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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 aspects of tibial tendons in insects.

Taxon	TFS	Orientation		ET/FT	Sclerotization	
		ET	FT		ET	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

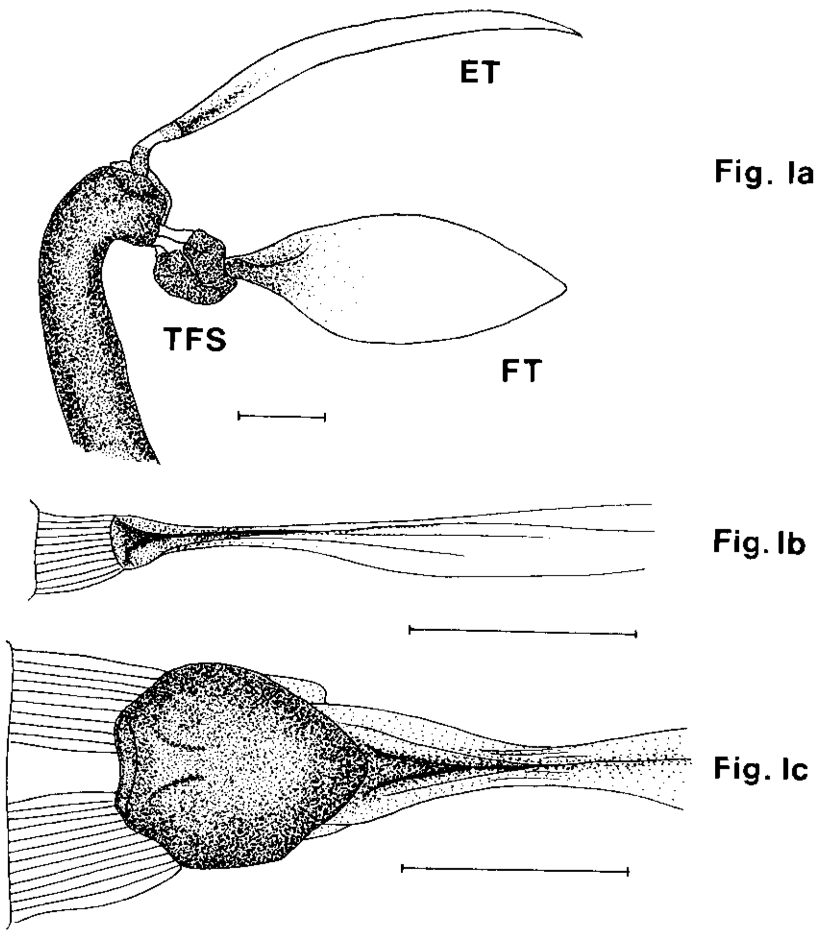

Fig. 1. *Sagra femorata*, metatibia. 1a, tibial base and tendons (ET = tibial extensor tendon, FT = tibial flexor tendon, TFS = tibial flexor sclerite); 1b, extensor tendon, ventral view; 1c, flexor sclerite and tendon, ventral view. Scale bars = 1 mm.

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

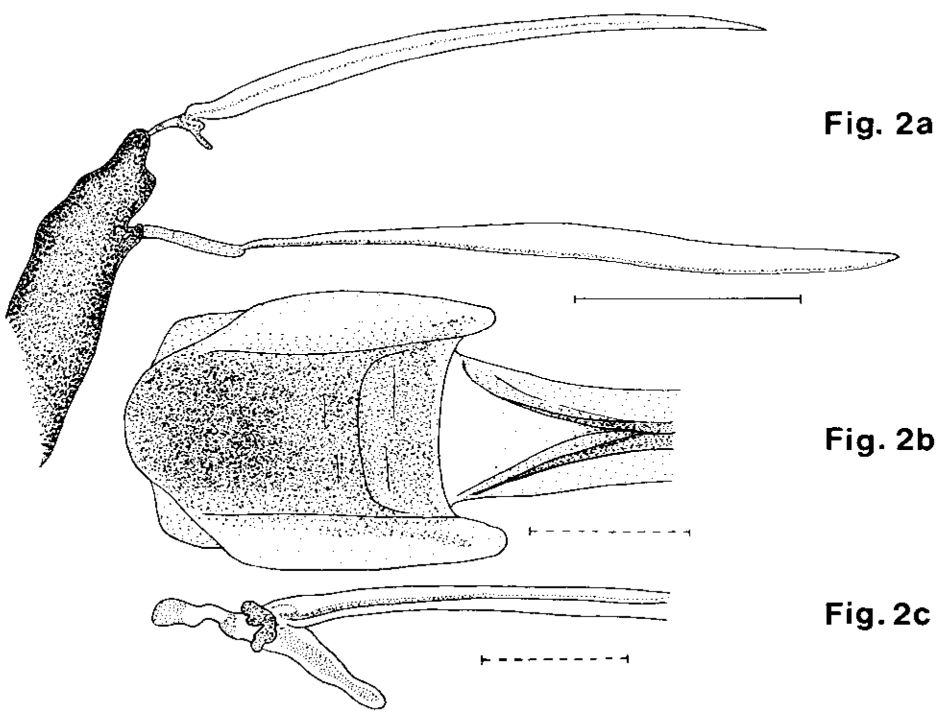

Fig. 2. *Brochymena quadripustulata*, metatibia. 2a, tibial base and tendons; 2b, flexor sclerite and tendon, base; 2c, extensor pendant sclerite and base of extensor tendon. Scale bars (broken) = 0.5 mm.

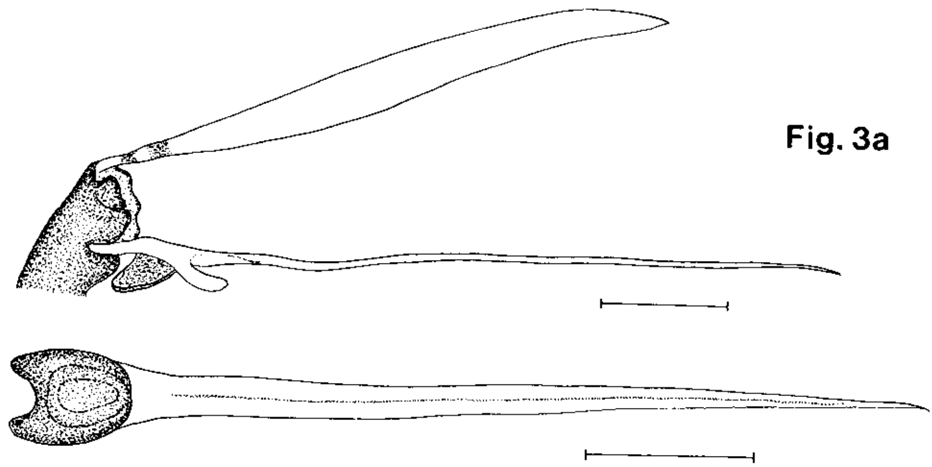

Fig. 3. *Monochamus titillator*, metatibia. 3a, tibial base and tendons; 3b, flexor sclerite and tendon, ventral view. Scale bars = 1 mm.

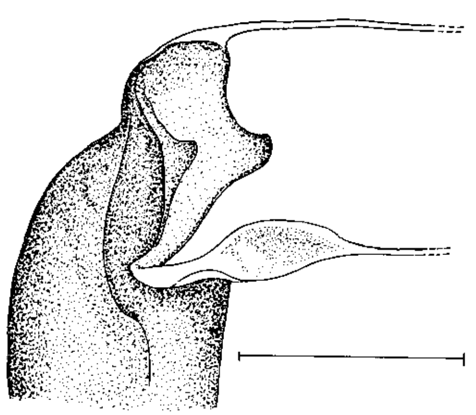

Fig. 4. *Pteronarcys* sp., metatibial base and tendons. Scale bar = 1 mm.

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-

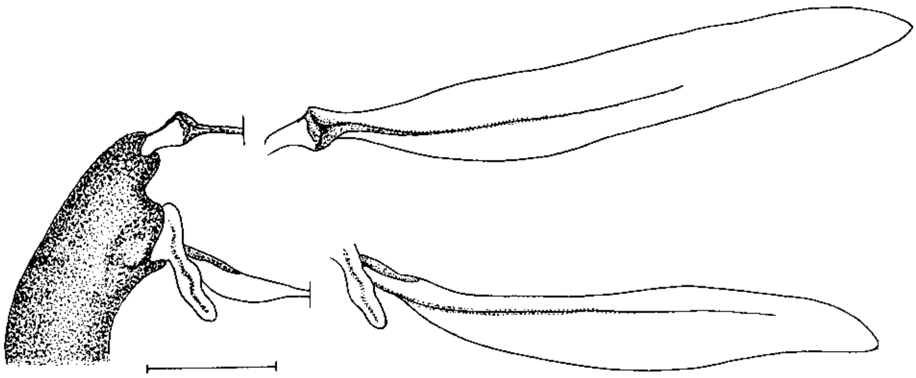

Fig. 5. *Sphecius speciosus*, metatibial base and tendons, right. Scale bar = 1 mm.

tibial joint or the tendons involved. One report of a potentially homologous structure is in the femur–patella joint of spiders, where the several patella/tibial flexor muscles are focused through attachment to the patellar base by a heavily sclerotized arcuate sclerite, thus strengthening the flexor action (Manton, 1968). In another treatment, of *Gryllus bimaculatus* De Geer, Thakare (1972) refers to a tibial depressor apodeme attached to the ventral aspect of the tibial base, which appears to be homologous to the base of the tibial flexor tendon, but there is no mention of whether this apodeme is sclerotized or differentiated from the tibial flexor tendon. In the spider and cricket examples mentioned above, the sclerites are respectively covered by or embedded in the ventral arthrodial membrane. One apparent treatment of the tibial flexor sclerite concerns aspects of locomotion in Carabidae (Adephaga) where Evans (1977) illustrates a 'sessamoid sclerite' attaching the base of the protibia to the tibial flexor muscles through an apodeme; the protibial extensor muscle is attached to the tibial base by another apodeme. Evans explains that this 'sessamoid sclerite' provides protection for the ventral arthrodial membrane. The only other mention of a possible TFS-type structure is Snodgrass (1942, 1956) in his descriptive studies of the anatomy of the honey bee in which he only briefly and simply indicates a 'genuflexor plate' attached to the tibial flexor tendon and in the membrane below the femoro-tibial joint.

Based on the present comparative study of homologous aspects of the tibial tendons, it is apparent that there is a broad spectrum of modifications of the tibial flexor (and extensor) tendon; this probably can be extrapolated to other arthropod groups. It is also apparent that such modifications are present in all (three pairs) of the legs of each insect group and our preliminary findings indicate that there are some patterns of anatomy (possibly phylogenetic) within each insect order. We assume that the differences in sclerotization of the flexor tendon and its parts are correlated with functional aspects of locomotion in each group.

Through the survey of the nineteen insect orders several general tendencies concerning anatomy and function of the tibial flexor and extensor tendons become apparent. However, at the same time there are a variety of conditions (e.g. presence of TFS) of these tendons among the different insect orders that do not conform to any evident pattern of lineage or relationship, but appear function-related. The primary focus of this study has been the tibial flexor tendon which performs a critical function in insect locomotion, namely the ability to flex the tibiae to the femur. This action is important for walking, running, swimming and jumping, as well as grasping. Necessarily the importance of such locomotory and grasping skills varies considerably in the insect world and even among and within the different insect orders, depending on the biology of different groups.

Lever's Organ (triangular plate) was originally described as a chitinized part of the tibial flexor tendon that was a separate plate or sclerite (Lever, 1930). In the present study we consider the 'tibial flexor sclerite' (Lever's Organ) to be a heavily sclerotized plate or sclerite at the broadened base of the tibial flexor tendon which can potentially be moved somewhat independently from its ligament origin on the base of the tibia and from its insertion/connection to the remainder of the flexor tendon. Essentially this tibial flexor sclerite (TFS) is homologous with the broad basal portion of the tibial flexor tendon, which has sclerotized, specialized and separated into a plate. In a variety of insect orders (e.g. Phasmatodea, Blattaria, Odonata, Ephemeroptera, Plecoptera, Trichoptera, Mecoptera, Diptera, Lepidoptera, some Coleoptera), while the base of the tibial flexor tendon may be somewhat sclerotized, it has not differentiated enough to be an independent sclerite as it has in others (e.g. Megaloptera, Neuroptera, Heteroptera, Hymenoptera, some Coleoptera). There does not seem to be any apparent relationship among the orders that do or do not have this independent sclerite. In fact, it is possible that when many families/genera of certain insect orders are examined there will be a variety of the TFS development found within an order (e.g. as with Coleoptera in this study, see Table 1). However, preliminary indications are of a general pattern in most insect orders (e.g. Heteroptera – four families with the same TFS condition, but with other modifications).

Although all aspects of the TFS are not yet understood, it potentially serves several functions. It presumably provides a strengthened base for the flexor tendon that is particularly effective in groups exerting great tension during tibial flexion (e.g. Bruchidae and sagrine Chrysomelidae for holding onto vegetation or alticine Chrysomelidae for jumping). Related to the previous function, the TFS serves as a point of indirect attachment to the tibia basally through a ligament and apically through the flexor tendon and muscle, and thus is part of the leg flexor system. The TFS also offers considerable protection to the ventral soft, generally exposed, femoro-tibial joint.

In most insect orders the orientation of both flexor and extensor tendons is horizontal (parallel to the ground in walking position) (see Table 1). In Coleoptera, the extensor tendon is usually oriented vertically; however, the flexor tendon varies in orientation and occasionally in groups with a well-developed, heavily sclerotized flexor tendon, this tendon is oriented horizontally at its base and then is twisted to vertical for the remainder of its length. The differences in tendon orientation presumably are related to the type and orientation of the locomotory muscles in the femur. The relative sizes of the flexor and extensor tendons (see Table 1), and their functional relationship will be discussed in further detail elsewhere (Furth & Suzuki, 1990).

This comparative morphological study of the tibial locomotor tendons of most insect orders is only a preliminary survey of these structures in the insect world. The patterns indicated here will be established more firmly or revised when a broader cross-section of each insect order is examined; this will lead to a better understanding of all the functional aspects of the TFS. However, this first general survey has been quite revealing concerning the tibial flexor sclerite's presence throughout the Insecta.

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