

VARIATION OF A MUSCLE IN HUMMINGBIRDS AND SWIFTS AND ITS SYSTEMATIC IMPLICATIONS

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Abstract.—Historically, features of the muscle tensor propatagialis pars brevis have been used to argue that swifts and hummingbirds comprise a single monophyletic order, the Apodiformes, and that this order is most closely related to the “pico-passeriforms.” We describe variations of this muscle in swifts and hummingbirds as well as in other orders and conclude that the new evidence does not support these claims. The variations observed, however, do show morphological trends that help to clarify relationships within both swifts and hummingbirds.

The phylogenetic relationships of hummingbirds and swifts to each other and to other avian orders are among the major unsolved ornithological problems in systematics. Subfamilial and generic relationships within swifts are fairly well understood (see Brooke 1970), but internal relationships of hummingbirds are still poorly known. Although we do not claim to have solved any of these problems, we have found that variation in a single muscle, *M. tensor patagii brevis*, bears on all of them. We report this variation and its systematic implications as a stimulus for further study of these problems, and as partial evidence toward their eventual solution.

The tensor patagii brevis muscle (TPB) extends from the shoulder to the forearm in birds and apparently can serve either to flex the forearm or to support the prepatagial membrane of the extended wing. This muscle exhibits marked variation among birds, especially in relation to its tendon or tendons of insertion. Garrod (1876) drew attention to this variation and to its taxonomic implications, and Fürbringer (1888) devoted six plates and considerable discussion to this muscle. Since then it has been further described in major systematic and anatomical works (e.g. Buri 1900; Beddard 1898; George and Berger 1966). In this paper we describe in some detail the variation of TPB in swifts and hummingbirds, and we test Lowe's (1939:329) contentions that the fleshy belly and tendon of insertion of TPB in hummingbirds is almost identical with that of the swift, that both are fundamentally passerine in design, and that the arrangement in non-passerines is quite different.

Hummingbirds

In hummingbirds the origin of TPB is consistently by a tendon from the head of the coracoid. The nearly parallel fibers of the short, wide belly pass distally and end on the surface of the extensor metacarpi radialis muscle (EMR) and on a short internal aponeurosis that fuses with the aponeurosis of origin of EMR. At this point of fusion the aponeurosis of TPB forms a tendon (the humeral tendon) that extends across the belly of EMR and inserts on the humerus. In hummingbirds another aponeurosis or tendon (the distal tendon) passes distally from the

same point of fusion along the surface of EMR toward the wrist. Within hummingbirds, four different patterns of insertion exist.

Type 1 (Fig. 1f) is characteristic of the Phaethornithinae or hermits (see Appendix for species examined). In these forms the humeral tendon of TPB is partially covered by fibers of EMR that arise from the process of origin of that muscle. The humeral tendon of TPB and the aponeurosis of origin of EMR are tightly bound together where they cross within the belly of EMR, thus forming a firm base for the attachment of overlying muscle fibers. The humeral tendon of TPB emerges from the belly of EMR, passes superficial to the distal-most fibers of origin of EMR and inserts on a tubercle of the humerus distal to the process of EMR. (Such terms as ectepicondylar process, lateral epicondyle, and dorsal supracondylar process are sometimes used for the points of attachment of EMR and TPB on the humerus. Until a better understanding of the homologies of projections on the distal end of the humerus is obtained throughout birds we prefer to avoid these terms and refer simply to the process of EMR and the tubercle of TPB.)

The distal "tendon" of TPB in hermits is so transparent that we initially considered it absent. Closer examination revealed a short tendon from the junction of the bellies of TPB and EMR that quickly fans out into a broad aponeurotic sheet and invests most of the distal half of the belly of EMR. Proximally it is free of a superficial dorsal aponeurosis of EMR, but distally the two aponeuroses fuse.

Eutoxeres is the only phaethornithine exception to the Type 1 format. In this genus the humeral tendon of TPB is visible for its entire length. Although not covered by fibers of EMR, it serves as a point of origin for some of the superficial fibers of that muscle. The humeral tendon and the aponeurosis of origin of EMR are fused where they cross as in other hermits.

Type 2 (Fig. 1g) occurs in some of the Trochilinae: *Anthracothonax*, *Doryfera*, *Androdon*, *Eulampis*, *Sericotes*, *Chrysolampis*, *Polytmus*, *Topaza*, *Heliothryx*, *Colibri*, and *Florisuga*. In these forms the humeral tendon of TPB is clearly visible on the surface of the proximal end of EMR. Unlike Type 1 the humeral tendon is essentially free of the aponeurosis of origin of EMR, attaching only to its cranial edge. The insertion of the humeral tendon is on a tubercle of the humerus. As in other trochiline hummingbirds a distinct distal tendon of TPB is formed. This tendon broadens distally and fuses with the dorsal surface of a superficial aponeurosis of EMR that contributes to its tendon of insertion near the wrist. This distal tendon of TPB lies on the dorsal surface of EMR so that the tendon appears to divide the belly of EMR unequally into cranial (smaller) and caudal (larger) portions. This is not the case with Type 3 birds.

Type 3 (Fig. 1h) is found in all trochiline genera listed in the Appendix except those of Types 2 and 4. The distal tendon of TPB is well developed and, at least proximally, free of the belly of EMR. It passes along the cranial edge of the belly of EMR rather than along the dorsal surface. Only near the distal end of the radius does it fuse with the craniodorsal portion of the tendon of insertion of EMR. The relations of the humeral tendon of TPB are like Type 2. This is the type illustrated by Garrod (1876).

Type 4 (Fig. 1i) is restricted to trochiline hummingbirds of the genera *Aces-trura*, *Chaetocercus*, *Calliphlox*, and possibly others. Here the relations of the

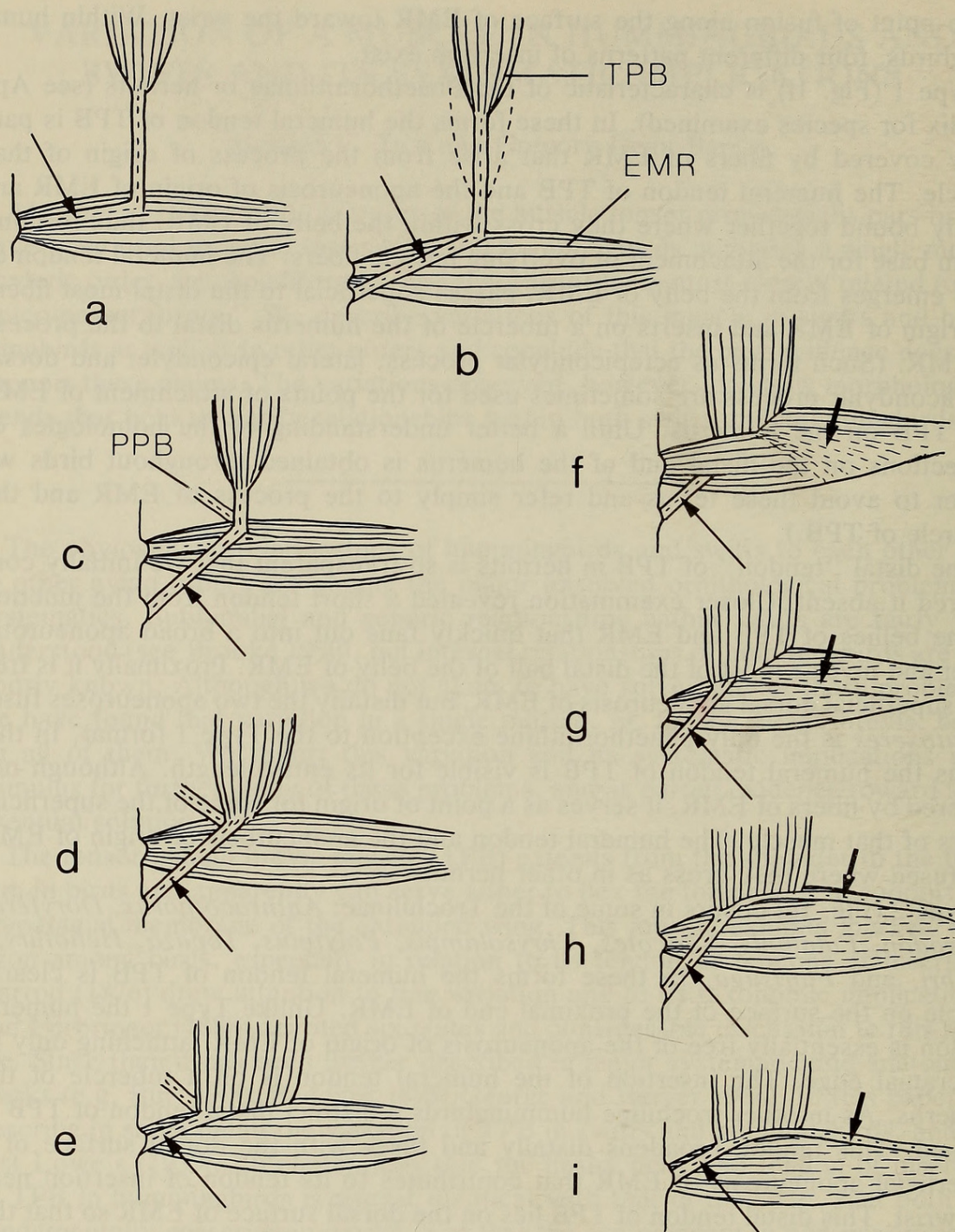


Fig. 1. Diagrams showing *M. tensor propatagialis pars brevis* and *M. extensor metacarpi radialis* (right, dorsal view): a, Piciformes and some Passeriformes; b, Most Passeriformes (dotted outline represents *Hirundinidae* and *Lonchurae*); c, *Hemiprocridae* (Type A); d, *Cypseloidinae* (Type B); e, *Apodinae* (Type C); f, *Trochilidae* (Type 1); g, *Trochilidae* (Type 2); h, *Trochilidae* (Type 3); i, *Trochilidae* (Type 4). EMR = *M. extensor metacarpi radialis*; PPB = *M. pectoralis pars propatagialis brevis*; TPB = *M. tensor propatagialis pars brevis*. Long arrow indicates humeral tendon of TPB; short arrow indicates distal tendon of TPB.

distal tendon of TPB are similar to Type 3, but a difference exists in the humeral tendon. In these forms, that tendon lies directly superficial to and almost parallel with the aponeurosis of origin of EMR, to which it is firmly fused. The short tendon of TPB inserts on the process of origin of EMR rather than on a separate tubercle.

Swifts

The condition of TPB in swifts is significantly different from that of hummingbirds. According to Cohn (1968) the muscle arises from the head of the coracoid and from the adjacent dorsal arm of the furcula in larger swifts, and only from the coracoid in some smaller swifts. Furthermore, *M. pectoralis pars propatagialis longus* and *M. pectoralis pars propatagialis brevis* are present in swifts but neither is present in hummingbirds. In swifts the latter muscle is represented by a short tendon that extends from *M. pectoralis* near the deltoid crest to the tendon of insertion of TPB. In those instances where the tendon of insertion of TPB is absent, the propatagialis brevis joins TPB at its juncture with EMR. In all of the swifts we examined there was no trace of a distal tendon of TPB. Within the swifts the TPB differs in other ways as well, and we recognize three basic types.

Type A (Fig. 1c) is found in the crested swifts (Hemiprocnidae). In these forms the belly of TPB ends on a short tendon that receives the pectoralis pars propatagialis brevis tendon and continues to the cranial surface of EMR. The humeral tendon then passes across the surface of EMR to insert on a tubercle of the humerus.

Type B (Fig. 1d) is found in the Cypseloidinae. It is similar to Type A except that the belly of TPB reaches the surface of EMR without first forming a tendon of insertion. Instead, the belly tapers to a narrow, semitendinous insertion on EMR. At this juncture pars propatagialis brevis attaches and a well-defined humeral tendon of TPB arises and crosses EMR to insert on a tubercle of the humerus.

Type C (Fig. 1e) is seen in the Apodinae (sensu Morony *et al.* 1975; includes Collocaliini, Chaeturini, and Apodini). Type C resembles Type B except that the belly of TPB makes broad contact with EMR rather than tapering to its insertion. In addition, the humeral tendon of TPB almost parallels that of EMR and inserts directly on the process of origin of EMR, much like Type 4 in hummingbirds. *Hirundapus giganteus* and *H. caudacutus* are somewhat different. In these species the humeral tendon of TPB attaches slightly distal to the process of EMR or on its distal edge. However, the extent of separation between that tendon and the aponeurosis of origin of EMR is not nearly as great as it is in Types A and B.

The use of *Hirundapus giganteus* to illustrate the TPB of swifts by Lowe (1939) was unfortunate because that species is atypical of either subfamily. Although used to support the presence of a humeral tendon of TPB in swifts, it probably represents a stage in the loss of that tendon.

Discussion

Separate humeral tendon of TPB.—The contention that passerine birds differ from most other birds in having a humeral tendon of TPB that is separate from rather than fused with the aponeurosis of origin of EMR (Fig. 1a, b) originated with Garrod (1876). Lowe (1939) used this feature to ally swifts and hummingbirds with the Passeriformes (which he broadened to include also the Capitonidae, Indicatoridae, and Picidae). Not all passeriforms (sensu strictu) have a separate tendon; we found it fused in Eurylaimidae and Rhinocryptidae. Garrod (1876) said it was fused in Menuridae and Atrichornithidae but Raikow (pers. comm.) found it separate in *Atrichornis clamosus*. In the Caprimulgidae we found the

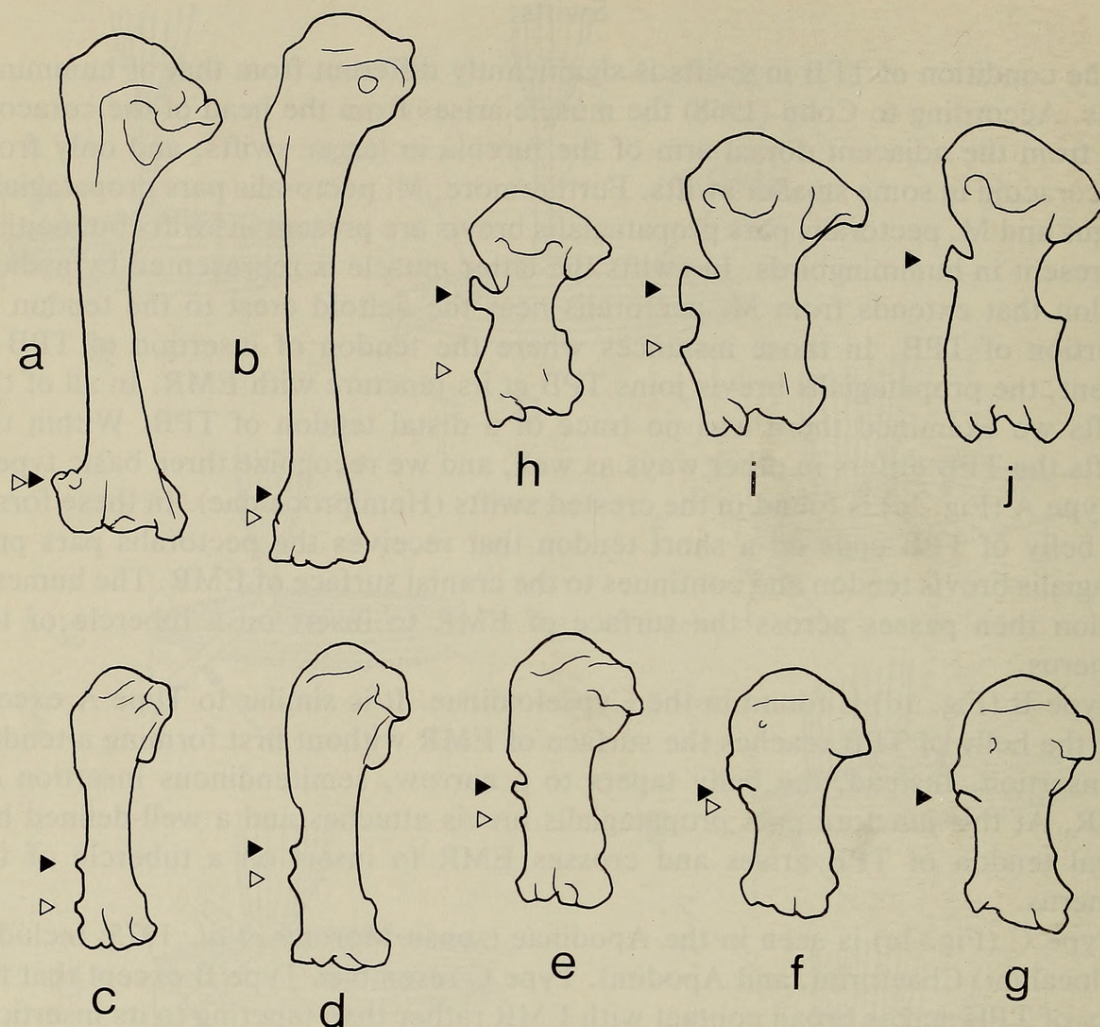


Fig. 2. Selected humeri (left, caudal view) showing positions of the process of *M. extensor metacarpi radialis* (opposite black triangle) and of tubercle of *M. tensor propatagialis pars brevis* (white triangle): a, *Coccothraustes vespertinus*; b, *Cordeiles minor*; c, *Hemiprocne comata*; d, *Hemiprocne longipennis*; e, *Nephoecetes niger*; f, *Hirundapus caudacutus*; g, *Apus apus*; h, *Glaucis hirsuta*; i, *Coeligena wilsoni*; j, *Chaetocercus jourdanii*. Some sizes have been adjusted to make them roughly comparable, but all are not drawn to same humerus length because that measure varies greatly in relation to body size.

tendon to be fused in *Caprimulgus* but completely separate in *Cordeiles*. Thus separate tendons, while probably derived within birds, have evidently evolved independently in at least the Caprimulgidae and Passeriformes.

Comparison among passerines, caprimulgids, crested swifts, and swifts strongly suggests that the degree of separation of the humeral attachments of TPB and EMR results mainly from proximal displacement of EMR. The humeral attachment of TPB also moves proximally (in an evolutionary sense), but it lags behind, creating a gap between the attachments. Eventually it may reach the level of the process of EMR. Such stages can be represented, as in Fig. 2, by: a, a passerine; b, *Cordeiles*; c, *Hemiprocne comata* and *mystacea*; d, *H. longipennis*; e, Cypseloidinae; f, Apodinae (*Hirundapus*); and g, all other Apodinae. In this morphological series, separate tendons in b–e appear to be derived relative to the fused tendons of most non-passerines, and the fused tendons of f and g derived relative to the separate tendons of b–e. A somewhat parallel trend occurs in hummingbirds

although there is considerable variation among closely related species. Types 1 and 2 tend to have the process of EMR and the tubercle of TPB widely separated, while in Type 3 they are usually closer together (Fig. 2h and i). In hummingbirds, as in swifts, loss or fusion of the humeral tendon of TPB (Type 4) probably represents a derived condition (Fig. 2j). These differences are caused mainly by proximal migration of the TPB tubercle because the process of EMR is located far proximally in all hummingbirds. (Any quantitative comparison of the proximal shift of these processes should compare their distance from the distal end of the humerus to some measure of body size rather than to humeral length because the humerus itself has become relatively shorter, to differing degrees, in the evolution of swifts and hummingbirds.)

Attachment of TPB on EMR.—The broad attachment of the belly of TPB on that of EMR in both swifts and hummingbirds is stated to be unique to those families and is used to support their placement in the order Apodiformes. However, other birds show various approaches to the condition in swifts and hummingbirds. Several passerines have only a short tendon between the bellies of TPB and EMR (swallows, pers. obs.; many *Lonchurae* [Bentz 1979]). In *Colius* the fleshy belly of TPB extends distally as far as EMR on the dorsal surfaces of two tendons, and in some pigeons the belly of TPB attaches on a broad tendon almost to EMR. Thus we see that an approach toward attachment of the belly of TPB on EMR has been made in at least three orders apart from swifts and hummingbirds.

Within the Apodidae a broad fleshy attachment is characteristic of the Apodinae, as described by Lowe (1939), who dissected only members of that subfamily. The Cypseloidinae, however, have a narrow and tendinous attachment of TPB (noted by us in *Cypseloides*, *Nephoecetes*, and *Streptoprocne*) and in the Hemiprocidae there is a short tendon. Thus, if we assume that the presence of one or more tendons between the bellies of TPB and EMR as found in most birds was the ancestral condition for swifts, we have a morphological series within the Apodiformes from primitive (tendon) to intermediate (tapered semitendinous belly) to advanced (broad attachment of the belly).

All hummingbirds display a broad attachment resembling that of the most specialized swifts. In the morphology of the humeral tendon, however, the more primitive stages in hummingbirds resemble the stage seen in the less specialized swifts. Unless the ancestral hummingbirds underwent a reversal (from stage g to h in Fig. 2) of the evolutionary trend in the humeral tendon seen in swifts, followed by another reversal to parallel the trend in swifts (compare h-j and e-g in Fig. 2), we conclude that the resemblance of the belly of TPB in hummingbirds and the Apodinae is the result of either parallel or convergent evolution.

Distal tendon of TPB.—The early illustration of *Patagona gigas* in Garrod (1876) and subsequent work based largely on dissections of trochiline hummingbirds of Type 3 (Beddard 1898; Cohn 1968) give the impression that the presence of a distal tendon of TPB is found in all hummingbirds and is unique to that family. We have seen that the "tendon" is a diffuse, expansive, and essentially transparent sheet in hermits. This structure might have become stronger and better defined (as in Type 2), and further specialized into a strong tendon (Types 3 and 4) as an expression of its increasing role in supplementing extension of the hand by EMR. We think it unlikely that evolution proceeded in the opposite direction because reduction of a well-defined distal tendon without a change in

its function would probably result in loss of the tendon rather than in production of a broadly investing, diaphanous sheet. We hypothesize that Types 1, 2, and 3 represent progressive evolutionary stages in the specialization of the distal tendon of TPB.

Systematic conclusions.—The direct connection of the belly of TPB with that of EMR in swifts and hummingbirds proves to represent an autapomorphy in each group. Whether these apomorphies were derived from a common ancestor (in which a tendon was present) or arose twice in different lineages cannot be determined from this muscle alone. Thus this aspect of the muscle gives no definite evidence for monophyly of the Apodiformes.

The alleged passerine nature of the humeral tendon of TPB in swifts and hummingbirds must be discounted because some nonpasserines have a similar form of the tendon. Furthermore, separation of the humeral tendons of TPB and EMR is related to a proximal shift in position of origin of EMR, which has occurred in unrelated orders or families. Once again, this feature of TPB is not by itself a good indicator of the ordinal affinities of either swifts or hummingbirds.

Within the Apodidae, our interpretation of the evolution of specialization of the belly and of the humeral tendon of TPB corresponds with Brooke's (1970) concept of a more primitive subfamily, Cypseloidinae, and a more advanced Apodinae. Our data are not useful in determining whether the Collocaliini, Chaeturini, and Apodini should be regarded as tribes of a single subfamily (Brooke 1970) or as two subfamilies (Collins 1976). Unfortunately, Brooke followed Lowe (1939) in regarding the Hemiprocnidae as more nearly passerine, and therefore more advanced, than the Apodidae. The characters used by Lowe are, in fact, found in many other orders besides the Passeriformes, and are thus primitive relative to the corresponding derived states in the Apodidae. The Hemiprocnidae should precede rather than follow the Apodidae in a linear classification.

Within the hummingbirds, our interpretation of the variation in TPB would support a hypothesis of a primitive phaethornithine group (hermits) and a more advanced trochiline group. Within the trochilines those genera with a dorsal distal tendon (Type 2) are more likely to be primitive (see Appendix). The presence of superficial muscle fibers of EMR covering part of the humeral tendon of TPB in most hermits (Fig. 1f) might best be regarded as a specialization of an otherwise primitive condition in hermits.

Acknowledgments

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Appendix

Listed below are the species dissected by us for *M. tensor propatagialis pars brevis* and *M. extensor metacarpi radialis*. We follow the terminology of Morony *et al.* (1975).

Trochilidae

Type 1.—*Ramphodon naevius*, *Glaucis hirsuta*, *Threnetes ruckeri*, *Phaethornis yaruqui*, *P. malaris*, *P. ruber*, *P. longuemareus*, *Eutoxeres aquila*, *E. condensini*.

Type 2.—*Androdon aequatorialis*, *Doryfera johannae*, *D. ludovicae*, *Florisuga mellivora*, *Colibri delphinae*, *C. thalassinus*, *C. coruscans*, *Anthracothorax nigricollis*, *A. dominicus*, *A. viridis*, *A. mango*, *Eulampis jugularis*, *Sericotes holosericeus*, *Chrysolampis mosquitus*, *Polytmus guainumbi*, *Topaza pella*, *T. pyra*, *Heliothrix barroti*.

Type 3.—*Campylopterus duidae*, *Orthorhynchus cristatus*, *Stephanoxis lalandi*, *Lophornis ornata*, *L. pavonina*, *Popelaria* sp., *Chlorostilbon swainsonii*, *C. maugaeus*, *Cyananthus latirostris*, *Cyanophaea bicolor*, *Thalurania furcata*, *Panterpe insignis*, *Damophila julie*, *Lepidopygia coeruleogularis*, *Hylocharis chrysura*, *Chrysura oenone*, *Goldmania violiceps*, *Trochilus polytmus*, *Leucochloris albicollis*, *Leucippus fallax*, *Amazilia amabilis*, *A. viridigaster*, *A. tzacatl*, *Elvira cupreiceps*, *Chalybura buffonii*, *Lampornis castaneoventris*, *Adelomyia melanogenys*, *Heliodoxa rubinoides*, *H. xanthogonys*, *H. branickii*, *Eugenes fulgens*, *Sternoclyta cyanopectus*, *Oreotrochilus estella*, *Patagona gigas*, *Aglaeactis cupripennis*, *Lafresnaya lafresnayi*, *Pterophanes cyanopectus*, *Coeligena coeligena*, *C. violifer*, *Ensifera ensifera*, *Sephanoides sephanoides*, *Heliangelus amethysticollis*, *Eriocnemis luciani*, *Haplophaedia aureliae*, *H. lugens*, *Ocreatus underwoodii*, *Lesbia victoriae*, *Sappho sparganura*, *Metallura tyrianthina*, *Aglaiocercus kingi*, *Heliothraupis longirostris*, *Philodice evelynae*, *Calothorax lucifer*, *Archilochus alexandri*, *Mellisuga minima*, *Calypte costae*, *Stellula calliope*, *Myrtis fanny*, *Selasphorus rufus*.

Type 4.—*Calliphlox amethystina*, *Acestrura mulsant*, *Chaetocercus jourdanii*.

Hemiprocridae and Apodidae

Type A.—*Hemiprocne comata*.

Type B.—Cypseloidinae: *Cypseloides rutilus*, *Nephoecetes niger*, *Streptoprocne zonaris*, *S. semicollaris*.

Type C.—Apodinae: *Collocalia brevirostris*, *C. whiteheadi*, *C. esculenta*, *Hirundapus caudacutus*,

H. giganteus, *Chaetura martinica*, *C. pelagica*, *Aeronautes montivagus*, *A. saxatilis*, *Tachornis phoenicobia*, *T. squamata*, *Cypsiurus parvus*, *Apus pallidus*, *A. pacificus*.

Other families

Columbidae: *Columba nigristrois*, *Columbina minuta*; Cuculidae: *Coccyzus erythrophthalmus*; Podargidae: *Batrachostomus septimus*; Nyctibiidae: *Nyctibius griseus*; Caprimulgidae: *Chordeiles pusillus*, *Caprimulgus europaeus*; Coliidae: *Colius striatus*; Trogonidae: *Trogon viridis*; Alcedinidae: *Chloroceryle aenea*; Todidae: *Todus mexicanus*; Momotidae: *Electron platyrhynchum*; Meropidae: *Merops apiaster*; Coraciidae: *Coracias garrulus*; Upupidae: *Upupa epops*; Phoeniculidae: *Phoeniculus purpureus*; Bucerotidae: *Tockus erythrorhynchus*; Galbulidae: *Galbula ruficauda*; Bucconidae: *Chelidoptera tenebrosa*; Capitonidae: *Megalaima haemacephala*; Indicatoridae: *Indicator archipelagicus*; Ramphastidae: *Bailloni bailloni*; Picidae: *Jynx torquilla*, *Melanerpes striatus*; Eurylaimidae: *Smithornis capensis*, *Eurylaimus ochromalus*, *Calypomena whiteheadi*; Furnariidae: *Certhiaxis subcristata*; Formicariidae: *Thamnophilus punctatus*, *Myrmotherula huxwelli*; Rhinocryptidae: *Sce-lorchilus rubecula*, *Scytalopus latebricola*; Cotingidae: *Pachyramphus cinnamomeus*; Pipridae: *Chiroxiphia linearis*; Tyrannidae: *Ochthoeca rufipectoralis*, *Tyrannus dominicensis*, *Todirostrum cinereum*, *Sublegatus arenarum*; Alaudidae: *Lullula arborea*; Hirundinidae: *Progne dominicensis*, *Riparia riparia*; Laniidae: *Lanius cristatus*; Muscicapidae: *Niltava grandis*; Nectariniidae: *Nectarinia jugularis*; Meliphagidae: *Melidectes fuscus*; Parulidae: *Basileuterus coronatus*; Sturnidae: *Acridotheres tristis*; Corvidae: *Garrulus glandarius*.

ERRATA FOR VOLUME 94(4)

page 1229 (Table 2, line 4)

“Second maxilliped,” should read “Second maxilliped exopod,”

page 1229 (Table 2, line 6)

“Third maxilliped,” should read “Third maxilliped exopod,”

page 1231 (Table 3, line 10)

“Second maxilliped,” should read “Second maxilliped exopod,”

page 1231 (Table 3, line 12)

“Third maxilliped,” should read “Third maxilliped exopod,”



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