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Comparative morphology of the tibial flexor and extensor tendons in insects

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Abstract. The relative size, orientation, and degrees of sclerotization of the tibial flexor and extensor tendons are compared in nineteen orders of insects. The sclerotized, independently movable tibial flexor sclerite, known previously only from Alticinae and Carabidae (Coleoptera), is found in some other Coleoptera, Megaloptera, Neuroptera, Hymenoptera and Heteroptera. The Heteroptera also have another small sclerite at the base of the tibial extensor tendon. The tibial flexor sclerite is presumed to provide additional strength and leverage to the flexion of the tibia in certain insect groups; it may also provide protection for the ventral side of the femoro-tibial joint of the leg.

Introduction

The internal morphology of the femoro-tibial joint of the insect leg has apparently received less attention than other aspects of the thorax; i.e. the coxa/trochanter/femur interface. Most studies of insect locomotion usually have focused on morphology of these various other parts closer to the thorax (e.g. Hughes, 1952). However, the action of the tibiae, with the associated tarsi, is as important or more so to insect locomotion. The muscles that control tibial movement (flexion and extension or levation and depression, respectively) are located in the femur and fill the femoral capsule. These tibial flexor and extensor muscles are attached to the base of the tibia by tendons. While a number of previous studies discuss various aspects of the tibial flexor and extensor muscles and their tendons, concerning a relatively few insect and other arthropod orders (Morison, 1927 [Hymenoptera]; Snodgrass, 1935 [Orthoptera], 1942, 1956 [Hymenoptera]; Hughes, 1965 [general insect kinetics]; Manton, 1968 [Araneae], 1972 [Apterygota]; Thakare, 1972 [Orthoptera]; Heitler, 1977 [Orthoptera]; Evans, 1977 [Coleoptera]; Burns & Usherwood, 1978 [Orthoptera]; Bowerman & Root, 1978 [Scorpiones]; Forsythe, 1983 [Coleoptera], Toro & Magunacelaya, 1987 [Hymenoptera], very few studies give morphological details about other orders. In the present study we examine and discuss the tibial locomotory tendons and their modifications in many insect orders. We prefer to use the term tibial extensor and flexor tendons, rather than levator/depressor or abductor/adductor used in a similar case for the locust jump (Heitler, 1977), to describe the functional aspects of the present study.

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In order to properly understand the true functional mechanism of the insect leg, it is necessary to study its anatomy in great detail (Pringle, 1939). Because of the differences in shape of legs in different insect groups, one can only decipher a general functional view of the leg muscles; i.e. flexors and extensors, that basically raise and lower the insect from the ground (Pringle, 1939). Even though Snodgrass (1935) gave more detailed morphological descriptions and figures of the insect leg than most workers, he did so primarily based on only the locust *Dissosteira* and his 1942 and 1956 studies gave skeleto-muscular details of only the honey bee. Homologous muscles may serve different functions in different insect groups, e.g. the jumping muscle of the grasshopper is the tibial extensor which is normally a levator (Pringle, 1939).

The insect's movement is governed by a variety of factors, and even though all muscles are striated and capable of rapid contraction there is a wide range of the rate of contraction achieved. The rate of movement associated with a particular joint is also determined by the associated musculature and the different tensions they exert (Hughes, 1965). It is at the femoro-tibial joint, through the action exerted on the tibia by the muscles and through their tendons, that the type of locomotion is determined (e.g. lifting, walking, running, jumping, etc.) and the thrust against the substrate is produced.

This research originated from studies of specialized modifications of the tibial extensor and flexor tendons associated with the metafemora and the jumping habits of flea beetles (Chrysomelidae: Alticinae). Maulik (1929) described a special structure that he referred to as a 'chitinized tendon' located in the metafemora of the Alticinae. This structure has been mentioned in the literature and referred to by various names: Costa Lima's Organ (Barth, 1954); extensor apodeme (Wilcox, 1965); Maulik's Organ (Paulian, 1942; Scherer, 1971); and metafemoral spring (Furth, 1982, 1985, 1988). In fact, Maulik's original description is quite accurate because it appears that this structure is a chitinized elaboration of the tibial extensor tendon, responsible for the generally good jumping ability of flea beetles. The Alticinae are generally distinguished from their apparent closest relatives the Galerucinae by the swollen metafemora which contain the large tibial extensor muscles, presumably for jumping. Furth (1985) defined the Alticinae as those members of the Chrysomelidae possessing this metafemoral spring. Another metatibial structure was described from the Alticinae by Lever (1930). He found a triangular plate linking a ventral muscle in the metafemur to the base of the tibia, and presumed it also to be a kind of 'chitinized tendon' probably involved in jumping. Lever mentioned that this 'chitinized tendon' is absent from the Galerucinae; however, we report different findings in this paper. Paulian (1942) describes this 'Lever's Organ' in detail in the Sagrinae. Elsewhere this structure has been rarely mentioned in the literature but has been referred to as 'Plate T' (Barth, 1954) and recently as Lever's triangular plate (Furth, 1980, 1982, 1988). This structure is apparently a modification/specialization of the tibial flexor tendon in Alticinae. However, the functional aspects of this tibial flexor plate or its presence in other taxa have never been investigated.

Methods

The insect legs were boiled or soaked overnight in 10% KOH (to remove muscle tissue), then dissected in water under a binocular dissecting microscope. The femoral capsule was opened longitudinally and the tibia, with its flexor and extensor tendon attachments, was separated. Detailed comparative observations were recorded as to the presence or absence of the tibial flexor sclerite, the relative size, orientation, and the degree of sclerotization of the tibial flexor and extensor tendons. Drawings were made of the tibia and its tendons using a Bausch and Lomb binocular dissecting microscope with an ocular square grid (10 × 10). We decided to make a superficial survey of insects by studying a wide variety of insect orders representing most of the major lineages. To this end we examined specimens of nineteen orders of insects, usually dissecting at least two individuals of each taxon or two taxa from each order. We studied the legs (tibiae) of these orders by using the left hind leg; however, in several cases the fore and middle legs were also examined in order to be certain that all legs had the same tibial tendon situation.

We searched the literature for any reference to structures similar to the tibial flexor sclerite by using *Entomology Abstracts* and *Biological Abstracts* (past 30 years) and checking references for jumping, locomotion and tibiae.

Results

Although the tibial flexor tendon has been the primary focus of our study, the tibial extensor tendon was also examined in each dissection

Table 1. Comparative aspec

Taxon
1. Odonata: Aeschnidae
2. Ephemeroptera: Hexage
3. Orthoptera: Acrididae 1
4. Orthoptera: Acrididae 2
5. Mantodea: Mantidae
6. Phasmatodea: Heteronem
7. Blattaria: Blattidae
8. Dermaptera: Carcinopho
9. Isoptera: Rhinotermitida
10. Plecoptera: Pteronarcida
11. Hemiptera: Cicadidae
12. Hemiptera: Lygaeidae
13. Hemiptera: Reduviidae
14. Hemiptera: Pentatomida
15. Hemiptera: Coreidae 1
16. Hemiptera: Coreidae 2
17. Mecoptera: Panorpidae
18. Neuroptera: Myrmeleon
19. Megaloptera: Corydalida
20. Hymenoptera: Sphecida
21. Diptera: Asilidae
22. Lepidoptera: Saturniida
23. Trichoptera: Limnephili
24. Coleoptera: Tenebrioni
25. Coleoptera: Chrysomeli
26. Coleoptera: Cerambyci
27. Coleoptera: Cerambyci
28. Coleoptera: Cerambyci
29. Coleoptera: Cerambyci
30. Coleoptera: Curculioni
31. Coleoptera: Curculioni
32. Coleoptera: Curculioni
33. Coleoptera: Curculioni

* All nineteen subfamilies

Explanation of symbols: T

+ = presence; V = vertical;

Sclerotization states: 1 =

only; 5 = TFS and most of t

Species names of taxa in T

McNeil; 4, *Paradalophora a*

Say; 7, *Periplaneta american*

Pteronarcys sp.; 11, *Tibice*

Brochymena quadripustulata

claripennis Hine; 18, *Vella te*

Promachus aldrichi Hine; 2

group; 25, *Sagra femorata* (

Megacyllene robinae (Forste

sulcatus (Fabricius); 32, *Hyp*

Table 1. Comparative aspects of tibial tendons in insects.

Taxon	TFS	Orientation ET	Orientation FT	ET/FT	Sclerotization ET	Sclerotization FT
1. Odonata: Aeschnidae	–	H	H	ET<FT	1	2
2. Ephemeroptera: Hexageniidae	–	H	H	ET=FT	1	1
3. Orthoptera: Acrididae 1	–	V	H	ET>FT	2	2
4. Orthoptera: Acrididae 2	–	V	H	ET>FT	2	2
5. Mantodea: Mantidae	–	H	H	ET<FT	2	2
6. Phasmatodea: Heteronemiidae	–	H	H	ET<FT	1	2
7. Blattaria: Blattidae	–	H	H	ET=FT	1	1
8. Dermaptera: Carcinophoridae	–	H	H	ET=FT	2	2
9. Isoptera: Rhinotermitidae	–	H	H	ET=FT	2	2
10. Plecoptera: Pteronarcidae	–	H	H	ET<FT	1	2
11. Hemiptera: Cicadidae	–	V	V	ET<FT	2	2
12. Hemiptera: Lygaeidae	+	H	H	ET<FT	4	5
13. Hemiptera: Reduviidae	+	H	H	ET<FT	2	4
14. Hemiptera: Pentatomidae	+	V	V	ET<FT	4	5
15. Hemiptera: Coreidae 1	+	V	V	ET<FT	4	5
16. Hemiptera: Coreidae 2	+	V	V	ET<FT	4	5
17. Mecoptera: Panorpidae	–	H	H	ET=FT	1	1
18. Neuroptera: Myrmeleontidae	+	H	H	ET<FT	2	4
19. Megaloptera: Corydalidae	+	H	H	ET<FT	2	4
20. Hymenoptera: Sphecidae	+	H	H	ET=FT	2	4
21. Diptera: Asilidae	–	V	H	ET<FT	2	5
22. Lepidoptera: Saturniidae	–	H	H	ET<FT	2	1
23. Trichoptera: Limnephilidae	–	H	H	ET=FT	2	2
24. Coleoptera: Tenebrionidae	–	V	H	ET=FT	3	3
25. Coleoptera: Chrysomelidae*	+	V	V	ET<FT	2	4
26. Coleoptera: Cerambycidae 1	+	V	H	ET<FT	2	4
27. Coleoptera: Cerambycidae 2	–	V	V	ET<FT	2	3
28. Coleoptera: Cerambycidae 3	–	V	V	ET<FT	2	2
29. Coleoptera: Cerambycidae 4	–	H	V	ET<FT	2	2
30. Coleoptera: Curculionidae 1	–	H	H	ET<FT	2	1
31. Coleoptera: Curculionidae 2	–	V	H	ET=FT	2	1
32. Coleoptera: Curculionidae 3	–	V	H	ET=FT	2	1
33. Coleoptera: Curculionidae 4	–	V	H	ET=FT	2	1

* All nineteen subfamilies of the Chrysomelidae have a TFS.

Explanation of symbols: TFS = tibial flexor sclerite; FT = flexor tendon; ET = extensor tendon; – = absence; + = presence; V = vertical; H = hozizontal; ET<FT = flexor tendon larger than extensor tendon.

Sclerotization states: 1 = none; 2 = slightly at base only; 3 = most of tendon, no TFS, thick base; 4 = TFS only; 5 = TFS and most of tendon.

Species names of taxa in Table 1: 1, *Anax junius* Drury; 2, *Hexagenia limbata* Guerin; 3, *Trimerotropis saxatilis* McNeil; 4, *Paradalophora apiculata* Harris; 5, *Tenodera aridifolia sinensis* Saussure; 6, *Diapheromera femorata* Say; 7, *Periplaneta americana* (Linnaeus); 8, *Anisolabis maritima* (Gene); 9, *Reticulitermes flavipes* (Kollar); 10, *Pteronarcys* sp.; 11, *Tibicen lyricen* (DeGeer); 12, *Oncopeltus fasciatus* (Dallas); 13, *Apiomerus* sp., 14, *Brochymena quadripustulata* (Fabricius); 15, *Piezogaster* sp.; 16, *Acanthocephala thomasi* (Uhler); 17, *Panorpa claripennis* Hine; 18, *Vella texana* (Hagen); 19, *Corydalus cornutus* Linnaeus; 20, *Specius speciosus* (Drury); 21, *Promachus aldrichi* Hine; 22, *Samia cynthia* (Drury); 23, *Platycentropus radiatus* (Say); 24, *Eleodes obscura* group; 25, *Sagra femorata* (Drury); 26, *Monochamus titillator* Fabricius; 27, *Orthosoma brunneum* (Forster); 28, *Megacyllene robinae* (Forster); 29, *Desmocerus palliatus* (Forster); 30, *Lixus concavus* Say; 31, *Otiorhynchus sulcatus* (Fabricius); 32, *Hypera punctulata* (Fabricius); 33, *Curculio sulcatus* (Fabricius).

and compared with the flexor (see Table 1). The flexor tendon is always attached to the ventral part of the base ('head') of the tibiae and the extensor tendon is attached to the dorsal part (Fig. 1). The actual material of attachment of the tendons is not sclerotized and we prefer to refer to it as a ligament in each case. The two tibial tendons extend from the point of attachment into the femoral capsule and may be oriented horizontally or vertically, relative to the axis of the femur in a walking position (see Table 1). In most insect orders the tendons are horizontally oriented, but in some (e.g. Heteroptera) both may be vertical (Fig. 2). Some orders may also have the extensor tendon vertical and the flexor tendon horizontal (Fig. 3 and e.g. Orthoptera) or the reverse (see Table 1). In general vertical tendons usually are basally horizontal for the first quarter or third of their length, then apically twist or fold (sometimes asymetrically) to become functionally vertical and broadened (Figs 1b, 1c). On the ventral side of the femoro-tibial joint, usually covering the point of attachment of the flexor tendon, is a soft arthrodial membrane; the remainder of the joint is also protected by this soft intersegmental membrane.

One of the most important aspects of our

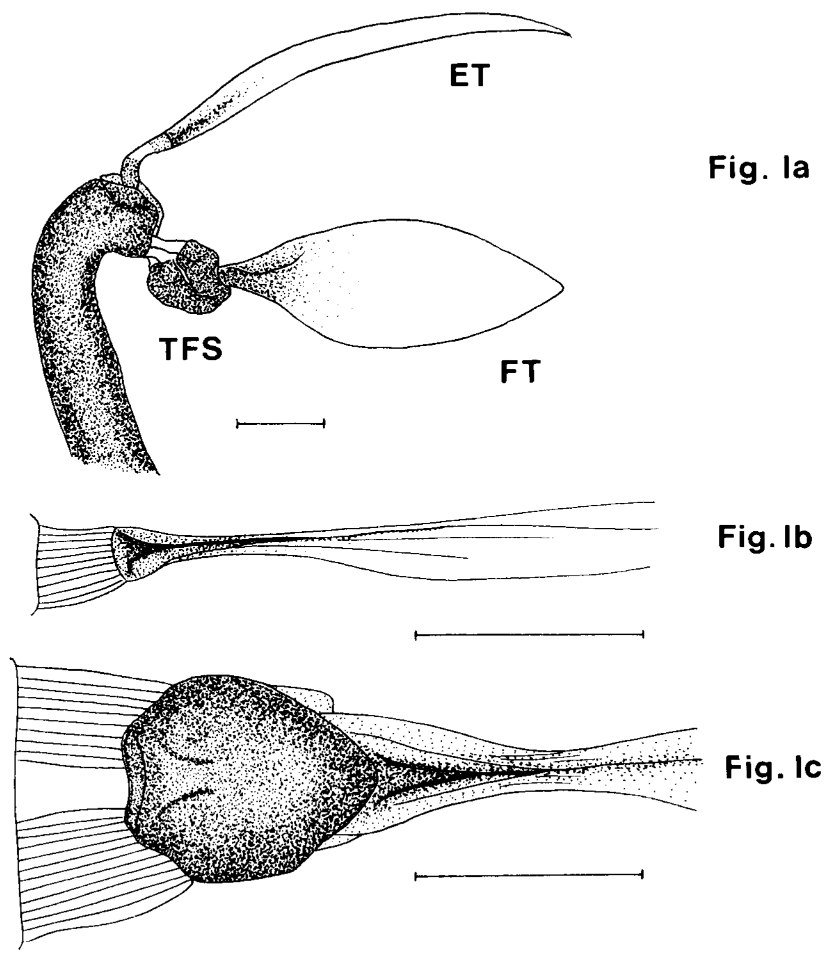

Fig. 1. *Sagra femorata*, metatibia. 1a, tibial base and tendons (ET = tibial extensor tendon, FT = tibial flexor tendon, TFS = tibial flexor sclerite); 1b, extensor tendon, ventral view; 1c, flexor sclerite and tendon, ventral view. Scale bars = 1 mm.

findings is that there is great variety in the degree of sclerotization of the tibial flexor tendon in different insect groups (see sclerotization states 1–5 in Table 1). It is sometimes difficult to interpret cases where there is an intermediate condition (state) of sclerotization of the two tendons. Usually the colour of the tendon is a good indicator of the degree of sclerotization; however, the darker colour may be affected (leached) by excessive boiling in KOH. Therefore, we also noted the consistency (hardness) of the base of the flexor tendon, the region of special concentration. In both tendons the base is usually broadly expanded and in certain cases may be thickened. As shown in the Table 1, in many insect orders there is some sclerotization (usually indicated by darker colour) at the base of the flexor tendon, but frequently there is only a slight indication of this, in the form of a small, basal, darkened area (Fig. 4) (e.g. Plecoptera, Isoptera, Phasmatodea, Odonata), in other orders there is slight sclerotization at the base of both tendons (e.g. Orthoptera, Mantodea, Dermaptera, Isoptera, Trichoptera), and in some there is no basal sclerotization (e.g. Ephemeroptera, Mecoptera). In some cases only the base of the extensor tendon shows any sclerotization (e.g. Lepidoptera). In the most advanced cases of sclerotization the entire tendon is darkened (sclerotized), such as in Diptera, and Coleoptera – some Cerambycidae, where the entire flexor tendon is heavily sclerotized.

In some advanced cases (e.g. Coleoptera – Chrysomelidae, Heteroptera, Hymenoptera – Figs 1, 2, 5) the tendon base is considerably thickened, possibly also elaborated and forming an independently movable plate or sclerite, the tibial flexor sclerite (TFS). When this TFS exists, it is exposed ventrally at the femoro-tibial joint and only partially covered on its ends by the soft arthrodial membrane (embedded in the membrane).

The Hemiptera proved to be exceptional and interesting in several aspects. In all cases the Heteroptera have an independently movable

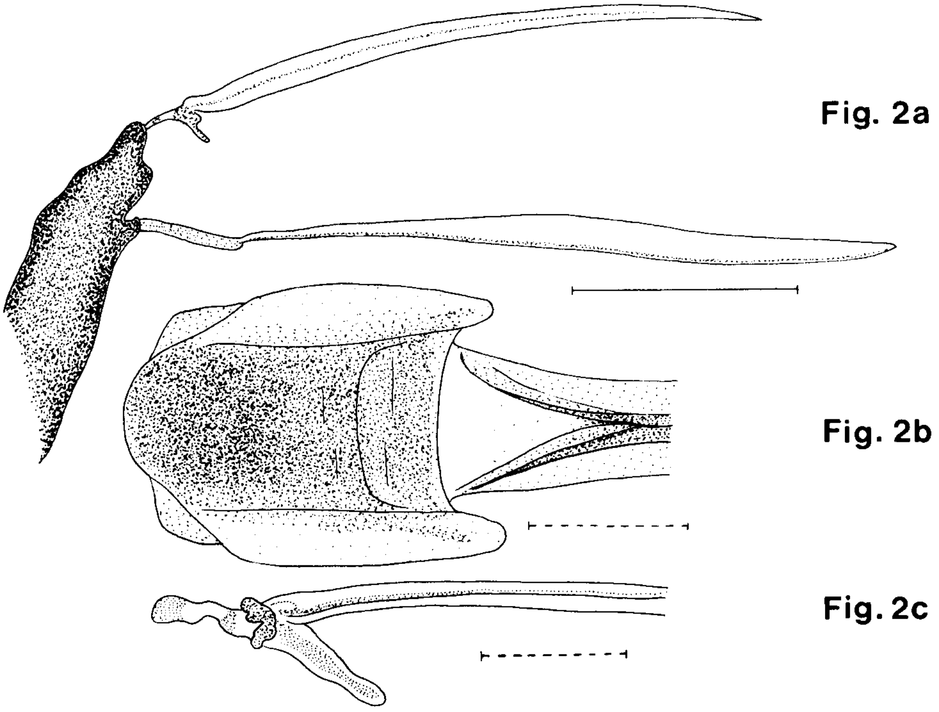

Fig. 2. *Brochymena quadripustulata*, metatibia. 2a, tibial base and tendons; 2b, flexor sclerite and tendon, base; 2c, extensor pendant sclerite and base of extensor tendon. Scale bars (broken) = 0.5 mm.

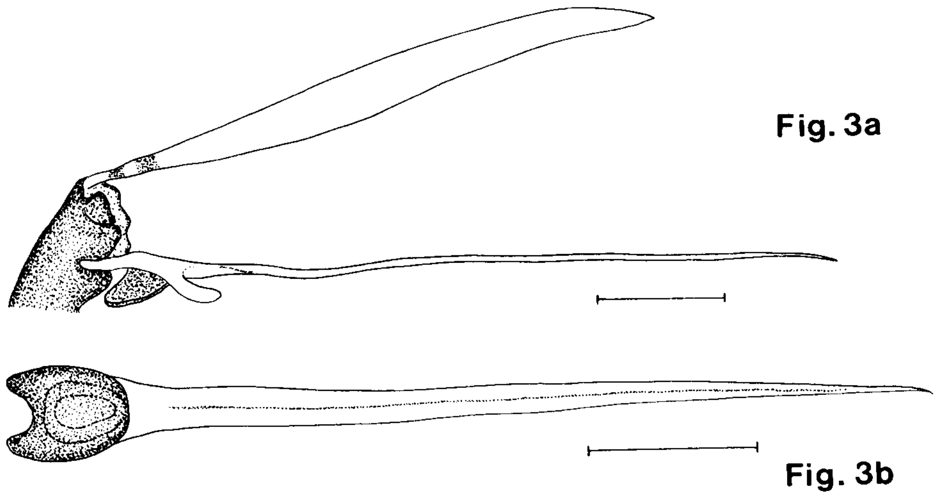

Fig. 3. *Monochamus titillator*, metatibia. 3a, tibial base and tendons; 3b, flexor sclerite and tendon, ventral view. Scale bars = 1 mm.

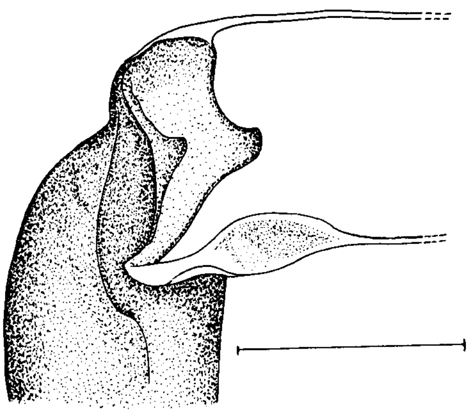

Fig. 4. *Pteronarcys* sp., metatibial base and tendons. Scale bar = 1 mm.

tibial flexor sclerite which is strongly sclerotized as in several other orders (Fig. 2 and see Table 1). Unique to the Heteroptera is another sclerotized structure which hangs down ventrally between the sclerotized base of the extensor tendon and the main body of this tendon ('tibial extensor pendant sclerite', TEPS). The TEPS is developed in all Heteroptera examined to date except *Apiomerus* where it appears to be vestigial (see Table 1 and Fig. 2c). In one unusual case (Reduviidae: *Apiomerus*), the base of the tibial extensor tendon is also heavily sclerotized and developed into an independently movable sclerite ('tibial extensor sclerite', TES). The TES is basically analogous to the TFS and possibly homologous to the metafemoral spring of flea beetles (see Furth, 1985).

Our preliminary results suggest that the condition of tibial flexor and extensor tendon sclerotization and the presence or absence of a tibial flexor sclerite is consistent throughout all three pairs of legs.

We have summarized the results of this study of nineteen insect orders in the Table 1 in order to show concisely the comparative state of the tibial flexor and extensor tendons and the presence or absence of the tibial flexor sclerite.

Discussion

An extensive search of the recent literature (*c.* 30 years) produced almost no mention of the tibial flexor sclerite. There is, of course, the possibility that it has been mentioned in large monographs concerning a restricted taxon or concerning comparative morphology, but if so such facts are effectively buried beyond easy retrieval. One such monograph, about the locomotor organs of Gyrinidae and other Coleoptera (Larsen, 1966), did not even discuss the femoro-