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Evolution of the Digital Tendon Locking Mechanism in Bats and Dermopterans: A Phylogenetic Perspective

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A tendon locking mechanism (TLM) in the digits of the feet has been described previously only in bats and birds. In bats, this mechanism typically consists of a patch of tuberculated fibrocartilage cells on the plantar surface of the proximal flexor tendons, and a corresponding plicated portion of the adjacent flexor tendon sheath. The two components mesh together like parts of a ratchet, locking the digit in a flexed position until the mechanism is disengaged. This system apparently allows bats to hang for long periods of time with reduced muscular activity. In this study, we document for the first time the presence of a similar tendon lock in dermopterans, an occurrence that provides additional support for the hypothesis that dermopterans and bats are sister taxa. The present work also includes observations on the morphology of the digital tendon system in chiropteran species not previously examined, including members of the Craseonycteridae, Mystacinidae and Kerivoulinae. Unlike other bats that have a TLM, *Craseonycteris* and *Kerivoula* have a plicated proximal tendon sheath but lack distinct tubercles on the flexor tendon. This condition may be related to small body size or may represent an evolutionary intermediate between the presence of a well-developed TLM and the complete absence of this structure. Phyllostomids apparently lack the ratchet-like TLM typical of other bats, instead exhibiting modifications of the tendon sheath that may contribute to its function as a friction lock. Consideration of the distribution of TLM structures in the context of previous phylogenetic hypotheses suggests that a ratchet-type tendon lock was lost and reexpressed at least once and perhaps several times within Microchiroptera. The friction lock is an autapomorphy of Phyllostomidae.

KEY WORDS: digital tendon locking mechanism; Chiroptera; Dermoptera; phylogeny.

INTRODUCTION

Bats spend much of their time roosting suspended from their hindlimbs. Hanging for long periods is apparently facilitated by a digital tendon locking mechanism (TLM) in members of most chiropteran families (Schaffer, 1905; Schutt, 1992, 1993; Bennett, 1993; Quinn and Baumel, 1993). The functional unit (Fig. 1A) typically consists of two components, a tuberculated fibrocartilage patch on the proximal plantar surface of the combined tendons of the flexor digitorum longus and plantaris muscles (Fig. 1B), and an adjacent plicated portion of the synovial layer of the flexor tendon sheath (Fig. 1C).

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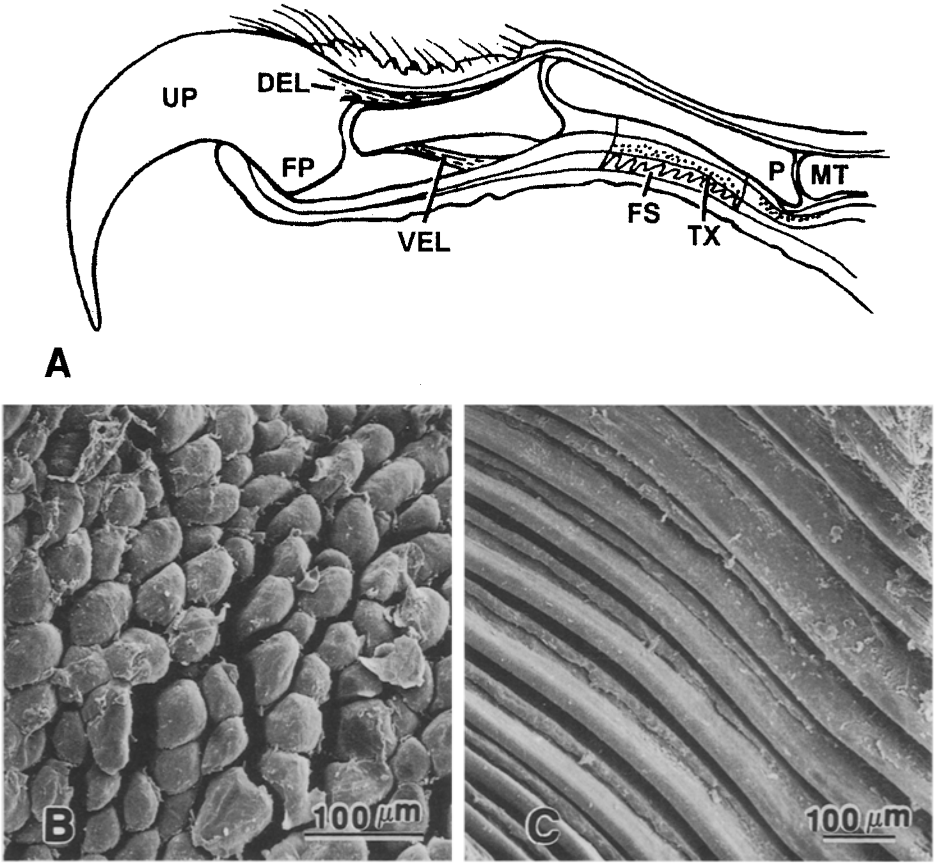

Fig. 1. Structure of the ratchet-like TLM in Chiroptera. (A) Diagram of a generalized pedal digit with a TLM. DEL, dorsal elastic ligament; FP, flexor process; FS, plicated portion of flexor tendon sheath; MT, metatarsal; P, proximal phalanx; TX, textured patch on plantar surface of flexor tendon; UP, ungual (distal) phalanx; VEL, ventral elastic ligament. (B) Patch of fibrocartilage tubercles on proximal plantar surface of digital flexor tendon of *Pteropus giganteus* (AMNH 83947). (C) Plicated portion of adjacent tendon sheath in *Pteropus giganteus* (AMNH 83947).

The locking mechanism on each digit consists of a single functional unit (tendon with tubercles, sheath with plicae) located on the proximal phalanx.[4] The tendon lock is engaged when the flexor tendon is pulled proximally, as occurs when the digit is flexed (Bennett, 1993; Quinn and Baumel, 1993; Schutt, 1993). This action aligns the components of the mechanism, pulls the flexor tendon away from the surface of the phalanx, and pushes the tuberculated surface of the tendon against the plicae on the inner surface of the flexor tendon sheath. Once the tendon tubercles engage with the plicae, the tendon remains locked in place as long as the claw is under tension (i.e., as long as the body weight of the animal is suspended from the flexed claw). Release of the tendon lock is apparently effected by an upward shift in body weight, passive elastic recoil of the dorsal

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[4] Although Schutt (1993) indicated that there are three locking units in *Myotis lucifugus*, we observed only one tuberculae/plicae complex in this species.

and ventral elastic ligaments, and active extension of the distal phalanx via the extensor tendons (Quinn and Baumel, 1993).

At least one member of every avian order also has a ratchet-like TLM (Ranvier, 1889; Schaffer, 1903; Shepherd, 1981; Quinn and Baumel, 1990). In contrast to the usual chiropteran condition, birds frequently have multiple complete TLM units on the same digit, and the lock is located on the middle (rather than proximal) phalanx when there is only one unit per digit (Quinn and Baumel, 1990). The mode of engagement of the locking mechanism is also somewhat different in birds. The avian tendon lock is engaged by a combination of pressure on the podothecal pads as they are deformed by the perch, proximal pull on the flexor tendon, and bowing of the tendon during digital flexion (Quinn and Baumel, 1990). Even without these differences, there is little doubt that the avian and chiropteran TLM evolved independently since this mechanism is absent in reptiles and most mammalian orders.

Although the tendon lock seen in bats is clearly a derived feature, the evolutionary history of this mechanism is uncertain because it is not present in all bats (Quinn and Baumel, 1993). Quinn and Baumel (1993) and Schutt (1993) investigated potential associations between TLM presence and substrate use, hibernation, dietary habits, and body weight but found few significant patterns. There seems to be no correlation between TLM presence and substrate use or dietary habits (Quinn and Baumel, 1993). All bats that hibernate apparently have a tendon locking mechanism, but many nonhibernating bats do as well (Quinn and Baumel, 1993; Schutt, 1993). Most large-bodied bats have a tendon lock, but this is also true of small-bodied forms (Quinn and Baumel, 1993). This suggests that other factors—including phylogenetic history—may be responsible for the patterns of TLM distribution observed in extant bats.

Understanding the evolutionary origins and history of any feature requires a phylogenetic perspective (Lauder, 1981; Brooks and McLennan, 1991). We cannot assume that structures are homologous simply because they are similar in form or function, nor can we assume that they are homoplastic if there are slight differences between them (Rieppel, 1980; Patterson, 1982; Simmons, 1993). The absence of a feature in a particular group may be either primitive or secondarily derived, and features that have been lost during evolution may later be re-expressed through activation of previously suppressed developmental pathways (Hall, 1984; Wake and Larson, 1987; Stiassny, 1992). Only a phylogeny can provide the framework necessary for sorting out these possibilities and developing hypotheses of historical patterns of gain and loss of a particular trait.

Higher-level phylogenetic relationships among bats have been controversial for many years. The possibility that bats are diphyletic has been the subject of considerable recent debate (e.g., Wible and Novacek, 1988; Pettigrew *et al.*, 1989; Baker *et al.*, 1991; Pettigrew, 1991a, b; Simmons *et al.*, 1991), but it is now clear that the majority of biochemical, molecular, and morphological data support monophyly of Chiroptera (Simmons, 1994). In contrast, there is little consensus concerning interrelationships of the 16 microchiropteran families. Several competing hypotheses have been developed based on different data sets (e.g., Smith, 1976; Van Valen, 1979; Luckett, 1980; Novacek, 1980; Pierson, 1986; Griffiths and Smith, 1991; Griffiths *et al.*, 1992). These phylogenies provide the appropriate framework for investigating homology and patterns of evolution of the tendon lock within bats.

A remaining question concerns possible presence of the TLM in non-chiropteran mammals. Schaffer (1905) dissected several non-volant mammals and did not find a TLM in any of these taxa. However, many taxa that may be closely related to bats (e.g., dermopterans, primates, tree shrews) have never been surveyed for the presence of a digital tendon lock. Understanding the origin(s) of the TLM in mammals requires knowledge of the taxonomic distribution of the TLM not only in bats, but also in putative sister taxa of Chiroptera. In this context, the principal goals of this study are to complete a survey of the distribution and structure of the TLM among families and subfamilies of extant bats, investigate a number of non-chiropteran mammals (particularly putative sister taxa of bats) for the presence of a TLM, and interpret the pattern of distribution of the TLM in the context of previous hypotheses of bat relationships.

MATERIALS AND METHODS

The third digit of the hindlimb was dissected in representatives of selected species to investigate TLM distribution and structure (Tables I and II). All of the specimens utilized in the present study were adult (as judged by epiphyseal closure) individuals preserved in 70% ethanol. Tissue was removed by microdissection and immediately

Table I. Distribution of the TLM in Chiroptera[a]

Taxon	Specimen(s)	TLM[b]
Pteropodidae		
Pteropodinae		
Pteropus giganteus	AMNH 83947	Plicae + tubercles
Pteropus poliocephalus	NA[c]	Plicae + tubercles[c]
Pteropus alecto	NA[c]	Plicae + tubercles[c]
Pteropus scapulatus	NA[c]	Plicae + tubercles[c]
Rousettus aegyptiacus	NA[d]	Plicae + tubercles[d]
Eidolon helvum	NA[d]	Plicae + tubercles[d]
Hypsignathus monstrosus	NA[d]	Plicae + tubercles[d]
Epomophorus wahlbergi	UNSM 20215	Plicae + tubercles
Cynopterus brachyotis	UNSM 20214	Plicae + tubercles
Cynopterus sphinx	NA[d]	Plicae + tubercles[d]
Macroglossinae		
Macroglossus minimus	AMNH 192755	Plicae + tubercles
Rhinopomatidae		
Rhinopoma microphyllum	NA[e]	Plicae + tubercles[e]
Rhinopoma hardwickei	AMNH 235563	Plicae + tubercles
Craseonycteridae		
Craseonycteris thonglongyai	BMNH 77.2999	Plicae only
Emballonuridae		
Taphozous nudiventris	NA[e]	Plicae + tubercles[e]
Balantiopteryx plicata	KU 145424	Plicae + tubercles
Nycteridae		
Nycteris gambiensis	USNM 478656	Plicae + tubercles
Megadermatidae		
Cardioderma cor	NA[d]	Plicae + tubercles[d]
Macroderma gigas	AMNH 197210	Plicae + tubercles
Megaderma spasma	USNM 573679	Plicae + tubercles
Rhinolophidae		
Rhinolophinae		
Rhinolophus ferrumequinum	KU 64420	Plicae + tubercles
Hipposiderinae		
Hipposideros diadema	AMNH 237819	Plicae + tubercles

Table I. Continued

Taxon	Specimen(s)	TLM[b]
Noctilionidae		
Noctilio leporinus	USNM 392924	Plicae + tubercles
Noctilio albiventris	AMNH 182706	Plicae + tubercles
Mormoopidae		
Pteronotus davyi[f]	KU 145427[f]	Absent
Mormoops megalophylla	KU 145426	Absent
Phyllostomidae		
Phyllostominae		
Chrotopterus auritus	NA[d]	Absent; see text[d]
Vampyrum spectrum	NA[d]	Absent; see text[d]
Macrotus waterhousii	NA[d]	Absent; see text[d]
Phyllostomus discolor	USNM 491234	Absent; see text
Glossophaginae		
Glossophaga soricina[g]	KU 145429[g]	Absent; see text
Anoura caudifer	USNM 491713	Absent; see text
Stenodermatinae		
Artibeus jamaicensis	UNSM 16723	Absent; see text
Desmodontinae		
Desmodus rotundus	USNM 329487	Absent; see text
Diaemus youngi	NA[d]	Absent; see text[d]
Diphylla ecaudata	NA[d]	Absent; see text[d]
Natalidae		
Natalus stramineus	KU 145428	Absent
Furipteridae		
Furipterus horrens	USNM 549598	Absent
Thyropteridae		
Thyroptera tricolor	USNM 281939	Absent
Myzopodidae		
Myzopoda aurita	USNM 448886	Absent
Vespertilionidae		
Vespertilioninae		
Myotis daubentoni	NA[e]	Plicae + tubercles[e]
Myotis mystacinus	NA[e]	Plicae + tubercles[e]
Myotis lucifugus	AMNH 244863, KU 145431	Plicae + tubercles
Eptesicus fuscus	KU 145430, USNM 17925–17929	Plicae + tubercles
Pipistrellus pipistrellus	NA[e]	Plicae + tubercles[e]
Pipistrellus subflavus	KU 145432	Plicae + tubercles
Nyctalus noctula	NA[e]	Plicae + tubercles[e]
Antrozous pallidus	Personal collection (T.H.Q.)	Plicae + tubercles
Kerivoulinae		
Kerivoula hardwickei	AMNH 234209	Plicae only
Molossidae		
Tadarida brasiliensis	KU 145425	Plicae + tubercles
Mops mops	UNSM 20217	Plicae + tubercles
Mystacinidae		
Mystacina tuberculata	MNHN 1983-1464	Absent

[a] All specimens for which collection information is given were dissected and examined by at least one of the authors; sources of data for other observations are as noted. All specimens represent adult individuals as judged by epiphyseal closure.

[b] Refers to a ratchet-type tendon locking mechanism that typically consists of tubercles on the proximal flexor tendon and plicae on the adjacent tendon sheath.

[c] Data from Bennett (1993); no specimen numbers available.

[d] Data from Schutt (1992, 1993); no specimen numbers available.

[e] Data from Schaffer (1905); no specimen numbers available.

[f] This taxon was incorrectly identified as *Pteronotus gymnotus* in Table 1 of Quinn and Baumel (1993).

[g] This taxon was incorrectly identified as *Glossophaga leachii* in Table 1 of Quinn and Baumel (1993).

Table II. Distribution of the TLM in Non-chiropteran Mammals[a]

Taxon	Specimen	TLM[b]
Dermoptera		
Cynocephalus sp.	AMNH 207001, USNM 115603	Plicae + tubercles
Primates		
Lemuriformes		
Microcebus sp.	AMNH 100844	Absent
Tarsiiformes		
Tarsius syrichta	AMNH 150143	Absent
Anthropoidea		
Homo sapiens	NA	Absent
Scandentia		
Tupaia glis	AMNH 213642	Absent
Carnivora		
Felis domesticus	Personal collection (T.H.Q.)	Absent
Artiodactyla		
Sus scrofa	Personal collection (T.H.Q.)	Absent
Rodentia		
Sciuridae		
Sciurus vulgaris	Personal collection (T.H.Q.)	Absent
Petaurista elegans	AMNH 234549	Absent
Myoxidae		
Myoxus glis	NA[c]	Absent
Insectivora		
Sorex cinereus	Personal collection (T.H.Q.)	Absent
Edentata		
Bradypus tridactylus	NA[c]	Absent[c]
Marsupialia		
Trichosurus vulpecula	NA[c]	Absent[c]

[a] All specimens for which collection information is given were dissected and examined by at least one of the authors; sources of data for other observations are as noted. All specimens represent adult individuals as judged by epiphyseal closure.

[b] Refers to a ratchet-type tendon locking mechanism that consists of tubercles on the flexor tendon and plicae on the adjacent tendon sheath.

[c] Data from Schaffer (1905); no specimen numbers available.

immersed in fresh 70% ethanol. Drawings of selected specimens were prepared with the aid of a dissecting microscope equipped with a camera lucida. Specimens to be observed in the SEM were further dehydrated in a graded series of ethanol solutions up to 100%, dried in liquid CO_2 in a Polaron critical point drier, and coated with AuPd alloy in a Polaron E5100 Coating Unit. A JEOL JSM 840A scanning electron microscope was used for viewing and photography. The anatomical terms used in this study follow those of Vaughan (1970) for bats, Leche (1886) for dermopterans, and the Nomina Anatomica Veterinaria (1983) for other taxa.

Historical patterns of gain and loss of the TLM in mammals were investigated by mapping the distribution of this feature on phylogenetic trees generated in previous studies of bat relationships (e.g., Smith, 1976; Van Valen, 1979; Luckett, 1980; Novacek, 1980; Pierson, 1986). Monophyly of Chiroptera was assumed following Simmons (1994). A sister-group relationship between Chiroptera and Dermoptera was tentatively accepted based on results of previous studies (e.g., Wible and Novacek, 1988; Johnson and Kirsch, 1993; Szalay and Lucas, 1993; Simmons, 1993, 1994, 1995; Novacek, 1994; Vrana, 1994), although alternative hypotheses were also considered (see Discussion below). MacClade Version 3.0 (Maddison and Maddison, 1992) was used to map TLM distribution, identify points of character transformation, and calculate the number of steps (evolutionary events) required to account for TLM distribution in the context of each phylogenetic hypothesis. No attempt was made to generate a new phylogeny of bats, although TLM data should prove useful in this regard in the future.

Abbreviations

The following institutional abbreviations are used in this paper: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; KU, University of Kansas Museum of Natural History, Lawrence, Kansas; MNHN, Muséum National d'Histoire Naturelle, Paris; UNSM, University of Nebraska State Museum, Lincoln; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

RESULTS

The TLM in Bats

The structure of the tendon lock was described previously for many bat species by Schaffer (1905), Bennett (1993), Schutt (1993), and Quinn and Baumel (1993). Here we describe the results of our study of several additional taxa.

Craseonycteris thonglongyai

This diminutive species (±2 g adult body weight) is the only member of the monotypic family Craseonycteridae (Nowak, 1991; Koopman, 1993). Despite the small size, transverse ridges are well-defined on the digital flexor tendon sheath in *Craseonycteris* (Fig. 2A). The plantar aspect of the flexor tendon (Fig. 2B) is covered by a layer of closely packed cells whose free surfaces barely rise above the tendon surface. Individual tubercles cannot be discerned per se, and the free surfaces of cells are not domed or elongated as are those of the majority of larger bats. However, a layer of superficial cells—distinct from the longitudinally running dense collagen of the tendon proper—is present. It seems likely that this layer is homologous with the thicker tubercular layer seen in larger bats with a TLM. Mammals that lack a TLM typically have a thin, nontextured cellular layer (epitenon) on the surface of the tendons. This smooth layer presumably facilitates tendon gliding within the synovial tendon sheath. It is not clear whether the epitenon is homologous with the rougher, thicker superficial cell layer seen in forms with a TLM.

Kerivoula hardwickei

This species is 1 of 22 referred to Kerivoulinae, a group typically considered a subfamily of Vespertilionidae (Koopman, 1992; although see Van Valen, 1979). The TLM in this small bat [4-6 g (Nowak, 1991)] differs somewhat from that observed in other vespertilionids. The surface of the flexor tendon in *Kerivoula* does not exhibit a distinct tubercular layer in which cell surfaces are domed or markedly protrude from the

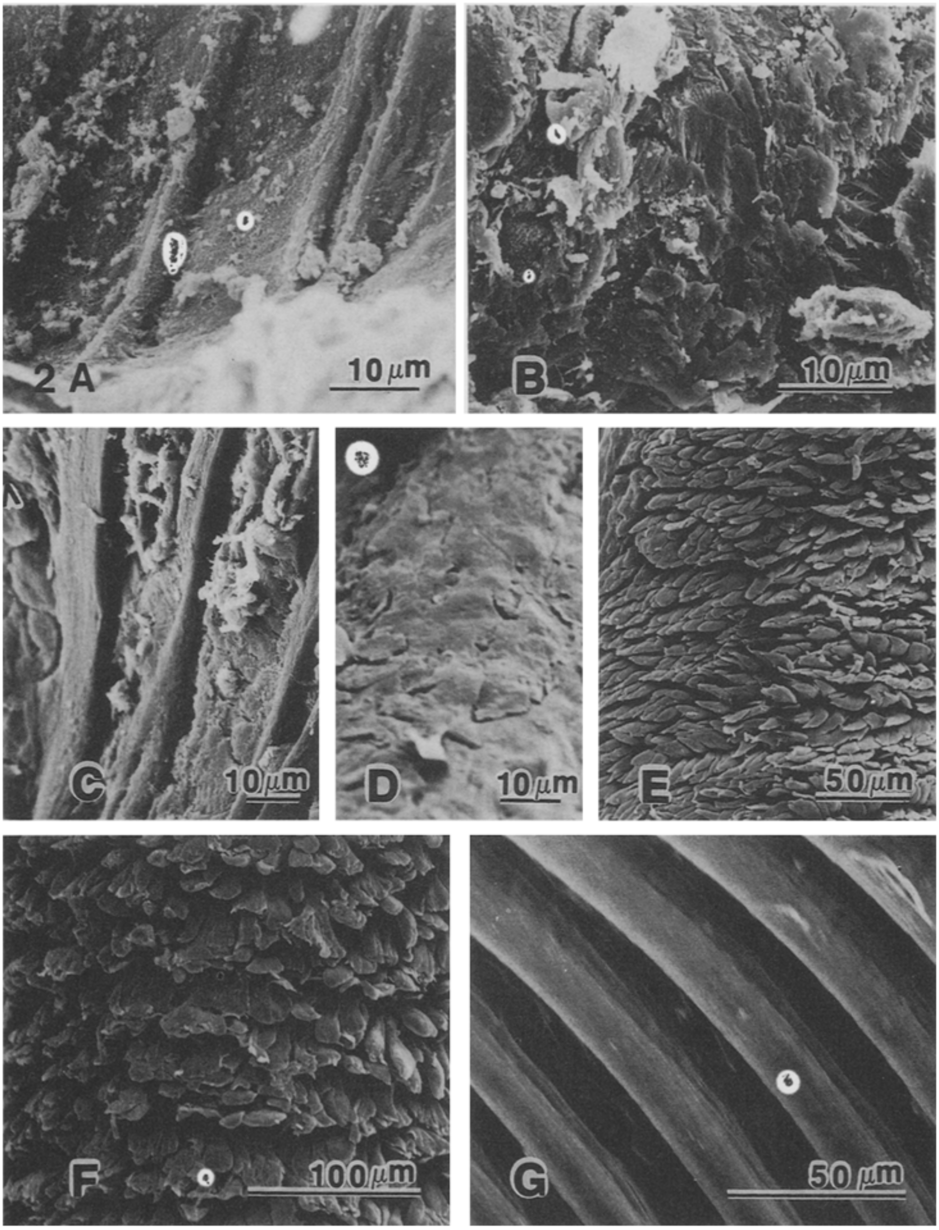

Fig. 2. Closeup views of the proximal pedal flexor tendon and adjacent tendon sheath in selected bats. (A) Tendon sheath with plicae in *Craseonycteris thonglongyai* (BMNH 77.2999). (B) Textured area of flexor tendon in *Craseonycteris thonglongyai* (BMNH 77.2999). (C) Tendon sheath with plicae in *Kerivoula hardwickei* (AMNH 234209). (D) Adjacent tendon surface in *Kerivoula hardwickei* (AMNH 234209); note the relatively smooth texture. (E) Textured tendon surface in *Mops mops* (UNSM 20217); note the foliate form of the tubercles. (F) Textured tendon surface in *Macroderma gigas* (AMNH 197210); note the tufted, pedunculate form of the tubercles. (G) Tendon sheath with plicae in *Macroderma gigas* (AMNH 197210).

plane of the underlying collagen fibers. Some texture is evident, and a distinct layer of surface cells is present (Fig. 2D). In contrast, distinct tubercles are present on the tendon surface in all other vespertilionids observed to date (Table I). The transverse folds of the flexor tendon sheath in *Kerivoula* (Fig. 2C) are regularly spaced and a relatively large number of squamous epithelial cells are present between the folds. The presence of these cells tends to make the troughs between the folds less pronounced than those described in other, larger bats.

Macroderma gigas

One of the largest microchiropterans, *Macroderma gigas* (70–130 g) is one of five species referred to the family Megadermatidae (Nowak, 1991; Koopman, 1993). The specimen that we examined has a robust TLM. The plicated portion of the flexor sheath extends from the base of the proximal phalanx to the proximal interphalangeal joint and comprises approximately 20 reinforced transverse folds (Fig. 2G). These mesh with prominent tubercles present on the plantar surface of the flexor digitorum longus tendon (Fig. 2F). The size and morphology of the TLM in *Macroderma* resembles that observed in *Pteropus* (Figs. 1B and C).

Phyllostomids

We dissected at least one member of each of four phyllostomid subfamilies (Table I) and did not observe a ratchet-type TLM (with plicae and tubercles) in any of these species. We did find, however, that the proximal annular portion of the flexor tendon sheath is modified to form a band-like structure (''retinaculum'' of Schutt, 1993) which is thickest in its central portion and tapers from anterior to posterior, much like a ferrule. Given this configuration, it seems likely that the tendon sheath in phyllostomids functions as a type of friction apparatus in addition to its role as a pulley for the tendon near the proximal metacarpophalangeal joint. As the flexor digitorum longus tendon is flexed, the free edge of the retinaculum may be slightly tilted to engage the tendon surface. The taper in sheath thickness would facilitate a broad area of contact between these elements. This configuration may constitute a sort of locking mechanism, albeit not as effective as the ratchet-type TLM seen in other bat families. Manipulative experiments with the digits of our specimens support this conclusion.

Mystacina tuberculatum

This species is one of only two that comprise the family Mystacinidae (Koopman, 1993). No tendon lock is present in the specimen that we examined. No plicae are present on the flexor sheath, and there is no evidence of tubercles or a roughened plantar surface on the tendon. The plantar surface of the proximal flexor tendon is covered by a uniformly thick tendon sheath similar to that observed in other bats that lack a TLM.

Other Bats

In addition to those taxa discussed above, we also dissected specimens of *Macroglossus minimus* (Pteropodidae: Macroglossinae), *Rhinopoma hardwickei* (Rhinopomatidae), *Hipposideros diadema* (Rhinolophidae: Hipposiderinae), *Noctilio albiventris*

(Noctilionidae), and *Eptesicus fuscus* (Vespertilionidae; Table I). Each of these species was found to have a TLM similar to those previously described for other members of their respective families.

Summary

Data concerning TLM distribution and structure are now available from members of all 17 extant chiropteran families (Table I). A ratchet-type TLM (with plicae on the tendon sheath and tubercles on the tendon surface) is present on the proximal phalanx in Pteropodidae (including Macroglossinae), Rhinopomatidae, Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae (including Hipposiderinae), Noctilionidae, Vespertilionidae, and Molossidae. A ratchet-type TLM is absent in Mormoopidae, Natalidae, Furipteridae, Thyropteridae, Myzopodidae, Mystacinidae, and all phyllostomids that we examined (although see discussion below). Craseonycteridae and Kerivoulinae exhibit what may be an intermediate condition in which plicae are present on the tendon sheath but distinct tubercles are absent from the tendon surface.

All bats that lack a TLM have a thickened annular sheath covering the flexor tendon where it crosses the proximal phalanx. Friction between this thickened area and the underlying tendon may function to help retard extension of the distal phalanx during hanging (Quinn and Baumel, 1993). In phyllostomids, the annular sheath is unusual in that it is modified to form a retinaculum that is thickest in its central portion and tapers from anterior to posterior. This configuration may facilitate function of the sheath as a sort of friction lock on the flexor tendon.

Although a ratchet-type TLM is not present in all bats, it is similar in most species which do possess it. We found that the TLM has generally the same components (i.e., tubercular patch on flexor tendon, plicae on adjacent tendon sheath) and configuration (single locking element present on proximal phalanx) in large and small microchiropterans and megachiropterans alike. Interspecific differences were found principally in tubercle texture, which varies among and within families (Fig. 2). For example, all pteropodids that we have examined have robut domed or cobblestone-like tubercles (Fig. 1A), while *Mops* (Molossidae; Fig. 2E) has foliate tubercles, and *Tadarida* (Molossidae), *Megaderma* (Megadermatidae),and *Macroderma* (Megadermatidae; Fig. 2F) have tufted, pedunculate tubercles. The absence of tubercles in *Craseonycteris* and *Kerivoula* may represent simply another variation of tendon texture (perhaps related to small body size), or the condition in these forms may represent an evolutionary intermediate between the presence of a well-developed TLM and the complete absence of this mechanism. Tendon sheath plicae appear to vary principally in number, although this aspect of TLM morphology was not explicitly investigated in the current study.

The TLM in Dermoptera

The fore and hind feet of specimens of *Cynocephalus* sp. were dissected and a ratchet-type TLM was found in association with the plantar aspect of the proximal phalanx in all digits of both limbs. The presence of this mechanism was recently reported by one of us in an abstract (Quinn, 1993); we describe here the specific morphology of the digital tendons and TLM of the third toe of the hindlimb (Figs. 3A–C).

The tendons of the flexor digitorum superficialis (FDS) and flexor digitorum pro-

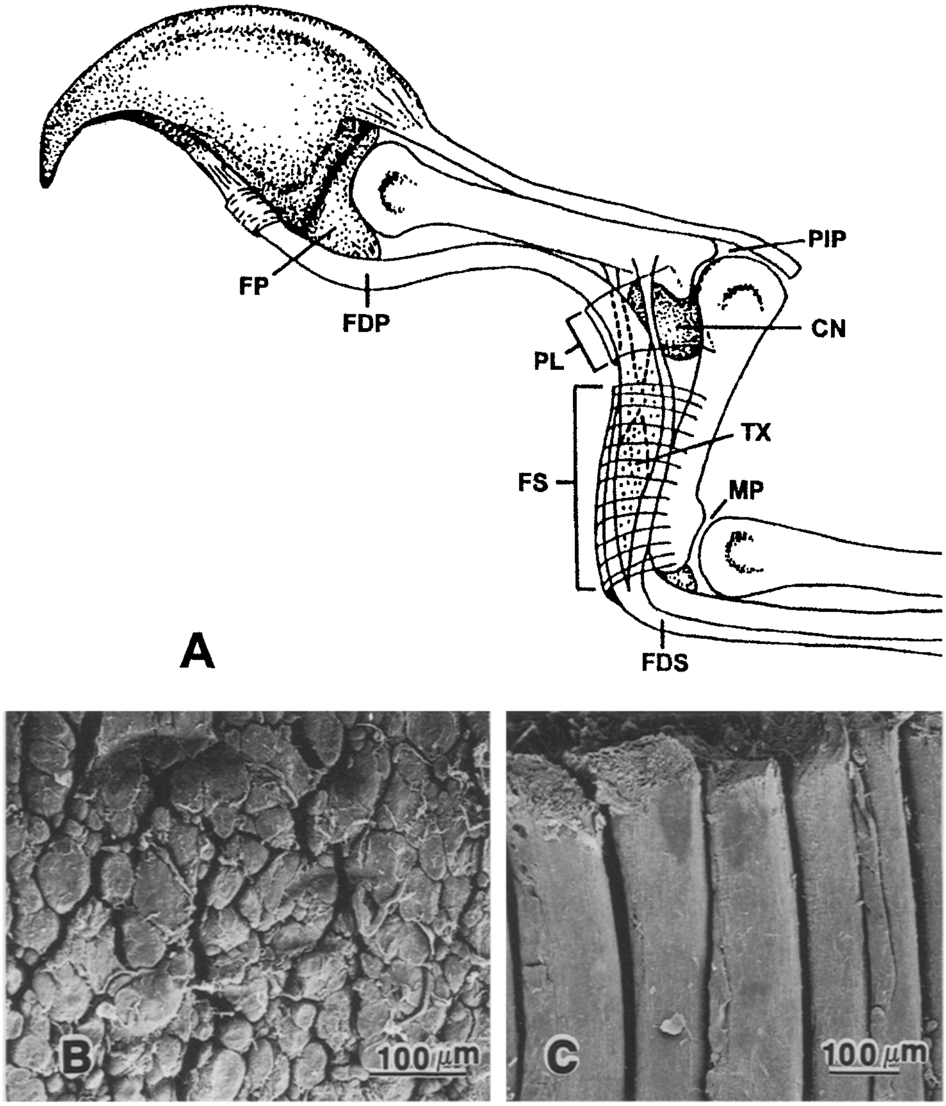

Fig. 3. Structure of the dermopteran TLM. (A) Diagram of a pedal digit in the resting position (i.e., hyperextended at the metatarsophalangeal joint). CN, cartilaginous nodule; FDP, flexor digitorum profundus tendon; FDS, flexor digitorum superficialis tendon; FS, flexor sheath with plicae; FP, flexor process; PIP, proximal interphalangeal joint; PL, pulley for PIP joint; TX, textured area (stippled) of tendon. (B) Textured portion of the FDP tendon in *Cynocephalus* sp. (USNM 115603). (C) Plicated flexor tendon sheath in *Cynocephalus* sp. (USNM 115603).

fundus (FDP) are held tightly against the plantar surface of the proximal phalanx by the flexor tendon sheath. The tendon of FDS splits to allow the tendon of FDP to course through toward its insertion on the ungual phalanx. The bifurcated portions of FDS rejoin by way of a tendinous strip only to bifurcate once more and insert on either side of the base of the proximal interphalangeal (PIP) joint. An additional constituent of the PIP joint is a firm cartilaginous nodule (CN in Fig. 3A) which is present on the plantar aspect of the joint. This nodule and the tendons of insertion of the FDS are covered on their plantar surfaces by a thickened portion of the fibrous flexor tendon sheath. This pulley-like structure spans the PIP joint, inserting on the sides of the base and head of the apposed phalanges.

With the exception of the cartilage nodules and relatively more complex pattern of tendon division and insertion, the primary components of the dermopteran TLM are nearly identical to those observed in large bats. Where it runs under the proximal phalanx, the plantar surface of the FDP tendon in *Cynocephalus* is covered with pronounced, regularly-shaped fibrocartilage tubercles (Fig. 3B) that are quite similar in form to those seen in *Pteropus* (Fig. 1A). Each of the tubercles consists of a nest of fibrocartilage cells surrounded by a dense fibrous matrix. A superficial synovial covering (epitenon) cannot be discerned on the surface of the tubercles. There are deep plicae on the part of the flexor tendon sheath that is in contact with the FDP tendon as it crosses the proximal phalanx (Fig. 3C).

When at rest, the dermopteran toe is hyperextended at the metacarpophalangeal (MP) joint and semiflexed at the proximal interphalangeal (PIP) joint (Fig. 3A). In an animal hanging suspended from a tree limb, apposition of the TLM components is effected by contact of the palm with the substrate and tension on the flexor tendons produced by the weight of the suspended body. Contraction of the long flexors apparently aligns the sheath plications and the tubercles to lock the TLM more fully. Full range of motion on flexing is not possible due to the presence of a hemispherical cartilaginous mass in the plantar joint spaces of the MP and PIP joints. These masses may act as fulcrum points or may hold the toe in a position from which it can provide a spring or shock absorber function when the colugo lands on a tree. They may also function as sesamoids to reduce tendon wear from friction.

Digital Morphology in Other Mammals

We examined the pedal flexor tendons and tendon sheaths of representatives of six additional orders of mammals (Primates, Scandentia, Carnivora, Artiodactyla, Rodentia, and Insectivora) but did not find a TLM in any of these taxa (Table II). There is considerable interspecific variation in the mechanical and physiological constraints on the flexor tendon apparatus, yet the morphology of the flexor tendons and their synovial sheaths were observed to vary little from each other. In most taxa the annular components of the tendon sheath resemble the cuff-like bands of collagen seen in human digital tendon sheaths. This is especially true of the other primate taxa dissected in this study (Table II).

DISCUSSION

The TLM in Phyllostomidae

Quinn and Baumel (1993) reported that a tendon lock (i.e., ratchet-type TLM) is absent in the five phyllostomids that they dissected (*Phyllostomus discolor*, *Glossophaga soricina*, *Anoura caudifer*, *Artibeus jamaicensis*, and *Desmodus rotundus*). Schutt (1993) similarly noted that the TLM appeared to be absent in several phyllostomids (*Desmodus rotundus*, *Diaemus youngi*, *Diphylla ecaudata*, and *Macrotus waterhousii*) but reported different results for three other taxa. Schutt (1993) indicated that the flexor tendon sheath in *Artibeus jamaicensis* is invested with a few plicae at the proximal border, although the flexor tendon lacks scales or foliations. Schutt (1993, p. 225) further reported that the digital lock is present but "modified" in *Vampyrum spectrum* and *Chrotopterus auritus*, although he did not describe these modifications.

In the current study we reexamined the phyllostomid specimens originally dissected by Quinn and Baumel (1993) and found no evidence of a ratchet-type TLM. As a result of Schutt's (1993) report, we looked closely for plicae on the proximal border of the annular tendon sheath in *Artibeus jamaicensis*, but found none in our individual. However, in all our phyllostomid specimens we noted presence of a retinaculum that is thickest in its central portion and tapers from anterior to posterior. As described above, we suggest that this configuration may act as a sort of friction lock on the tendon.

Schutt (personal communication) informs us that the tendon is smooth and the retinaculum lacks plicae in the digits of *Vampyrum* and *Chrotopterus*. However, the flexor sheath distal to the retinaculum is divided into unique plate-like segments that *are* plicated (Schutt, personal communication). This structure may represent yet another type of tendon locking mechanism. Based on these and other observations, we conclude that (1) phyllostomids lack the ratchet-like TLM (with plicated proximal tendon sheath and tubercles on the tendon) typical of other bats, (2) phyllostomids possess a uniquely thickened retinaculum that may act as a friction lock, and (3) some phyllostomids (i.e., the large "phyllostomines") have a unique structure distal to the retinaculum that may also function as a TLM.

Phylogenetic Relationships of Dermoptera and Chiroptera

The only mammalian taxa known to possess a ratchet-like TLM (with tendon sheath plicae and tubercles on the tendon surface) are dermopterans, megachiropterans, and members of 9 of 16 microchiropteran families (Tables I and II). The absence of a TLM in marsupials and most eutherian orders (Table II) indicates that the lack of this structure is primitive for mammals; presence of a TLM is clearly a derived feature.

As noted above, monophyly of Chiroptera was assumed at the outset of this study following Simmons (1994). Although some authors continue to support the hypothesis that bats are diphyletic (Pettigrew *et al.*, 1989; Pettigrew, 1991a, b, 1995), the majority of phylogenetic studies agree that bats are monophyletic (Simmons, 1994). The position of Chiroptera within Eutheria is less clear, however, and identity of the sister group of bats is still the subject of considerable debate.

A sister-group relationship between Dermoptera and Chiroptera has been supported in studies based on a broad range of morphological data (e.g., Gregory, 1910; Novacek and Wyss, 1986; Novacek, 1986, 1990, 1992; Wible and Novacek, 1988; Johnson and Kirsch, 1993; Simmons, 1993, 1995; Szalay and Lucas, 1993). Analyses that combined molecular and diverse morphological data reached the same conclusion (Novacek, 1994). However, some studies based on more limited morphological data sets have suggested that the sister group of bats may be either Dermoptera + Primates (Beard, 1993) or Primates + Scandentia (Kay *et al.*, 1992). Beard's (1993) data set included only postcranial and cranial osteological characters, while Kay *et al.* (1992) considered only cranial data. In contrast, the studies of Novacek and others—which support a sister-group relationship between bats and dermopterans—included characters of the cranium, dentition, postcranial skeleton, musculature, vascular system, fetal membranes, and nervous system (Novacek and Wyss, 1986; Novacek, 1986, 1990, 1992; Wible and Novacek, 1988; Johnson and Kirsch, 1993; Simmons, 1993).

Analyses of molecular data have produced a broad range of results (for a review see Simmons, 1994). Among studies that have included both bats and dermopterans, a clade containing Dermoptera plus other orders (e.g., Primates, Scandentia) was indicated as the sister group of bats in studies based on 12S rDNA sequences (Ammerman and Hillis, 1992) and ϵ-globin gene sequences (Bailey *et al.*, 1992). Different taxa (e.g., Artiodactyla, Carnivora) have been identified as the sister group of bats based on analyses of cytochrome oxidase II and interphotoreceptor binding protein gene sequences (Stanhope *et al.*, 1992; Adkins and Honeycutt, 1993). The conflicting phylogenetic results of these studies may have been caused by relatively sparse, uneven taxonomic sampling and long branch attraction (Simmons, 1994; Vrana, 1994). In an effort to resolve these problems, Vrana (1994) used a dense sampling approach, simultaneously analyzing 12S rDNA sequences from 158 species (representing 20 orders) under a variety of search parameters. Dermoptera grouped with bats in all of the most parsimonious trees generated in this study.

Novacek (1986) revived the name Volitantia Illiger 1811 to describe the clade containing Dermoptera + Chiroptera. The presence of a ratchet-type TLM in bats and dermopterans provides additional support for monophyly of this clade. With the exception of Dermoptera, none of the other putative sister taxa of bats appear to have a TLM (Table II). If Dermoptera and Chiroptera are not sister taxa, we must hypothesize that a ratchet-like TLM evolved at least twice within mammals, or that it evolved once and was lost at least once among non-chiropteran mammals. Either of these alternative hypotheses is less parsimonious than supposing that the TLM evolved in the ancestral volitantian lineage. Including the presence of the TLM, 17 morphological synapomorphies of Volitantia have now been identified (Table III). These characters represent a wide variety of anatomical systems including the dentition (one character), ear region (three characters), cranial vascular system (one character), axial skeleton (two characters), forelimb and patagia (seven characters), and feet (three characters).

Pedal Function in Volitantia

It seems likely that the pedal characters shared by bats and dermopterans are related to the evolution of underbranch hanging behavior (Szalay and Lucas, 1993; Simmons, 1995). Both colugos and bats spend a great deal of time hanging suspended from various substrates. Microchiropteran bats apparently hang almost exclusively from their hindlimbs; megachiropterans generally roost suspended by the hindlimbs, but often move about in trees using a pendant quadrupedal gait (Hill and Smith, 1984; Bennett, 1993; Pettigrew, 1995). Dermopterans also adopt a suspended quadrupedal posture when feeding or moving about on branches, and are apparently incapable of effective upright quadrupedal locomotion (Lekagul and McNeely, 1977).

Characters unique to the volitantian pes include the following: (1) elongation of the fourth and fifth pedal rays, (2) ungual phalanges that are deep both proximally and distally and compressed mediolaterally, and (3) the presence of a tendon locking mechanism on the digits (Table III). Several authors have argued previously that a TLM

Table III. Morphological Synapomorphies of Volitantia (Chiroptera + Dermoptera)[a]

1. Tooth enamel with horseshoe-shaped prisms with associated minor boundary planes (seams)[b]
2. Fenestra cochlea (round window) faces directly posteriorly[c]
3. Subarcuate fossa greatly expanded and dorsal semicircular canal clearly separated from endocranial wall of squamosal[c]
4. Tegmen tympani reduced, tapered to a round process, does not form roof over mallear-incudal articulation or entire ossicle chain[d]
5. Ramus infraorbitalis of the stapedial artery passes through the cranial cavity dorsal to the alisphenoid[e,f]
6. Neural spines on cervical vertebrate 3–7 weak or absent[c]
7. Ribs flattened, especially near vertebral ends[c,g]
8. Forelimbs markedly elongated[c]
9. Proximal displacement of the areas of insertion for the pectoral and deltoid muscles; coalesced single proximal humeral torus[g]
10. Presence of humeropatagialis muscle[c]
11. Reduction of proximal ulna[c]
12. Modification of distal radius and ulna: fusion of distal ulna to distal radius; distal radius transversely widened, manus effectively rotated 90°; deep grooves for carpal extensors on dorsal surface of distal radius; disengagement and reduction of the ulna from anterior humeral contact[f,g]
13. Fusion of scaphoid, centrale, and lunate into scaphocentralunate[g]
14. Patagium continuously attached between digits of manus[c,g]
15. Elongation of the fourth and fifth pedal rays[g]
16. Ungual phalanges both proximally and distally deep, compressed mediolaterally[g]
17. Presence of a ratchet-type tendon locking mechanism on digits of feet

[a] Features listed have been discussed by other authors as noted. Dermoptera is defined here to include extant gliding lemurs (Galeopithecidae = *Cynocephalus*) + extinct Paromomyidae. This grouping is equivalent to Eudermoptera sensu Beard (1993). Several fossil taxa included in Dermoptera by Beard (micromomyids, plesiadapids, carpolestids, and saxonellids) are excluded here due to ambiguity concerning their relationships (Simmons, 1993).
[b] Source: Lester *et al.* (1988).
[c] Source: Wible and Novacek (1988).
[d] Source: Wible and Martin (1993).
[e] Source: Wible (1993).
[f] Source: Simmons (1994).
[g] Source: Szalay and Lucas (1993).

facilitates hanging with little or no muscular effort (Schaffer, 1905; Schutt, 1992, 1993; Bennett, 1993; Quinn and Baumel, 1993). Although no *in vivo* experiments have been conducted to test this hypothesis, the morphological evidence is compelling and the hypothesis appears to be widely accepted (Schutt, 1992, 1993; Bennett, 1993; Quinn and Baumel, 1993). Elongation of the fourth and fifth pedal rays also appears to be related to hanging behavior (Szalay and Lucas, 1993; Simmons, 1995). As a result of elongation of the lateral digits, digits II–V are subequal in length and their claws are aligned. This arrangement apparently facilitates hanging by allowing the digits to work together as a single gripping unit with tensile forces evenly distributed among the digits. Finally, the shape of the ungual phalanges may contribute to hanging ability by increasing resistance of the claws to bending stresses. The relatively great depth of the strongly recurved ungual phalanx and the presence of a relatively large flexor process may also contribute to the function of the TLM by increasing the distance between the point of insertion of the flexor tendon and the distal interphalangeal joint. When the digit is flexed, this configuration causes the tendon to "bowstring," thus effectively increasing the amount of pressure that the tendon exerts on the flexor sheath.

Microchiropteran Phylogeny and TLM Evolution

Recognition of the ratchet-like TLM as a synapomorphy of Volitantia implies that a TLM was present ancestrally in bats. Given this assumption, we can investigate possible patterns of TLM evolution within microchiropteran bats by considering distribution of this apparatus in the context of different phylogenetic hypotheses. The classification of Koopman (1984) will be accepted for the purpose of providing superfamilial group names for the following discussion (Table IV). "TLM" is used below to refer exclusively to the ratchet-type TLM typical of most bats; the friction apparatus of phyllostomids (and the unique distal structures seen in *Vampyrum* and *Chrotopterus*) are interpreted as autapomorphies in all of the scenarios presented below.

Smith (1976, p. 56) presented a cladogram of bat families that was intended to represent the "generally accepted view" of bat phylogeny (Fig. 4). This tree was presumably based principally on consideration of external and craniodental morphology, although no explicit analysis was conducted. In the context of Smith's (1976) phylogeny, the most parsimonious interpretation is that a TLM was present primitively in Microchiroptera and has been retained in all yinochiropteran bats (emballonuroids and rhinolophoids). In contrast, the TLM seems to have been lost in the lineage leading to Yangochiroptera (phyllostomoids and vespertilionoids). However, three yangochiropteran families—Noctilionidae, Molossidae, and Vespertilionidae—have a TLM. If

Table IV. A Higher-Level Classification of Recent Bats[a]

- Order Chiroptera
  - Suborder Megachiroptera
    - Family Pteropodidae
  - Suborder Microchiroptera
    - Infraorder Yinochiroptera
      - Superfamily Emballonuroidea
        - Family Emballonuridae
        - Family Craseonycteridae
        - Family Rhinopomatidae
      - Superfamily Rhinolophoidea
        - Family Nycteridae
        - Family Megadermatidae
        - Family Rhinolophidae
          - Subfamily Rhinolophinae
          - Subfamily Hipposiderinae
    - Infraorder Yangochiroptera
      - Superfamily Phyllostomoidea
        - Family Mormoopidae
        - Family Noctilionidae
        - Family Phyllostomidae
      - Superfamily Vespertilionoidea
        - Family Thyropteridae
        - Family Myzopodidae
        - Family Furipteridae
        - Family Mystacinidae
        - Family Natalidae
        - Family Molossidae
        - Family Vespertilionidae

[a] From Koopman (1984).

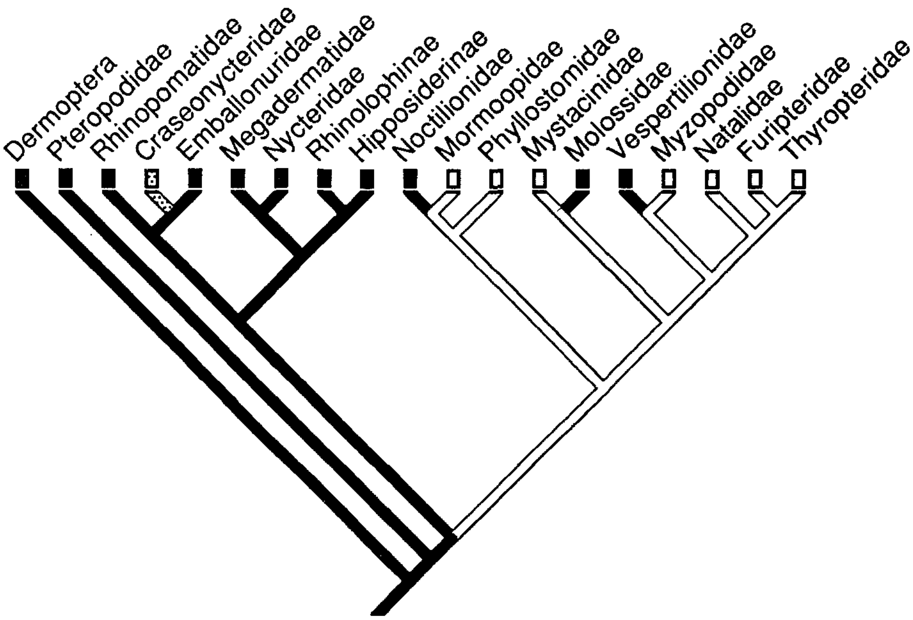

Fig. 4. Distribution of the ratchet-type TLM mapped on the phylogeny of bats presented by Smith (1976). In this and the following figures, monophyly of Chiroptera is assumed following Simmons (1994), and a sister-group relationship between Chiroptera and Dermoptera is accepted. In each tree the presence of a TLM (with both tendon sheath plicae and tendon tubercles) is indicated by black boxes, and lineages presumed to have a TLM are indicated by black branches. The absence of the TLM is indicated by white boxes and white branches. The presence of a partially developed TLM (with plicae but no tubercles) is indicated by the stippled boxes and branches. The rank endings of various taxonomic names (e.g., Hipposiderinae versus Hipposideridae) are portrayed as originally presented by each author.

Smith's (1976) phylogeny is accepted, the TLM must have reappeared independently in each of these forms. The presence of a partially developed TLM (with plicae but no tubercles) in Craseonycteridae appears to be an autapomorphy. In contrast, the partially developed TLM in Kerivoulinae might represent an intermediate condition associated with the reacquisition of the TLM in Vespertilionidae. In total, Smith's (1976) phylogeny minimally requires six evolutionary steps (transformations), including a single origin of the TLM in the ancestral volitantian lineage, loss of the TLM in the ancestral yangochiropteran lineage, and reappearance of the TLM in three yangochiropteran families.

Van Valen (1979) presented a phylogeny (Fig. 5) based on an analysis of diverse morphological features using unspecified cladistic methods. Van Valen's phylogeny differs from that of Smith (1976) in several ways, particularly in the placement of Phyllostomoidea, which Van Valen (1979) associated with emballonuroids and rhinolophoids rather than vespertilionoids. In the context of Van Valen's (1979) phylogeny, the most parsimonious interpretation is that the TLM was present primitively in all four of the microchiropteran superfamilies (Fig. 5). Subsequent evolution led to loss of the TLM within phyllostomoids (in the lineage leading to Mormoopidae + Phyllostomidae) and within vespertilionoids (in mystacinids and in a lineage leading to several other families).

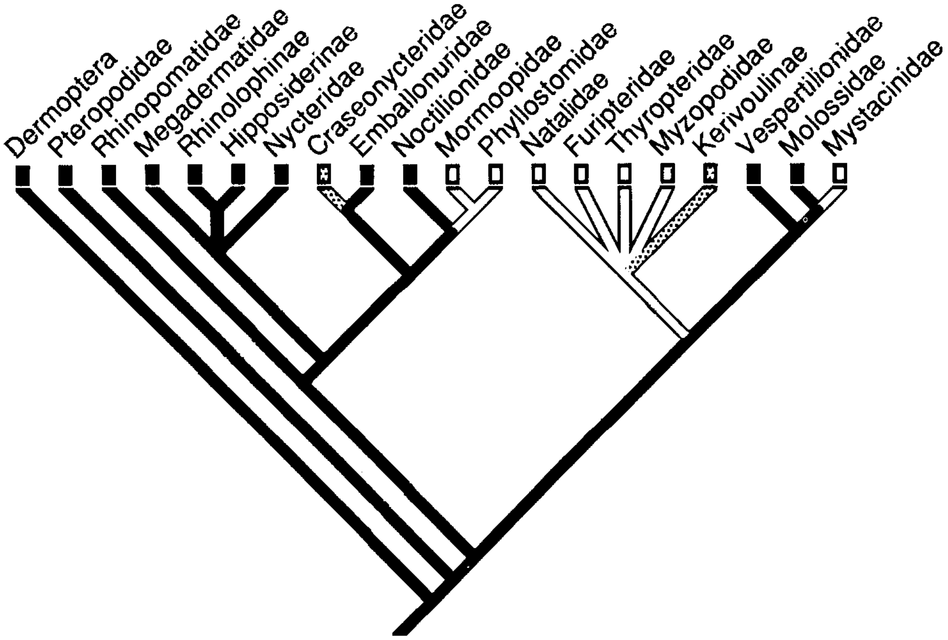

Fig. 5. Distribution of the TLM mapped on the phylogeny proposed by Van Valen (1979).

Within the latter group, a partially developed TLM (with plicae but no tubercles) seems to have reappeared in Kerivoulinae. Presence of a partially developed TLM in Craseonycteridae appears to be an autapomorphy. In total, Van Valen's (1979) phylogeny minimally requires six evolutionary steps including the origin of the TLM in the ancestral volitantian lineage.

Novacek (1980) analyzed chiropteran relationships using characters of the auditory region. The cladogram produced in his study (Fig. 6) differs significantly from those proposed previously, and Novacek (1980) warned against using this cladogram as a basis for a new phylogenetic reconstruction or classification. Nevertheless, Novacek's (1980) tree provides an opportunity to investigate congruence between TLM distribution and another character system, i.e., the auditory region. The pattern of TLM distribution as mapped on Novacek's (1980) tree indicates that the presence of a TLM is primitive for most lineages of microchiropteran bats. Loss of the TLM appears to have occurred independently five times—once in the lineage leading to Mystacinidae + Mormoopidae, once in phyllostomids, once in furipterids, once in thyropterids, and once in natalids. A minimum of six evolutionary steps is thus required by Novacek's (1980) cladogram. However, it should be noted that Novacek's (1980) study did not include Kerivoulinae, Craseonycteridae, or Myzopodidae. Inclusion of these taxa might change perceived patterns of transformation of the TLM.

Luckett (1980) analyzed the ontogeny and morphology of the fetal membranes of 10 families of bats and constructed a poorly resolved cladogram from these data (Fig. 7). Interpretation of TLM distribution in the context of this tree indicates that the presence of a TLM is primitive for all major microchiropteran lineages and that loss of this

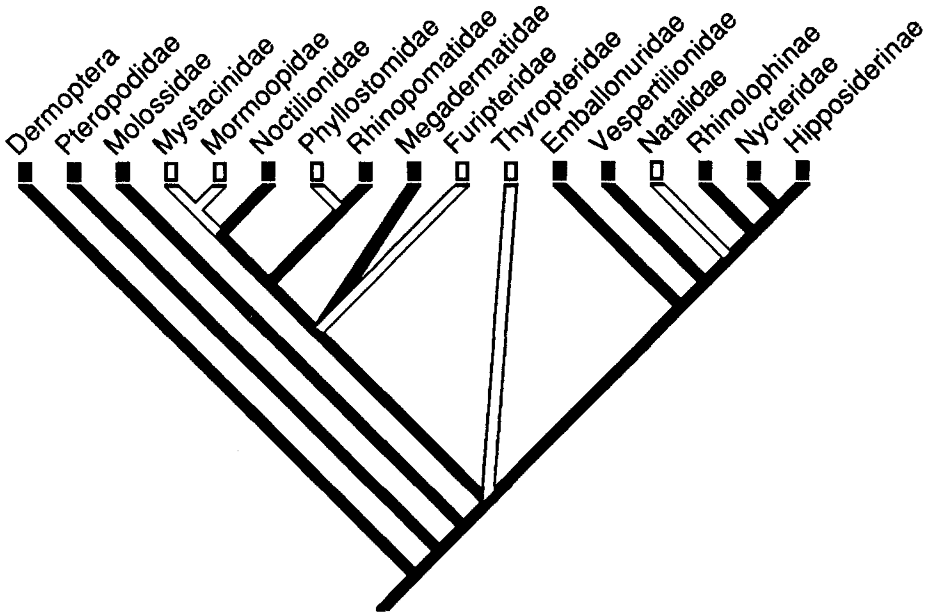

Fig. 6. Distribution of the TLM mapped on a phylogenetic tree derived from auditory characters by Novacek (1980).

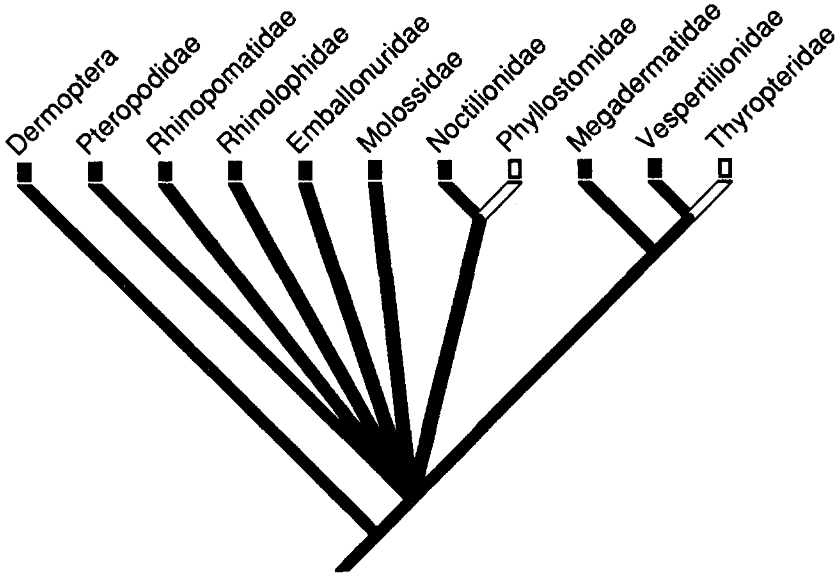

Fig. 7. Distribution of the TLM mapped on a phylogenetic tree derived from fetal membrane characters by Luckett (1980).

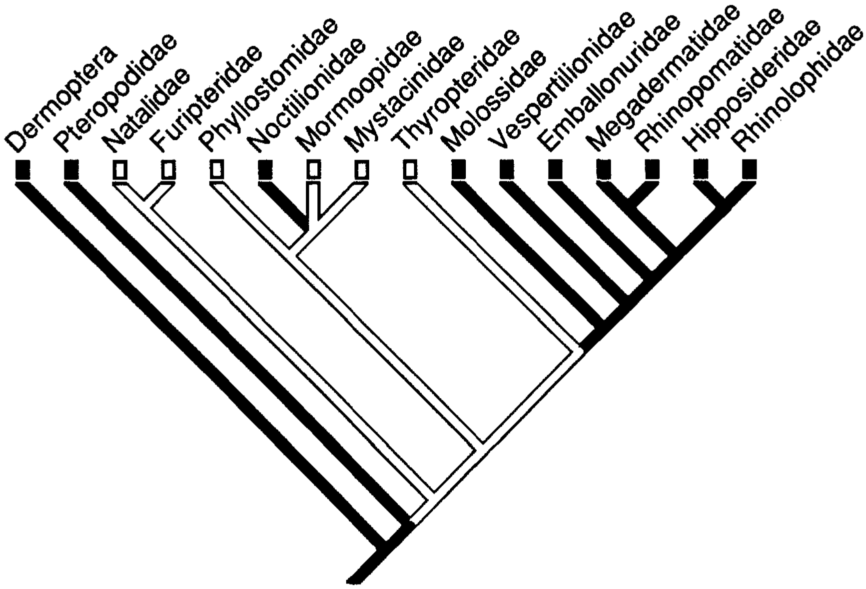

Fig. 8. Distribution of the ratchet-type TLM mapped on a phylogeny proposed by Pierson (1986) on the basis of transferrin immunological distances.

structure occurred at least twice, once in phyllostomids and once in thyropterids. However, this interpretation might change significantly if the seven families of bats omitted from this tree were considered, since five of these taxa lack a TLM.

Another phylogeny of bats was proposed by Pierson (1986) on the basis of immunological distance data (Fig. 8). Unfortunately, this study did not include representatives of Nycteridae, Craseonycteridae, Myzopodidae, or Kerivoulinae. The pattern of distribution of the TLM as mapped on Pierson's (1986) tree suggests that the TLM was lost in the earliest members of the microchiropteran lineage, and the TLM subsequently reappeared twice, once in Noctilionidae and once in the lineage leading to Molossidae, Vespertilionidae, Emballonuridae, and Rhinolophoidea. A minimum of four evolutionary steps is thus implied by this phylogeny.

Each of the phylogenetic hypotheses discussed above indicates that homoplasy exists in evolution of the TLM. Smith's (1976) phylogeny implies that the ratchet-like TLM evolved once, was lost once, and then reappeared three times. In contrast, Van Valen's (1979) tree indicates that the TLM evolved once, was lost three times, and subsequently reappeared only once. Pierson's (1986) phylogeny implies that the TLM evolved once, was lost once, and reappeared twice. Only Novacek's (1980) and Luckett's (1980) trees do not require any "reappearances" of the TLM, instead implying multiple losses of this structure.

Evolution and Development

With the exception of the initial appearance of the TLM in the ancestral volitantian lineage, most of the TLM transformations implied by the phylogenies discussed above are homoplastic. These evolutionary events apparently represent either reversals to the ancestral mammalian condition (absence of a TLM) or reversals to the ancestral volitantian condition (presence of a TLM).

A phylogenetic character reversal is an evolutionary change from a derived state to a condition that was present in the ancestral lineage of a taxon. While the resultant state may be identical to the ancestral condition in all morphological details, its occurrence is secondarily derived. Reversals differ from cases of convergence or parallelism in that they apparently result from reactivation of developmental pathways that had been suppressed or modified previously (Hall, 1984; Wake and Larson, 1987; Stiassny, 1992). Reversals can apparently be brought about via many mechanisms, including genetic mutation, paedomorphosis, and perturbation of developmental regulatory systems (Hall, 1984; Wake and Larson, 1987; Stiassny, 1992). In the case of the chiropteran TLM, there is no evidence of paedomorphosis. Some underlying genetic component seems most likely given the apparent absence of any significant intraspecific variation in TLM structure.[5]

Extrinsic factors, such as chronic pressure, do not appear to be responsible for initiation of TLM formation although such factors may affect the degree of development of the components. It has been shown experimentally that fibroblasts may be transformed into chondroblasts when subjected to chronic pressure (Benjamin and Evans, 1990). Pressure exerted on adjacent surfaces of the flexor tendon sheath and tendon surface might cause such a transformation, facilitating TLM development by helping to activate local cartilage matrix production. However, TLM formation is already evident in fetal bats that we have examined, so chronic pressure—such as that produced by hanging from the digits—cannot be the only factor influencing TLM development. Nevertheless, pressure-mediated cellular transformations may be important in determining the form of the adult TLM. The components of the TLM appear most robust in large-bodied species such as *Pteropus* (Figs. 1B and C), *Macroderma* (Figs. 2E and F), and *Cynocephalus* (Fig. 3), perhaps as a result of the relatively high pressures generated on these components by the suspended body mass. Conversely, in tiny bats (e.g., *Craseonycteris*, *Kerivoula*; Figs. 2A–D) the absence of well-defined tubercles on the flexor tendon and lack of stiffening along the free edges of the plicae may result from an absence of pressure-mediated cellular transformations. These possibilities have yet to be adequately investigated.

CONCLUSIONS

Although this study completes a preliminary survey of the TLM in chiropteran families, considerable work remains to be done before we can hope to understand the evolutionary history of this mechanism. A well-substantiated hypothesis of chiropteran interfamilial relationships is essential for interpreting the taxonomic distribution of TLM structures. Unfortunately, existing hypotheses are largely incongruent, and problems involving taxonomic sampling, limited character sets, and phylogenetic methods make

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[5] Examination of large series of specimens (something well beyond the scope of the current study) will be necessary to evaluate properly intraspecific variation in TLM structure. We dissected six individuals of *Eptesicus fuscus* (Table I) and detected no significant difference in TLM structure between individuals. However, other species might show different patterns, and it is possible that variation may be greatest in taxa in which the TLM is only partially developed (e.g., *Kerivoula hardwickei*). Incongruence between our observations of *Artibeus jamaicensis* and those of Schutt (1993) further indicates that more work on tendon structures of phyllostomids is necessary.

it difficult to resolve the inconsistencies. Because interpretation of TLM evolution varies widely in the context of these different phylogenies (Figs. 4–6), it is difficult to draw any conclusions except to note that substantial homoplasy seems to have occurred in this system. There is no evidence that a ratchet-like tendon lock (with tubercles and plicae) has evolved de novo more than once in mammals. All of the homoplasy noted appears to involve reversals to either the ancestral mammalian condition (TLM absent) or the ancestral volitantian condition (TLM present). The development of substantive hypotheses concerning the causes of these transformations in various bat lineages must await better resolution of higher-level relationships among bats. Toward this end, data concerning structure and distribution of a TLM in different families may prove useful in future phylogenetic analyses.

Interspecific variability in TLM structure and function have yet to be adequately investigated. Some clear differences exist among species in the form of the tubercles and plicae that comprise the ratchet-type TLM, and structure of the friction apparatus seems to vary among phyllostomids. These and other features may prove to be phylogenetically significant at higher taxonomic levels, but evaluation of such patterns will require detailed sampling far beyond that undertaken in the current study. Additional work is also necessary to document any patterns of intraspecific variation that may exist.

Function of the tendon lock also requires additional study. As discussed above, the tendon lock in bats has long been assumed to function as a mechanism for reducing the muscular effort needed to cling to the substrate while hanging suspended. However, this mechanism has never been investigated experimentally. Electromyographic monitoring of flexor musculature in hanging bats could be used to indirectly investigate the function of the TLM in vivo. Detailed analyses of TLM function may provide a perspective necessary for interpreting the possible ecological and evolutionary significance of this interesting mechanism.

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