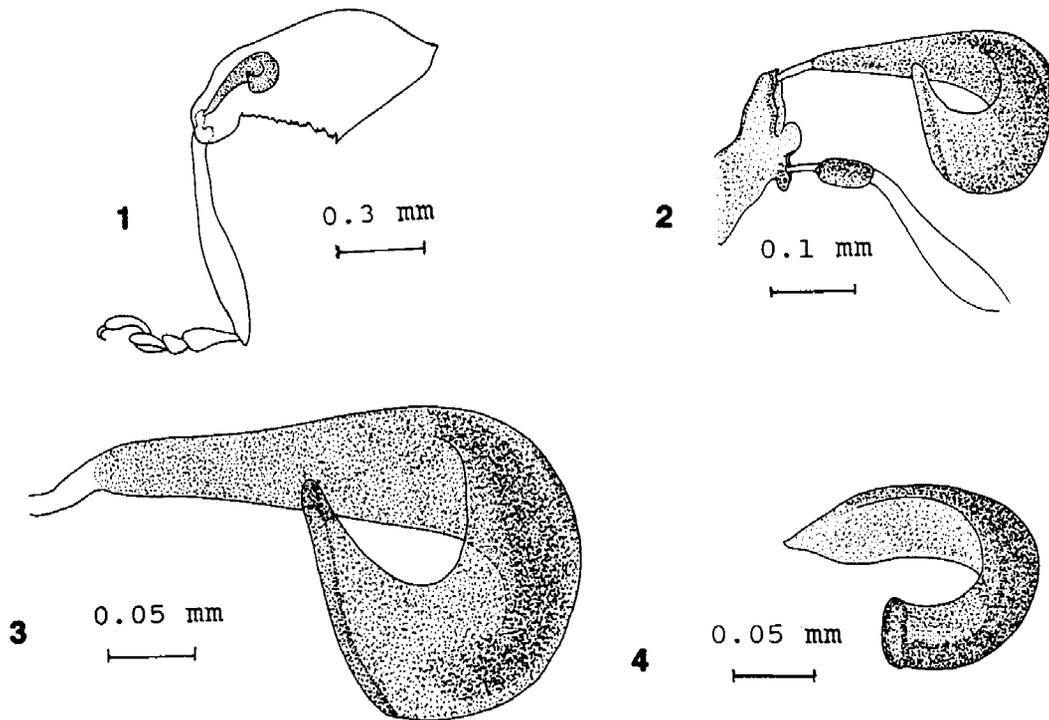
Results

Curculionidae: Rhynchaeninae

Four genera (sixteen species) or Rhynchaeninae were examined here and a metafemoral spring was found in each (Table 1). Figs 1–3 illustrate the basic morphology of a *Rhynchaenus* metafemoral spring. All eleven species of *Rhynchaenus* examined had the same hook-like simple morphology (Fig. 3) and a similar form was found in *Tachyerges* Schoenherr except that its dorsal lobe is more uniform in height rather than apically tapered. *Rhamphus* Clairville & Schellenberg (Fig. 4) has a more simple spring form than *Rhynchaenus*, as does *Isochnus* Thomson which is more uniform in height than *Rhynchaenus* throughout and with the apex of the ventral lobe not greatly expanded.

Curculionidae: Ceutorhynchinae

Twenty-six genera in all six tribes of New World Ceutorhynchinae were examined (Table 1); *Hypocoeliodes*



Figs 1–4. Curculionidae: Rhynchaeninae. 1, *Rhynchaenus quercus* hind leg with metafemoral spring; 2, *Rhynchaenus* sp. base of metatibia with metafemoral spring and tibial flexor sclerite (below); 3, *Rhynchaenus* sp. spring (posterior view); 4, *Rhamphus flavicornis* spring (posterior view).

Faust, *Auleutes* Dietz, and *Acanthoscelidius* Dalla Torre & Hustache, have been observed jumping (C. O'Brien, pers. comm.). Most tribes have members with a metafemoral spring, the notable exception being the Ceutorhynchini in which no genera have one. In the New World Scleropterini *Acallodes* LeConte and *Rutidosoma* Stephens have no metafemoral spring. *Amalus* Schoenherr (Fig. 13) has a spring (see discussion below) and the only other genus in the tribe, *Homorosoma* Frivaldszky (Fig. 12), contains a spring similar in form to certain Phytobiini. Hypurini and Mononychini are represented in the New World only by the typical genus of each; *Hypurus* Rey (Fig. 7) has a dorsally arched/convexed, strongly C-shaped spring, whereas *Mononychus* Germar (Fig. 8) has a more linear, elongate spring with a short ventral lobe somewhat similar to *Neophytobius* Wagner (Fig. 15) or *Amalus* (Fig. 13). Genera in the more diverse tribes Cnemogonini and Phytobiini seem to all have a metafemoral spring (Table 1) although the spring morphology varies considerably (Figs 9–11 and 14–16, respectively). Cnemogonini have somewhat diverse spring morphology, flattened dorsally and elongate with a relatively short ventral lobe that is ventrally rounded giving a hook-like shape to the entire spring (Figs 9–11). This is essentially different from most Phytobiini in which the spring has a thinner and more elongate dorsal lobe, with the ventral lobe even shorter relative to the total spring length and often not evenly

rounded at its base, the spring is less sclerotized than that of Cnemogonini and appears more delicate (Figs 14–16).

Other Curculionidae

As indicated in Table 1, the authors also examined members of Ceratopinae, Erihinae and Zygopinae possessing somewhat swollen metafemora, some of which have been observed to jump in the Neotropics (H. Hespeneide, pers. comm.). Only the genus *Pedinus* Faust possesses a metafemoral spring (Fig. 5); this genus, formerly in the Rhynchaeninae (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1989), recently transferred to the Erihinae (Derelomini) by Anderson (1989), is known to jump (C. O'Brien, pers. comm.) as implied by the species name *halticoides* (Champion).

Bruchidae

Terán (1964, 1967) indicated the presence of a metafemoral spring in all four species of the Neotropical genus *Eubaptus*. The metafemoral spring of *E. palliatus* Lacordaire is shown here to be a simple hook-shaped structure similar to that of *Rhynchaenus* but with the apex of the ventral lobe somewhat scoop-shaped and open

Table 1. Coleoptera groups with metafemoral spring.*

Taxon	No. spp. examined	Spring +/-
BRUCHIDAE		
Eubaptinae:		
<i>Eubaptus</i> †	1	+
CURCULIONIDAE		
[5 subfamilies; 11 tribes;		
40 genera; 77 species]		
Rhynchaeninae (16)		
<i>Rhynchaenus</i>	11	+
<i>Isochnus</i>	1	+
<i>Tachyerges</i>	3	+
<i>Rhamphus</i>	1	+
Ceratopinae (1)		
Ceratopini		
<i>Ceratopus</i>	1	-
Erirehinae (9)		
Derelomini		
<i>Pedetinus</i>	1	+
<i>Hypoleschus</i>	1	-
<i>Phyllotrox</i>	5	-
<i>Acalyptus</i>	1	-
<i>Derelomus</i>	1	-
Zygopinae (4)		
Zygopini		
<i>Cylindrocopturus</i>	1	-
<i>Peltophorus</i>	1	-
Lechriopini		
<i>Lechriops</i>	1	-
<i>Acoptus</i>	1	-
Ceutorhynchinae (47)		
Hypurini (1)		
<i>Hypurus</i>	1	+
Mononychini (1)		
<i>Mononychus</i>	1	+
Cnemogonini (20)		
<i>Craponius</i>	1	+
<i>Cnemogonus</i>	1	+
<i>Acanthoscelidius</i>	5	+
<i>Hypocoeliodes</i>	3	+
<i>Auleutes</i>	5	+
<i>Perigaster</i>	3	+
<i>Dietzella</i>	1	+
<i>Panophthalmus</i>	1	+
Ceutorhynchini (7)		
<i>Ceutorhynchidius</i>	1	-
<i>Ceutorhynchus</i>	2	-
<i>Sirocalodes</i>	1	-
<i>Trichosirocalus</i>	1	-
<i>Rileyonymus</i>	1	-
<i>Nedyus</i>	1	-
Scleropterini (6)		
<i>Homorosoma</i>	1	+
<i>Amalus</i>	1	+
<i>Ruidosoma</i>	1	-
<i>Acallodes</i>	3	-
Phytobiini (12)		
<i>Phytobius</i>	2	+
<i>Eurhychiopsis</i>	1	+
<i>Rhinoncus</i>	4	+
<i>Pelenomus</i>	3	+
<i>Neophytobius</i>	1	+
<i>Parenthis</i>	1	+

Table 1 (continued)

Taxon	No. spp. examined	Spring +/-
BUPRESTIDAE		
[5 subfamilies; 6 tribes;		
9 genera; 10 species]		
Chalcophorinae (1)		
Chalcophorini		
<i>Hippomelas</i>	1	-
Buprestinae (2)		
Melanophilini		
<i>Chalcogenia</i>	1	-
Anthaxini		
<i>Anthaxia</i>	1	-
Chrysobothrinae (2)		
Actenodini		
<i>Megactenodes</i>	2	-
Agrilinae (4)		
Coroebini		
<i>Sambus</i>	1	+
<i>Pseudagrilus</i>	1	+
<i>Nickerleola</i>	1	+
<i>Pseudagriloides</i>	1	+
Trachyinae (1)		
Aphanisticini		
<i>Anthaxomorphus</i>	1	+
ANTHRIBIDAE		
[5 species]		
Choraginae		
Choragini		
<i>Araecerus</i>	1	-
<i>Choragus</i>	2	-
? species	1	-
<i>Euxenus</i>	1	-
MELANDRYIDAE		
[2 species]		
<i>Lederia</i>	1	-
<i>Microscapha</i>	1	-

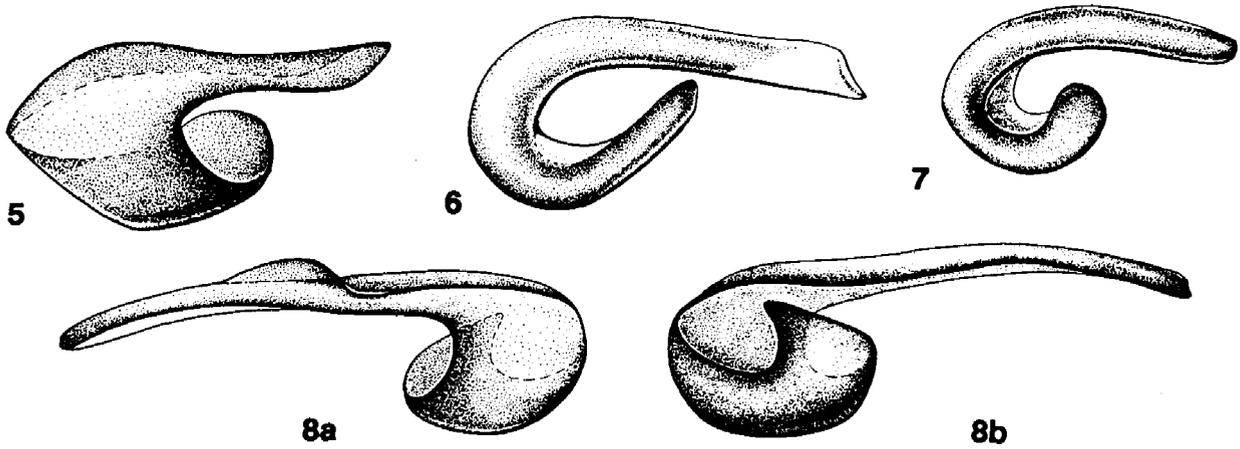
* Exclusive of Alticinae (see Furth, 1980).

† Terán (1964, 1967).

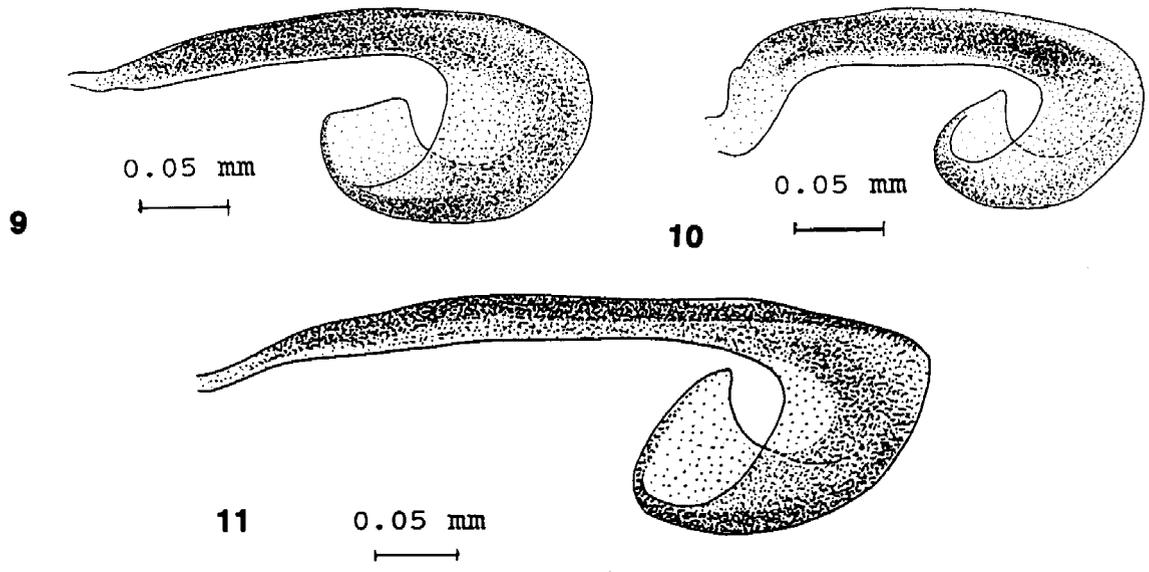
towards the anterior side but not expanded and with the entire spring of approximately equal thickness (height) (Fig. 6). *Eubaptus* spring morphology is clearly different from that of any Rhynchaeninae genera. Borowiec (*in litteris*) and Kingsolver (personal communication) assured the authors that *Eubaptus* is the only known bruchid genus with such a metafemoral spring.

Buprestidae

H. Sasaji (*in litteris*) told the authors of a jumping species of Buprestidae (*Sambus quadricolor* Saunders) (Agrilinae: Coroebini) and sent a specimen for study. Surprisingly this species does contain a metafemoral spring (Fig. 17). After considering other potentially jumping or swollen femora Buprestidae, Charles Bellamy (*in litteris*) suggested three other genera of primarily Afro-tropical



Figs 5-8. 5. *Pedetinus halioides* (Curculionidae: Erihiniinae) spring (anterior view). Length of spring (Lsp) = 0.33 mm. 6. *Eubaptus palliatus* (Bruchidae: Eubaptinae) spring (anterior view). Lsp = 0.40 mm. 7. *Hypurus* sp. (Curculionidae: Ceutorhynchinae: Hypurini) spring (anterior view). Lsp = 0.22 mm. 8. *Mononychus vulpeculus* (Curculionidae: Ceutorhynchinae: Mononychini) spring: a, posterior view; b, anterior view. Lsp = 0.48 mm.

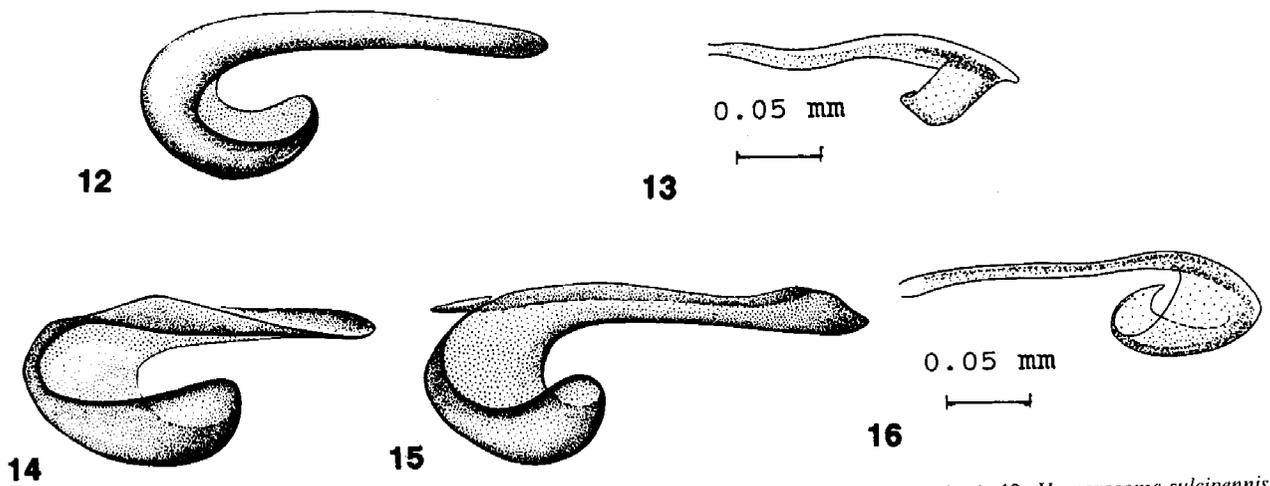


Figs 9-11 (Curculionidae: Ceutorhynchinae: Cnemogonini) spring (posterior view). 9. *Hypocoeliodes bicarinatus*; 10. *Auleutes asper*; 11. *Acanthoscelidius acephalus*.

Coroebini as well as some other genera in the Buprestinae, Chrysobothrinae and Trachyinae (Table 1). Of these last three subfamilies only *Anthaxomorphus* Deyrolle (Trachyinae: Aphanisticini) has a metafemoral spring (Fig. 18). The form of the spring in *Sambus* is simple, hook-shaped and somewhat similar to that of the Rhynchacninae and Ceutorhynchinae, although recognizably different; the other three genera of Coroebini (Agrilinae) are generally similar to *Sambus*, but with some evident differences. However, the spring morphology of *Anthaxomorphus* (Trachyinae) is quite different from all other buprestid genera. A tibial flexor sclerite is also found in all of these spring-containing buprestid genera.

Other Coleoptera

A variety of other beetles reported to jump in some fashion were examined for the presence of a spring, especially in their hind legs. Melandryidae, as well as Mordellidae, Scaptiidae, Eucinetidae, Limmichidae (Thaumastodinae) often referred to as jumpers, possess a variety of characteristics presumed to be associated with their jumping ability, such as expanded and/or modified metacoxae, long metatibial spurs, somewhat triangular abdomen (in cross-section), and some melandryid genera have the metafemur wider (dorso-ventrally) than other femora. The melandryid genus *Microscapha* LeConte



Figs 12-16. (Curculionidae: Ceutorhynchinae) spring (12, 14, 15: anterior view; 13, 16: posterior view). 12, *Homorosoma sulcipennis* (Scleropterini). Lsp = 0.33 mm. 13, *Amalus haemorrhous* (Scleropterini). 14, *Rhinoncus pericarpus* (Phytobiini). Lsp = 0.26 mm. 15, *Neophytobius cavifrons* (Phytobiini). Lsp = 0.26 mm. 16, *Parenthis vestitus* (Phytobiini).

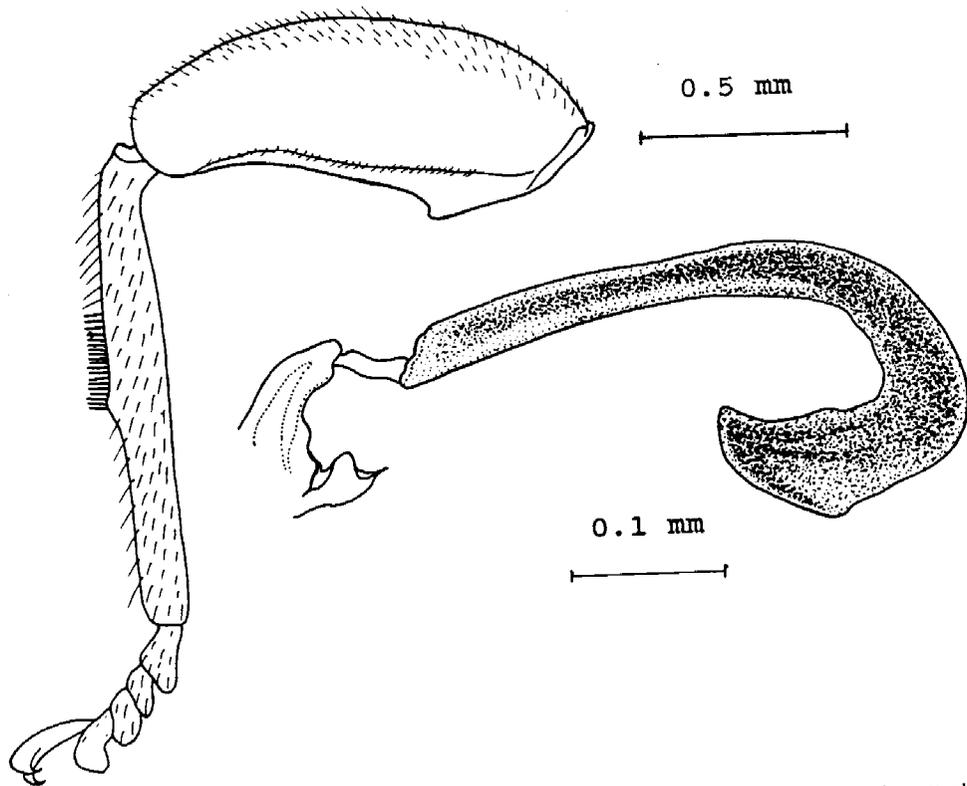


Fig. 17. *Sambus quadricolor* (Buprestidae: Agrilinae: Coroebini) hind leg and spring (posterior view of spring attached to metatibia).

has prominent metacoxae, but also has extremely long metatibial spurs (equal in length to the entire metatibia) and extremely long metatarsi (longer than the metafemur and metatibia together) - *Microscapha* and its close relative *Lederia* Reitter do not have a metafemoral spring (Table 1), nor do any of the families mentioned above.

Anthribidae are known to jump (B. Valentine, pers.

comm.) but dissection of metafemora in the known jumpers reveals no metafemoral spring (Table 1). The profemora of these anthribids are not modified or swollen differently than the metafemora, but the protibiae are distinctly longer (as long as profemora or longer) than the metatibiae (distinctly shorter than metafemora).

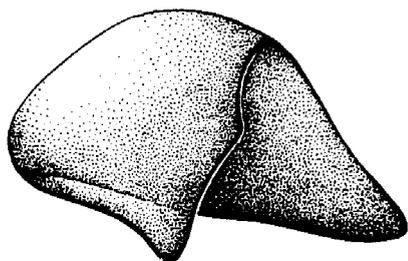


Fig. 18. *Anthaxomorpha paracoeruleus* (Buprestidae: Trachyinae: Aphanisticini) spring (anterior view). Lsp = 0.3 mm.

Discussion

As with insects in general, jumping behaviour/ability has arisen independently a number of times in the Coleoptera, the metafemoral spring mechanism being the most elaborate system reported to date. Even such an elaborate mechanism, through chitinization of the metatibial extensor tendon, could have (and almost certainly has) evolved independently in several families of the Coleoptera.

In the Bruchidae the metafemoral spring has been found in one genus (*Eubaptus*). *Eubaptus* is the only genus in the subfamily Eubaptinae, considered relatively advanced within the Bruchidae (Borowiec, 1987). Although the Bruchidae has often been included in the Chrysomelidae (Mann & Crowson, 1981) or has included certain chrysomelid subfamilies within it (Crowson, 1981), there is good evidence to retain Bruchidae as a separate family (Suzuki, 1988, unpublished, and see also Furth & Suzuki, 1990b). Thus, the metafemoral spring has certainly evolved separately in the Alticinae and the Bruchidae.

The study of the metafemoral spring of many species of the weevil subfamily Rhynchaeninae from four genera provides an interesting perspective on the evolution of the metafemoral spring. As with the Alticinae (Furth, 1980, 1982, 1988), the rhynchaenine spring has a constant intra-generic morphology but displays distinct inter-generic differences (Figs 3 and 4). As with *Eubaptus*, the basic morphology of the spring of the four genera of Rhynchaeninae is simplified in comparison to that of the Alticinae (Furth, 1988, 1989). These morphological principles correlate well with the spring of Alticinae, including the possibility that the simplified spring morphology may be a primitive condition (Furth, 1989; Furth & Suzuki, unpublished).

Other than *Pedetinus* (formerly Rhynchaeninae) a survey of the likely Erirhinae and Zygopinae genera produced no metafemoral spring. It is presumed that the Neotropical members of these weevil subfamilies observed to make small jumps do so through simple and sudden use of tibial extensor tendons and muscles.

The extent to which the metafemoral spring was discovered in the Ceutorhynchinae was unexpected, particularly because only three genera (*Hypocoeliodes*, *Auleutes* and *Acanthoscelidius*) have been observed to jump. One explanation of this may be that many of the genera have not been observed for long while alive; many collectors do

not keep specimens alive long enough and do not spend time observing behaviour in the field. In the Cnemogonini, other than the three genera mentioned above, *Craponius* LeConte and *Panophthalmus* Buchanan probably do jump but *Perigaster* Dietz does not (C. O'Brien, pers. comm.). The Phytobiini are all aquatic or semiaquatic as adult weevils and they swim well under water using different swimming techniques (C. O'Brien, pers. comm.). These techniques may include using all six legs independently, using the three pair of legs in a coordinated 'breast stroke' style, using the front legs only as a 'dog paddle', rowing with the middle pair of legs only, but none involve use of the hind legs only (C. O'Brien, pers. comm.). These weevils often have some morphological adaptations such as blade-like tibiae with hairs or setae and elongate tarsi that add efficiency to this swimming habit. Thus the metafemoral spring is unlikely to have any function in the swimming habit of this large tribe.

The metafemoral spring is present in all Ceutorhynchinae examined other than members of the Ceutorhynchini and two genera of the Scleropterini. In the case of the latter tribe, *Acallodes*, which lacks a spring, is an unusual genus which may eventually be placed in the Ceutorhynchini (C. O'Brien, pers. comm.), although the other springless genus, *Rutidosoma*, is not otherwise exceptional. *Amalus* was placed by Colonnelli (1979, 1984) in the Ceutorhynchini; however, recently Colonnelli (*in litteris*) suggests that the genus may be in Scleropterini and notes that it shares a foodplant family and morphological features with *Homorosoma* (Scleropterini). For these reasons, and because the presence of a spring would seem to exclude it from Ceutorhynchini, *Amalus* is considered here as Scleropterini.

Although spring morphology differs between genera and tribes of the Ceutorhynchinae, and between subfamilies (i.e. Rhynchaeninae), it is premature to attempt to establish morpho-groups as with the Alticinae. Phylogenetic analysis should consider the value of the spring morphology and whether it has been lost in certain groups such as the Ceutorhynchini, *Acallodes* and *Rutidosoma*. The mixture of presence and absence states of the spring within the Scleropterini is particularly suspect. However, also based on other characters the higher classification of the Curculionidae is known to need revision (C. O'Brien, pers. comm.).

The discovery of the metafemoral spring in five genera of two subfamilies of the Buprestidae was even more unexpected than in Ceutorhynchinae. Even though only members of the genus *Sambus* have been observed to jump, this ability is likely in species in the other four genera. Buprestids also demonstrate the principle of inter-generic spring morphological differences. Other subfamilies may be discovered to have a metafemoral spring after a more thorough survey.

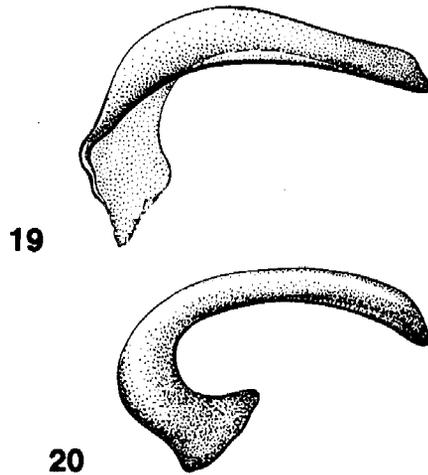
Several basic principles are evident from the present studies of the metafemoral spring in Coleoptera. Although the metafemoral spring has evolved from chitinization of the metatibial extensor tendon (Furth & Suzuki, 1990b), no group has been discovered with a 'vestigial' spring. The functional aspects of the metafemoral spring dic-

tate a minimum simplified morphology as found in the Coleoptera considered in the present study compared with the Alticinae (Fig. 21). As in the Alticinae each genus of these other beetle groups possesses a constant and characteristic spring morphology. The groups considered here appear to have spring morphological patterns associated with their higher categories; however, this requires more extensive investigation.

A more comprehensive survey of the tribes and genera of these other beetle families is necessary in order to determine if there is any phylogenetic value to the morphological similarities and differences of their metafemoral spring. The metafemoral spring has independently evolved in four different families of Coleoptera, probably in at least two different groups of the Curculionidae, and possibly two groups of the Buprestidae. Although the higher classification of these four families is currently unclear, there is no pattern of close relatedness among these beetle groups; therefore, this appears to be a good example of convergent evolution.

The authors think that the metafemoral spring functions only for jumping and that even though some groups may have lost the ability/need to jump, they still retain the spring mechanism. We also believe that such an internally chitinized functional mechanism arose only once within each higher group (i.e. subfamily and/or tribe) evolving inter-generic differences and did not appear and disappear repeatedly within each group; such monophyletic scenario is parsimonious. Therefore there is a potential phylogenetic value to character analysis of the metafemoral spring.

In the Alticinae only the 'primitive' *Buphonella* Jacoby (*sensu* Wilcox, 1975) (Fig. 19) and *Chaloesoma* Jacoby (aberrant in various alticine characters) (Fig. 20) have a



Figs 19–20. (Chrysomelidae: Alticinae) spring (anterior view). 19, *Buphonella murina*. Lsp = 0.63 mm. 20, *Chaloesoma metallica*. Lsp = 0.7 mm.

simplified spring morphology similar to that in the Curculionidae, Bruchidae and Buprestidae – all other Alticinae have relatively elaborate spring morphology (Furth, 1980, 1988) (Fig. 21). Even though these two alticine genera are morphologically different from each other and from the non-alticine families, they indicate that metafemoral spring evolution may have begun with a simplified spring and derived a more elaborate form. Therefore, metafemoral spring evolution may not have proceeded as far in the Curculionidae, Bruchidae and Buprestidae as it did in the Alticinae.

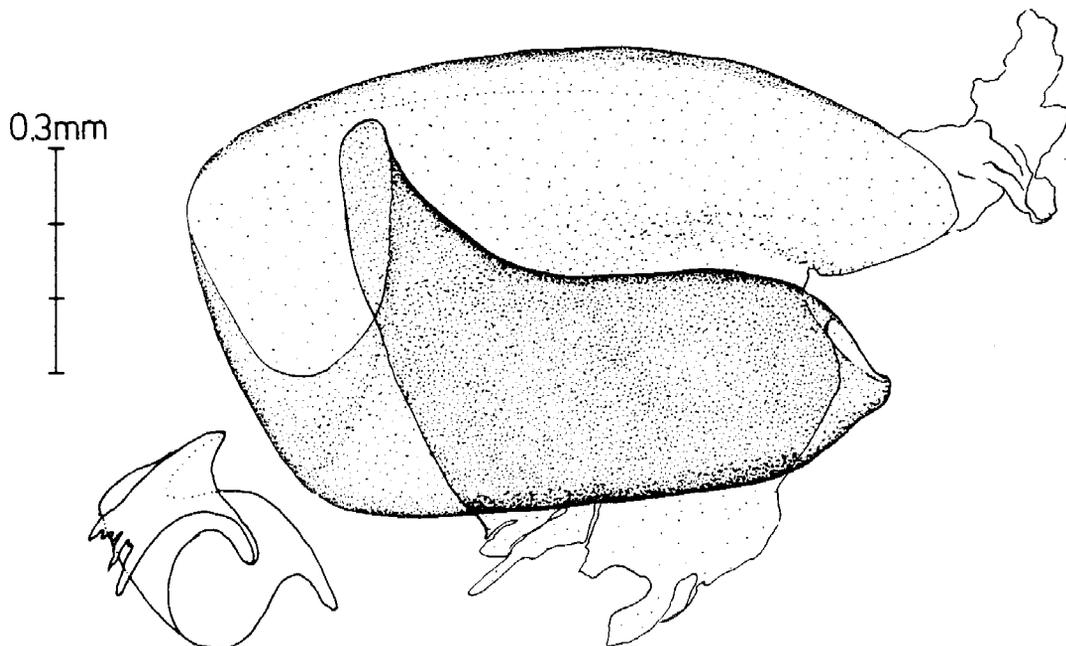


Fig. 21. *Psylliodes hyoscyamus* (Chrysomelidae: Alticinae) spring (anterior view with schematic diagram).

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References

- Anderson, R.S. (1989) Revision of the subfamily Rhynchaeninae in North America (Coleoptera: Curculionidae). *Transactions of the American Entomological Society*, **115**, 207–312.
- Bellamy, C.L. (1985) A catalogue of the higher taxa of the family Buprestidae (Coleoptera). *Navorsinge van die Nasionale Museum, Bloemfontein*, **4**, 405–472.
- Borowiec, L. (1987) The genera of seed-beetles (Coleoptera, Bruchidae). *Polskie Pismo Entomologiczne*, **57**, 3–207.
- Byers, G. (1983) The Crane Fly genus *Chionea* in North America. *The University of Kansas Science Bulletin*, **52**, 59–195.
- Colonnelli, E. (1979) Note su *Panophthalmus* e generi affini, con descrizione di una nuova tribù e di una nuova specie della sottofamiglia Ceutorhynchinae (Coleoptera, Curculionidae). *Bollettino Associazione Romana di Entomologia*, **34**, 1–9.
- Colonnelli, E. (1984) Notes sur quelques Ceutorhynchinae de l'Afrique tropicale (Coleoptera, Curculionidae). *Annales Historico-Naturales Musei Nationalis Hungarici*, **76**, 207–238.
- Crowson, R.A. (1981) *The Biology of Coleoptera*. Academic Press, London.
- Evans, M.E.G. (1972) The jump of the click beetle – a preliminary study. *Journal of Zoology, London*, **167**, 319–336.
- Evans, M.E.G. (1975) The jump of *Petrobius* (Thysanura, Machilidae). *Journal of Zoology, London*, **176**, 49–65.
- Furth, D.G. (1980) Inter-generic differences in the metafemoral apodeme of flea beetles (Chrysomelidae: Alticinae). *Systematic Entomology*, **5**, 263–271.
- Furth, D.G. (1982) The metafemoral spring of flea beetles (Chrysomelidae: Alticinae). *Spixiana (Supplement)*, **7**, 11–27.
- Furth, D.G. (1985) Relationships of Palearctic and Nearctic genera of Alticinae. *Entomography*, **3**, 375–392.
- Furth, D.G. (1988) The jumping apparatus of flea beetles (Alticinae): the metafemoral spring. *Biology of Chrysomelidae* (ed. by P. Jolivet, E. Petitpierre and T. H. Hsiao). Chapter 17, pp. 285–297. Kluwer Academic Publishers, Dordrecht.
- Furth, D.G. (1989) Metafemoral spring studies of some Neotropical genera of Alticinae. *Entomography*, **6**, 497–510.
- Furth, D.G. & Suzuki, K. (1990a) Comparative morphology of the tibial flexor and extensor tendons in insects. *Systematic Entomology*, **15**, 433–441.
- Furth, D.G. & Suzuki, K. (1990b) The metatibial extensor tendons in Coleoptera. *Systematic Entomology*, **15**, 443–448.
- Furth, D.G., Traub, W. & Harpaz, I. (1983) What makes *Blepharida* jump? A structural study of the metafemoral spring of a flea beetle. *Journal of Experimental Zoology*, **227**, 43–47.
- Gibson, G.A.P. (1986) Mesothoracic skeletomusculature and mechanics of flight and jumping in Eupelminae (Hymenoptera, Chalcidoidea: Eupelmidae). *The Canadian Entomologist*, **118**, 691–728.
- Lever, R. (1930) A new endoskeletal organ in the hind leg of the Halticinae. *Zoologische Anzeiger*, **92**, 287–288.
- Maulik, S. (1929) On the structure of the hind femur in halticine beetles. *Proceedings of the Zoological Society of London*, **2**, 305–308.
- Mann, J.S. & Crowson, R.A. (1981) The systematic positions of *Orsodacne* Latr. and *Syneta* Lac. (Coleoptera Chrysomelidae), in relation to characters of larvae, internal anatomy and tarsal vestiture. *Journal of Natural History*, **15**, 727–749.
- Manton, S.M. (1972) The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. *Zoological Journal of the Linnean Society*, **51**, 203–400.
- O'Brien, C.W. & Wibmer, G.J. (1982) Annotated checklist of the weevils (Curculionidae *sensu lato*) of North America, Central America, and the West Indies (Coleoptera: Curculionidae). *Memoirs of the American Entomological Institute*, **34**, 1–382.
- O'Brien, C.W. & Wibmer, G.J. (1986) Annotated checklist of the weevils (Curculionidae *sensu lato*) of North America, Central America, and the West Indies, Supplement 1. *The Southwestern Entomologist*, **9**, 286–307.
- Pomorski, R.J. (1978) Das Vorkommen des Maulikischen Sprungapparates bei den Springruesslern (Coleoptera, Curculionidae). *Polskie Pismo Entomologiczne*, **48**, 601–602.
- Riek, E.F. (1970) Hymenoptera. *The Insects of Australia* (ed. by D. F. Waterhouse), Chapter 37, pp. 867–943. Melbourne University Press, Carleton.
- Rothschild, M., Schlein, J., Parker, K., Neville, C. & Sternberg, S. (1975) The jumping mechanism of *Xenopsylla cheopsis*. III. Execution of the jump and activity. *Philosophical Transactions of the Royal Society, B*, **271**, 499–515.
- Suzuki, K. (1988) Comparative morphology of the internal reproductive system of the Chrysomelidae (Coleoptera). *Biology of Chrysomelidae* (ed. by P. Jolivet, E. Petitpierre and T. H. Hsiao), Chapter 19, pp. 317–355. Kluwer Academic Publishers, Dordrecht.
- Terán, A.L. (1964) Algunas novedades en el género *Eubaptus* Lac. (Col., Bruchidae). *Acta Zoologica Lilloana*, **20**, 177–186.
- Terán, A.L. (1967) Consideraciones sobre *Eubaptus palliatus* Lac., *Bruchus scapularis* Pic y description de los estados preimaginales de *Eubaptus rufithorax* (Pic). *Acta Zoologica Lilloana*, **21**, 71–89.
- Wibmer, G.J. & O'Brien, C.W. (1989) Additions and corrections to annotated checklists of the weevils of North America, Central America, and the West Indies, and of South America. *Southwestern Entomologist, Supplement*, **13**, 1–49.
- Wilcox, J.A. (1975) Chrysomelidae: Galerucinae. *Coleopterorum Catalogus, Supplementa*, **78**, (4), 667–770.