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The metatibial extensor and flexor tendons in Coleoptera

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Abstract. The metatibiae of genera in several families of Coleoptera with enlarged metafemora are examined, including Chrysomelidae (Alticinae, Galerucinae, Sagrinae), Bruchidae (Pachymerinae, Rhaebinae, Eubaptinae, Bruchinae), Scirtidae and Oedemeridae. There is an evident pattern concerning the relative size of the tibial extensor and flexor tendons that is dependent on the type of hind leg movement of a specific beetle group. Beetle groups that jump (e.g. Alticinae, Scirtidae) always have a greatly enlarged metatibial extensor tendon and associated musculature. However, other groups with swollen metafemora that do not jump have enlarged metatibial flexor tendons with the associated musculature for holding/grasping onto the vegetation (Sagrinae, Bruchidae) or onto the female during copulation (male *Oedemera*). This indicates a strong functional relationship between Sagrinae and Bruchidae, both with large flexor tendons, and between the Alticinae and Galerucinae, with relatively large extensor tendons; these two cases may also have phylogenetic meaning. This pattern of the metatibial extensor and flexor tendon size related to function is presumably true for at least all other Coleoptera.

Introduction

The authors have studied several aspects of leg morphology, especially the metafemora, of Coleoptera and certain other insect orders. These studies include aspects of the tibial extensor and flexor tendons, especially the tibial flexor sclerite (Furth & Suzuki, 1990), the metafemoral spring of the Alticinae (Furth, 1980, 1982, 1985, 1988, 1989) and certain other Coleoptera (Furth & Suzuki, in prep.), and the use of leg characters in character congruence chrysomelid higher classification (unpublished). In the accompanying study (Furth & Suzuki, 1990), although the major emphasis is on the tibial flexor sclerite, the tibial flexor and extensor tendons are also examined, including their relative size, orientation and degree of sclerotization. It has become apparent from this research on the legs, especially the metafemora, that there are patterns and relationships between the size of the metafemoral capsule and the tendons with their associated musculature. The dissection and drawing techniques are essentially the same as given in Furth & Suzuki (1990).

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Few aspects of the internal structure of the hind legs of Coleoptera have been studied that do not relate to the musculature or other soft part structures. Several studies have considered certain tendons or apodemes, but, as with most insect orders, this has primarily been concerned with the basic aspects of locomotion (see Evans, 1977; Larsen, 1966). Some of these (Larsen,

1966) have dealt with only the proximal parts of the legs (e.g. coxa, trochanters, etc.) rather than with the structure or function of femorotibial articulation. Snodgrass's (1935, 1952) treatments of the morphology of the femorotibial joint of the generalized insect leg were elaborated by Chapman (1969) to illustrate the basic functional aspects of tibial extension and flexion.

A structure present only in some Coleoptera legs is the femoral chordotonal organ which is attached to the tibial extensor tendon through a flexible sclerite, the arcellate apparatus. Through their ligament connections the chordotonal organ and arcellus sense the amount of stress exerted by muscular action on the tibial extensor tendon. There is great diversity in the morphology of the arcellus of different Coleoptera taxa (Frantsevich & Shumakova, 1988).

Maulik (1929) discovered a special structure inside the metafemora of the Alticinae (flea beetles) and described it as a 'chitinized tendon'. More recently, Furth (1980, 1985, 1988) has discussed the morphology and function of this metafemoral apodeme/spring which, through tension energy storage, enable Alticinae to be such effective jumpers and indicates its homology to a chitinized elaboration of the metatibial extensor tendon. Shortly after Maulik's discovery, Lever (1930) described another 'chitinized tendon' attached to the flea beetle metatibiae which is apparently a modification of the metatibial flexor tendon (Furth & Suzuki, 1990). In associated studies the authors investigated the tibial flexor and extensor tendons in a range of insects; however, in the present paper the authors have examined only one aspect of these tibial tendons as it pertains to the functions of the Coleopteran leg, especially the hind leg.

Results

After examination of a variety of beetle taxa (several families) with enlarged metafemora, it is apparent that there are several tendencies regarding their metatibial extensor and flexor tendons. The Sagrinae, represented by *Sagra femorata* (Fig. 1), have a distinctly enlarged metafemoral capsule containing a tibial flexor tendon that is several times larger than the antagonistic tibial extensor tendon; a large distinct, bulbous and heavily sclerotized tibial flexor sclerite is also present (see Furth & Suzuki, 1990, Fig. 1). Several genera of Bruchidae with enlarged metafemora, including *Carysobruchus* (Fig. 2), *Rhaebus*, *Caryedes* and *Eubaptus*, were examined. Except for *Eubaptus*, known to have a sclerotized extensor tendon (Terán, 1964) anatomically homologous to the metafemoral spring of Alticinae, these other bruchid genera have the tibial flexor tendon distinctly larger than the tibial extensor tendon.

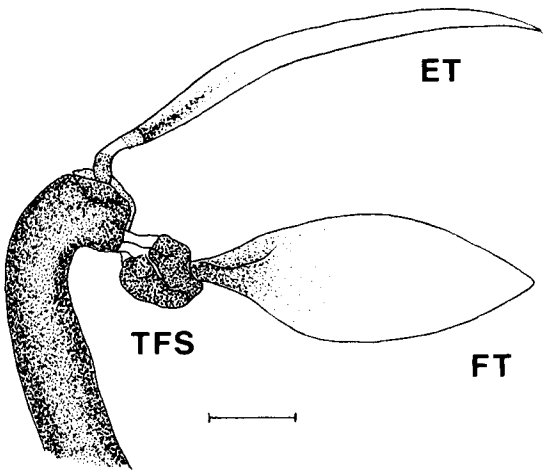

Fig. 1. *Sagra femorata* (Drury) (Chrysomelidae), metatibial base and tendons. (ET = tibial extensor tendon, FT = tibial flexor tendon, TFS = tibial flexor sclerite). Scale bar = 1 mm.

A somewhat different situation is present in certain Oedemeridae, particularly the Old World genus *Oedemera*, in which the hind femora of only the males are greatly enlarged. Upon dissection and examination of *Oedemera* it was discovered that their metafemur contains a complex flexor tendon divided into five parts (a central and two divided lateral longitudinal flanges) joined at the base near the ventral femoro-tibial articulation by a type of composite tibial flexor sclerite. Each of these parts of the tibial flexor tendon is almost equal to the size of the tibial extensor tendon, and taken together the tibial flexor tendon is much larger than the tibial extensor tendon.

Another beetle family containing genera with enlarged hind femora is the Scirtidae (formerly Helodidae) (e.g. *Scirtes* and *Cyphon*) species of which are well known to jump. Examination of *Scirtes* (Fig. 3) and *Cyphon* metafemora reveal

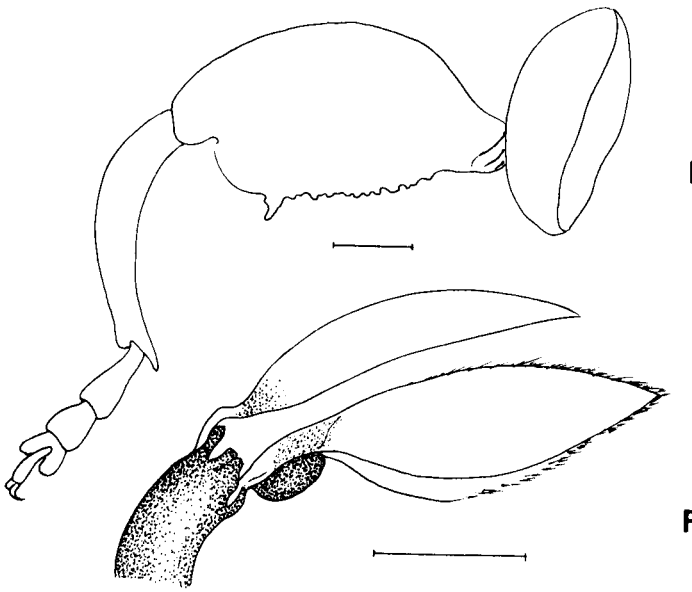

Fig. 2. *Carysobruchus gleditsiae* (Linn.) (Bruchidae). 2a, metafemur and metatibia; 2b, metatibial base and tendons. Scale bars = 1 mm.

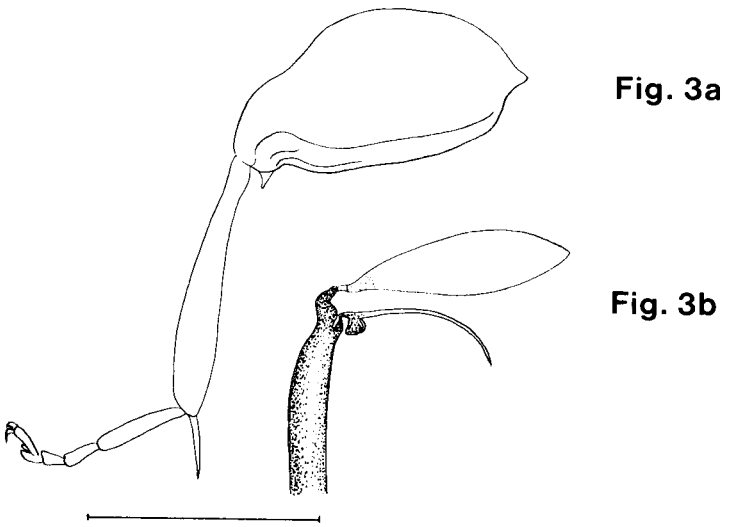

Fig. 3. *Scirtes tibialis* Guerin (Scirtidae). 3a, metafemur and metatibia; 3b, metatibial base and tendons. Scale bar = 1 mm.

that the tibial extensor tendon is much larger than the tibial flexor tendon, i.e. the opposite condition from the Sagrinae, Bruchidae and Oedemeridae mentioned above. Other genera of the Scirtidae without swollen metafemora and not known to jump were not examined.

Among the Chrysomelidae the Alticinae are known to have enlarged metafemora, to be

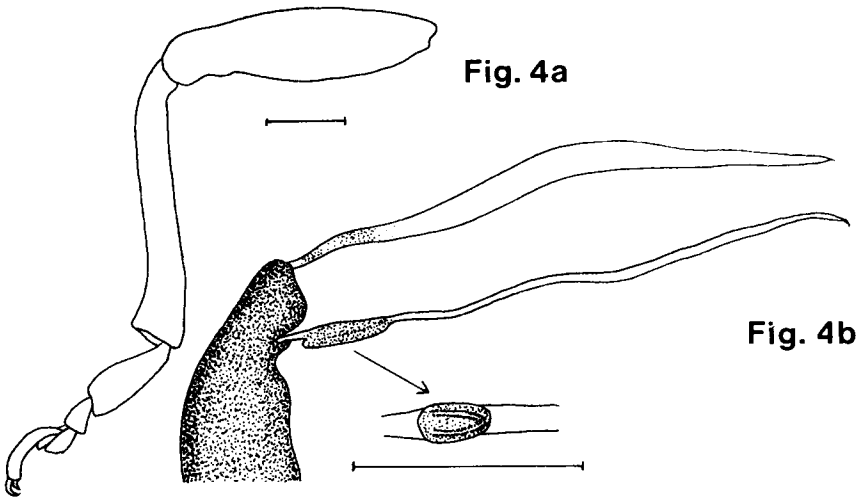

Fig. 4. *Galeruca sardoa* (Gene) (Chrysomelidae). 4a, metafemur and metatibia; 4b, metatibial base and tendons. Scale bars = 1 mm.

good jumpers, and to contain a metafemoral spring or modified tibial extensor tendon (Maulik, 1929; Furth, 1988). These characters of the flea beetles are used to separate them from the closest chrysomelid subfamily, the Galerucinae. The metafemora of several genera of Galerucinae have been examined (*Oides*, *Monolepta*, *Philocalis*) and their tibial extensor tendon is slender but significantly larger than the tibial flexor tendon, even though the metafemoral capsule is not noticeably swollen in these genera. There are genera of Alticinae that have been placed in the Galerucinae by previous workers because they have metafemora that are not significantly enlarged (Wilcox, 1975); however, these genera do have a tibial extensor apodeme/metafemoral spring (Wilcox, 1975; Furth & Suzuki, unpublished).

Discussion

An effort has been made to study representatives of a variety of Coleoptera families possessing enlarged metafemora in order to examine potentially different internal conditions of the tendons that are responsible for the movement of the hind legs. The first aspect of this study involved the relationship of the Sagrinae to the Bruchidae. The Sagrinae are considered by many workers to be one of the most primitive subfamilies of the Chrysomelidae (Seeno & Wilcox, 1982; Suzuki, 1988). The Bruchidae have been considered by some workers to be a subfamily of the Chrysomelidae and closely related to the Sagrinae (Monros, 1959; Mann & Crowson, 1981, 1983a, b). However, based on male and female reproductive structures Suzuki (1988, and unpublished) has shown that the Bruchidae are quite separate from the Sagrinae and the Chrysomelidae in general; Schmitt (1989) basically agrees with this separation. In the greatly enlarged metafemur of the Sagrinae the tibial flexor tendon is much larger than the tibial extensor tendon (Fig. 1); the major part of this swollen femur is occupied by the tibial flexor muscles attached to this large tendon. Similarly in the many Bruchidae with enlarged metafemora the tibial flexor tendon is larger than the tibial extensor tendon (Fig. 2) and the tibial flexor muscles are larger than the extensors. Kingsolver (personal communication) has dissected many Bruchidae with large metafemora and has also found the tibial flexor muscles to be much larger than the extensors. Therefore, most Sagrinae and some Bruchidae share the condition of large tibial flexor tendons and the associated musculature. The presumed explanation for the enlarged flexors in both the Sagrinae and Bruchidae is that the action of flexion

of the hind tibia is an important aspect of the biology of these groups, probably used primarily for holding onto stems of their foodplants.

In the case of *Oedemera*, where only the males have distinctly enlarged metafemora, the larger and complicated (five part) tibial flexor tendon with its associated musculature is certainly concerned with the male's ability to grasp and hold the female during copulation. At this point it is difficult to explain the exact reason for this unique anatomical complexity. Even though this is a quite different function for the legs, it is similar to that in Sagrinae–Bruchidae in that flexion is the primary action, and, therefore, the tibial flexor tendon is much more developed than the tibial extensor tendon.

In the jumping members of the Scirtidae (e.g. *Scirtes* and *Cyphon*) (see Fig. 3) the metafemora are greatly swollen and the tibial extensor tendon and its associated musculature are much larger and occupy significantly more space than the tibial flexor tendon and muscles. This difference from the two previously mentioned situations is quite logical because unlike the sagrine/bruchid group or *Oedemera* the primary hind leg action is extension (i.e. jumping).

The final case to be considered is that of the Alticinae–Galerucinae, which are closely-related chrysomelid subfamilies. The Alticinae (flea beetles) are well known to be good jumpers and are usually distinguished from the Galerucinae by their greatly enlarged metafemora. The alticine jumping mechanism inside the swollen hind legs was discovered by Maulik (1929) and more recently studied in detail by Furth (1988, 1989), who found that there are intergeneric morphological differences in this metafemoral spring; Furth (1982) discussed its anatomy and function, and Furth *et al.* (1983) its histology. Essentially the metafemoral spring is an enlarged, chitinized and elaborate modification of the tibial extensor tendon with large extensor muscles attached, increasing the jumping ability; it has also been found in one genus of the Bruchidae (Terán, 1964, 1967) and one genus of the Curculionidae (Pomorski, 1978). As a follow-up to Maulik's original discovery Lever (1930) described another 'chitinized tendon' from Alticinae also said to be associated with their jumping mechanism. Recently, this organ has been studied in detail (Furth & Suzuki, 1990) and discovered to be present in many other Coleoptera as well as certain other insect orders. This organ is actually an independently movable chitinized sclerite attached to the base of the tibia and to the tibial flexor tendon and muscles, and it is certainly derived from this tendon. The Galerucinae do not have obviously enlarged metafemora or a metafemoral spring, and do not jump; however, they do have a tibial extensor tendon that is noticeably larger than the tibial flexor tendon (Fig. 4). The Galerucinae are considered quite closely related to the Alticinae (Suzuki, 1988; Furth, 1989) and it is easy to imagine that the anatomically homologous metafemoral spring (with the jumping ability that it affords) arose from an already enlarged tibial extensor tendon as is present in the Galerucinae (see Furth, 1982, for figures of the Alticinae metafemoral spring).

There are certainly other aspects of these tibial tendons that can be studied and correlated to the behaviour and/or relationships of various taxa. For example, an aspect which has not been considered here is the correlation of size and shape of femora and tibiae within a taxon with the detailed behaviour and locomotion ability of those different Coleoptera groups. Forsythe (1983) discussed the relatively enlarged hind femora (length and width) of certain Carabidae that allowed the expansion of tibial extensor and flexor muscles necessary for increased pushing ability. In-depth study and examination of certain other beetle families may also reveal interesting morphological patterns that reflect behaviour and/or phylogeny. Nevertheless, the present study does reveal a morphological pattern, in Coleoptera with enlarged metafemora, of the relative sizes of the metatibial extensor and flexor tendons (and associated musculature) correlating well with jumping and grasping behaviour. For those who appreciate a little humour in science, this pattern might be called a tibial extensor/flexor 'tendoncy'.

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