Pointing the Way: The Distribution and Evolution of Some Characters of the Finger Muscles of Frogs

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ABSTRACT

The mm. transversi I and II of the hands of frogs have apparently shifted during the course of history from positions dorsal to the mm. flexores teretes III and IV to ventral positions—in the ancestor of Pipidae; and in the ancestor of a clade in Neobatrachia comprising Allophryne ruthveni, Brachycephalidae, Bufonidae, Centrolenidae, Hyliidae, Leptodactylidae, Pseudidae, Ranoidea, and Rhinoderma darwini, and excluding Heleophryne, Myobatrachidae, and Sooglossidae. Unique conditions of the m. transversus-m. flexor teres complex characterize Centrolenidae, Microhylidae, and a group of ranid frogs. The superficial flexors of the third finger are consistent in many families, but vary more than the deep muscles. There is an overall trend toward movement of the origins of the flexors from the palmar aponeurosis to the carpal. A hitherto undescribed muscle, the m. lumbricalis longus digit III, occurs in Batrachophrynus, Calyptocephalellini, Heleophrynidae, Lyncophrys, and Petropedetes. Shared conditions in the superficial flexors support the monophyly of Myobatrachidae, hylodine origin of the Dendrobatidae, and placement of Batrachophrynus and Lyncophrys in Calyptocephalellini.

INTRODUCTION

The paucity of our knowledge of the evolution of frogs is reflected in the polytomy presented by Ford and Cannatella (1993). These ambiguities indicate the need for new characters that can be used to resolve the uncertain relationships that now exist.

Hand muscles may seem unlikely to yield such characters, because the hands are in direct contact with the environment, so the muscles may be expected to be specialized for particular lifestyles, and hence subject to much convergence. Thus it seems reasonable to assume, for example, that the hand mus-

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cles of arboreal frogs of any family will be similar, and that the different evolutionary histories of the different families will be obscured by the adaptive similarities. Burton (1996, 1998) demonstrated that the contrary was true: hand muscles show surprisingly few recognizable adaptations to lifestyle. Burton (1998) identified two sets of hand muscles whose distribution in Leptodactylidae and associated families suggested that they might be phylogenetically informative. In particular, Calyptocephalellini (*Caudiverbera* and *Telmatobufo*) possesses characters suggesting that it probably has a closer affinity to Helophrynidae than to other Leptodactylidae.

Among the deepest muscles of a frog's hand are the mm. transversi metacarporum and the mm. flexores teretes. The mm. transversi are flat sheets of muscle that pass between the metacarpals of adjacent digits. Since there are four metacarpals, there are three mm. transversi. The m. transversus metacarpi I passes between Digits II and III; m. transversus II between Digits III and IV; and m. transversus III between Digits IV and V (fig. 1A). Contraction of the mm. transversi adducts the fingers, but depending on the positions of insertion of a m. transversus on the adjacent metacarpals, the palm may be closed (if the insertions are ventral on the metacarpals), opened (if they are dorsal), or rotated (if one insertion is dorsal and the other ventral).

The deepest flexor muscle of each finger is the m. flexor teres. This is always a slender muscle (the Latin word “teres” means “narrow”); usually it arises from the ventral or medial surface of the metacarpal, and inserts on the basal phalanx of the same digit. Contraction of a m. flexor teres bends the finger at the joint it crosses.

In some frogs, for example in myobatrachids (Egan, 1995), the attachments of the mm. transversi are relatively dorsal (fig. 1B). In these frogs the mm. flexores teretes digitorum III and IV arise from the ventral surface of the metacarpal, and lie ventral to the mm.
transversi metacarporum III and IV. In other frogs, for example in pelodryadines (Burton, 1996), the attachments of the mm. transversi are relatively ventral (fig. 1C). In these frogs, the origins of the mm. flexores teretes digitorum III and IV arise from more medially on the metacarpal, and lie dorsally to the mm. transversi. The mm. flexores teretes digitorum II and V always lie ventral to the adjacent mm. transversi. Egan (1995) and Burton (1996, 1998) demonstrated that these relationships between the muscles vary little within families.

The more superficial flexors of the third finger consist of a flexor tendon, the tendo superficialis digiti III, which passes from the distal edge of the palmar aponeurosis, and inserts upon the ventral surface of the ultimate phalanx (fig. 2A). This tendon is usually associated with a caput profundum, which arises from the carpals, and inserts on the dorsal side of the tendon. The m. lumbricalis brevis digiti III arises from the aponeurosis, or from the dorsal side of the tendon, or from the carpals, and inserts on the basal phalanx via a short tendon. Again, Egan (1995) and Burton (1996, 1998) reported little variation within families.

To test the potential of these sets of muscles as characters for use in phylogenetic analyses, I surveyed their relationships across all families of frogs.

**MATERIALS AND METHODS**

I examined the mm. flexores teretes III and IV and the mm. transversi metacarporum I and II in specimens of 378 species representing 183 genera from all of the living frog taxa represented in the phylogeny of Ford and Cannatella (1993). In many species, the deep muscles were exposed in the course of a dissection of the entire hand musculature, but in most species the muscles were ex-

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**Fig. 2.** Flexor muscles of third finger of left hands of frogs. A. *Bufo americanus* AMNH A124634; B. *Ascaphus truei* UMMZ 133050 (7392); C. *Scaphiopus hurteri* UMMZ 107147 (6445); D. *Limnodynes dumerili* AMNH A59128; E. *Caudiverbera caudiverbera* UMMZ 56620; F. *Aromobates nocturnus* AMNH A130036; G. *Mantidactylus curtis* UMMZ 212708. CP = caput profundum; LBB = m. lumbricalis brevis digiti III; LL = m. lumbricalus longus digiti III; FM = m. flexor ossis metacarpi III; TS = tendo superficialis digiti III. Scale bars = 2 mm, except in B scale bar = 1 mm.
posed by cutting through the skin along the metacarpals, and pushing the overlying muscles aside with fine forceps. The species used in this study are listed in appendix 1.

I also examined the superficial flexor musculature of the third finger of 337 species representing 159 genera of frogs from all of the living families. I exposed the musculature either in the course of a total dissection, or by a single incision in the skin, from the flexor surface of the wrist, and along the third finger to a point beyond the metacarpo-phalangeal joint. The skin was then held back by forceps to expose the muscles. In some specimens, the muscles were then cut, and pulled back to reveal their attachments; but in most specimens, I pushed and lifted muscle slips with forceps to find the attachments. The specimens examined are listed in appendix 1.

As salamanders are the most appropriate outgroup to use in comparisons with frogs, I examined the hand muscles of a number of caudates, and the figures and description of Salamandra salamandra of Francis (1934) (figures redrawn in Duellman and Trueb, 1986). Because the anatomical nomenclatures of salamanders and frogs have been derived independently, muscles that are identical in appearance and function, and are presumably homologous, bear different names. In describing the muscles of frogs, I use the nomenclature of Gaupp (1896). I follow Fabrezi and Alberch (1996) in numbering the digits of the frog hand from II to V, and Shubin (1994) in numbering the salamander fingers from I to IV.

RESULTS

Salamander-Frog Comparison

The smallest flexor of each finger of a salamander, the m. flexor digiti minimus, is a slender muscle that arises pennately from the metacarpal, and inserts via a short tendon on the basal phalanx. I assume that this muscle corresponds to the m. flexor teres of frogs. Between each pair of salamander metacarpals lies a flat muscle, the m. intermetacarpalis. I assume that this muscle corresponds to the m. transversus metacarpi of frogs.

The tendones superficiales of frogs correspond to the tendons of insertion of the m. flexor primordialis communis of salamanders. The only muscle in salamanders that corresponds with the mm. lumbricales longi of frogs is the m. flexor accessorius lateralis of the third finger of salamanders; this muscle corresponds to the m. lumbricalis longus digit IV. If these muscles are homologous, then the absence of the m. lumbricalis longus digit III appears to be the primitive condition in frogs. The mm. flexores breves superficiales of salamanders appear to correspond to the mm. lumbricales breves of frogs. In all of the salamanders examined, the mm. flexores breves arise from the tendon and adjacent aponeurosis; this appears to be the primitive condition in frogs.

DEEP MUSCULATURE

The relative positions of the origins of the mm. flexores teretes and mm. transversi are consistent within families (table 1), except in the following cases.

In Leptodactyliidae, the mm. flexores teretes are dorsal to the mm. transversi metacarporum except in Calyptocephallini and Eupsophus (Burton, 1998). This variation is recorded as “dorsal or ventral” in table 1.

In Ranidae, the m. flexor teres digit IV lies dorsal to the m. transversus metacarpi II, but, in addition, the following genera possess an extra slip of the m. flexor teres, which is ventral to the m. transversus—Altirana, Aubria, Ceratobatrachus, Conraua, Hildebrandtia, Mantella, Mantidactylus, Petropedetes, Ptychadena, Ptyxicephalus, and Rana (fig. 1C). In table 1, I record taxa with the single slip as Ranidae (a), the taxa with two slips as Ranidae (b), “dorsal + ventral.”

In Microhylidae (fig. 1D), the m. transversus metacarpi I usually consists of two slips, one slip passing between the distal ends of the metacarpals of Digits II and III, and a more proximal slip that arises proximally on the metacarpal of Digit III, and inserts on the metacarpus of Digit II just proximal to the other slip. Thus, I now interpret the unnamed muscle “M” of Burton (1983a, 1983b) as a slip of the m. transversus metacarpi I. In most species, the m. flexor teres digit III passes dorsally to the proximal slip of the m. transversus, and ventrally to the distal slip. In table 1, I record this condition as “dorsal/ventral.” The m. transversus metacarpi II of
TABLE 1
Positions of the Origins of the Mm. Flexores Teretes III and IV Relative to the Corresponding Mm. Transversi Metacarporum I and II

<table>
<thead>
<tr>
<th>Taxon</th>
<th>m. flexor teres III</th>
<th>m flexor teres IV</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Caudata</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Ascapalus truei</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Leiopelma</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Bombinatoridae</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Discoglossidae</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Megophryidae</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Pelobatidae</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Pelodytes</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Rhinophrynus dorsalis</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Pipidae</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Limnodynastinae</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Myobatrachinae</em></td>
<td>ventral</td>
<td>ventral</td>
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<tr>
<td><em>Sooglossidae</em></td>
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<td>ventral</td>
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<tr>
<td><em>Heleophrynus</em></td>
<td>ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Leptodactylidae</em></td>
<td>dorsal or ventral</td>
<td>dorsal or ventral</td>
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<tr>
<td><em>Bufo nidae</em></td>
<td>dorsal or ventral</td>
<td>dorsal or ventral</td>
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<tr>
<td><em>Allophryne ruthveni</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Brachycephalidae</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Rhinoderma</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Hylidae</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Pseudidae</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Centrolenidae</em></td>
<td>ventral</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Microhylidae</em></td>
<td>dorsal/ventral</td>
<td>ventral</td>
</tr>
<tr>
<td><em>Dendrobatidae</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Hemisus</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
<tr>
<td><em>Arthroleptidae</em></td>
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<td>dorsal</td>
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<tr>
<td><em>Ranidae (a)</em></td>
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<tr>
<td><em>Ranidae (b)</em></td>
<td>dorsal</td>
<td>dorsal + ventral</td>
</tr>
<tr>
<td><em>Hyperoliidae</em></td>
<td>dorsal</td>
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<tr>
<td><em>Rhacophoridae</em></td>
<td>dorsal</td>
<td>dorsal</td>
</tr>
</tbody>
</table>

Note: “dorsal/ventral” = the m. flexor teres passes between two slips of the m. transversus; “dorsal or ventral” = in some species the m. flexor teres is dorsal to the m. transversus, but in others it is ventral; “dorsal + ventral” = there are two slips of the m. flexor teres, one dorsal to the m. transversus, the other ventral.

**SUPERFICIAL MUSCULATURE OF THE THIRD FINGER**

Some frogs possess a superficial flexor muscle that has not previously been described. From the dorsal surface of the tendo arises a m. lumbricalis, in the form of a pair of slender slips that insert on the basal phalanx on both sides of the tendo. This muscle is identical in form to the m. lumbricalis longus digitii IV, except that it inserts on the basal phalanx. Digit IV contains three phalanges; Digit III contains two, thus in each case this m. lumbricalis inserts on the penultimate phalanx. I identify this muscle of Digit III as the m. lumbricalis longus digitii III. Andersen
(1978) figured and labeled a m. lumbricalis longus digiti III in a number of figures in his atlas, but claimed in the text that mm. lumbricales longi occur on only the fourth and fifth digits. The m. lumbricalis longus digiti III occurs in *Alytes*, *Batrachophrynum*, the Calyptocephalellini (fig. 2E), the Helophrynidae, *Lynchophrynum*, and *Petropedetes*.

In many species, a caput profundum arises from the carpals. Since the degree of fusion of the carpals varies between frogs, an attempt to identify the exact origin of the caput in each case would lead to unnecessary confusion, and give a false impression of variability. The caput always arises laterally to the tendo. In species that I have inspected, it originates from either the third carpals, or from fused bone that includes the third carpal.

The superficial flexors vary in the following characters: presence of caput profundum; presence of a m. lumbricalis longus digiti III; and the origin of the m. lumbricalis brevis digiti III, from the aponeurosis palmaris, the tendo superficialis, the carpals, or a combination of two of these. Little intraspecific variation was noted. Two of nine *Megaelosia goeldi* possess a small caput on one hand only, otherwise the caput is absent; the m. lumbricalis brevis digiti III arises in part from the carpals in *Astysternus diadematus* (AMNH A23618). In *Kassina senegalensis* (AMNH A68535), and *Afrixalus osoroi* (AMNH A9425 and A9437), the m. lumbricalis brevis digiti III arises from the tendo superficialis as well as the carpals, whereas in other specimens it arises from the carpals alone. In *Ceratophrys cornuta* (KU 196428), *Limnodynastes dumerili* (UMMZ 83395), and *Heleophrynum purcelli* (UMMZ 94139A and B), there is an additional slip from the aponeurosis to the medial side of this muscle. In most pelodyradines, the caput and tendo are sunken into the m. lumbricalis brevis to some degree, and in many species the latter is divided (Burton, 1996). Variation in this character occurs in *Litoria dahlii*, *L. ewingii*, *L. fallax*, *L. lesueurii*, *L. nannois*, *L. peroni*, *L. thesaurensis*, *Nyctimystes humeralis*, and *N. pulchra*.

1. Presence of caput profundum


B. Origin from carpals—other species.

2. Presence of m. lumbricalis longus digiti III

A. Present—*Batrachophrynum*, *Caudiverbera* (fig. 2E), *Heleophryne*, *Lynchophrynum*, *Petropedetes*, *Telmatobufo*.

B. Absent—other species.

3. Origin of m. lumbricalis brevis digiti III

A. From tendo superficialis or adjacent aponeurosis only—*Ascaphus* (fig. 2B), Bominatoridae, Discoglossidae, *Heleophryne*, *Hymenochirus*, *Leiopelma*, *Myobatrachidae* (fig. 2D), *Pipa*, *Rhinophrynum*, *Xenopus*.

B. Two origins: by narrow tendon from tendo superficialis or adjacent aponeurosis palmaris, and by tendon from carpals—*Batrachophrynum*, *Cardioglossus*, *Caudiverbera* (fig. 2E), *Discodeles*, *Hyperoliidae* (except *Kassina cochranae*), *Lynchophrynum*, *Manella baroni*, *M. femoralis*, *Mantidactylus* (fig. 2G), *Petropedetes*, *Phrynomerus*, *Platypelis*, *Plethodontyla*, *Rhacophoridae* (except *Agylyptodactylus*), *Scotobleps*, *Telmatobufo*, *Trichobatrachus*.

C. From carpals only—other species.

Most families can be diagnosed by only one combination of characters. Variation occurs in Arthroleptidae, Leptodactylidae, Microhylidae, Pipidae, and Ranidae.

**DISCUSSION**

The relative positions of the mm. flexores and the corresponding mm. transversi appear to be very conservative characters, conflicting little with what is known of frog evolution. Although the superficial flexors vary more than the deep muscles, data from the superficial flexors may contribute to understanding of frog relationships. The caput profundum appears to have evolved in Mesobatrachia, possibly from a slip detached from the m. palmaris profundum. There appears to have been a trend for the origin of the m. lumbricalis brevis digiti III to migrate from the aponeurosis palmaris to the carpals. However, the mesobatrachian families Pelobatidae, Pelodytidae, and Megophryidae pos-
sessed the condition prevalent in Neobatrachia, whereas the Myobatrachidae possess a condition more like that of Archaeobatrachia.

With caudates as the outgroup, the most parsimonious interpretation of the distribution of characters of the deep musculature is that the dorsal position of the mm. transversi relative to the mm. flexores teretes is the primitive condition in frogs. The ventral position appears to have evolved twice independently—in Pipirumpha, the ancestor of Pipidae, in which the hand is reversed for feeding; and once in Neobatrachia, in a common ancestor of the clade consisting of the following: Allophryne ruthveni; Brachycephalidae; Bufonidae; Leptodactylidae; the common ancestor of the Hylidae, Pseudidae, and Centrolenidae; Rhinoderma; and Ranidae. To reduce repetition in the discussion to follow, I refer to this putative clade as “the advanced Neobatrachia.” This same clade was identified, on the basis of position of amplexus, by Duellman and Trueb (1986), but Ford and Cannatella (1993) found the data relating to amplexus conflicting, and omitted this clade from their phylogeny.

By this interpretation, reversals may have occurred in Centrolenidae; Microhylidae; the bufonids Ansonia, Nectophryne, and Oreophrynella; and the leptodactylids Caudiverbera, Eupsophus, and Telmatobufo; or one or more of these taxa may be part of the sister group of the advanced Neobatrachia. Centrolenidae are probably part of the clade also containing Hylidae and Pseudidae (Ford and Cannatella, 1993), and, in that context, the ventral position of the mm. flexor teres digitii III is a probable apomorphy of Centrolenidae. The unique conditions of the mm. transversi of Microhylidae are two more apomorphies of this family.

Whether the ventral positions of the mm. flexores teretes in the bufonids Ansonia, Nectophryne, and Oreophrynella represent the primitive condition of Bufonidae, or a reversal, is unclear. Nectophryne africana is a highly unusual bufonid. Noble and Jaekle (1928) remarked on the striking similarity between the articular pads of Nectophryne and salamanders, and it is noteworthy that Nectophryne also displays a salamander-like condition of the deep hand musculature.

The mm. transversi of Eupsophus are so extensive that there is insufficient space to allow dorsal origins of the mm. flexores teretes (Burton, 1998). After examination of a wide range of frogs, I conclude that the broad mm. transversi of Eupsophus constitute a uniquely derived condition, with which the reversal of the mm. flexores teretes to the ventral positions is correlated.

The mm. transversi of Calyptocephalellini are not exceptionally developed, as in Eupsophus. Calyptocephalellini is “putatively the most primitive” tribe of the lower telmatobines (Lynch, 1978). The possession of the primitive condition of the deep hand muscles by members of Calyptocephalellini may be further evidence of the primitiveness of this tribe, and evidence that they are the part of the sister group of the advanced Neobatrachia.

However, possession of the mm. lumbricalis longus digitii III, which appears to be a derived condition, suggests a close relationship with Batrachophrynus and Lynchophrys. The most parsimonious of Lynch’s (1978) trees identifies a clade consisting of Calyptocephalellini and Batrachophrynus (including the species that now constitutes Lynchophrys). The addition of this new character would increase the superiority of this tree over the next most parsimonious tree, on which Lynch based his taxonomy, in which Batrachophrynus was excluded from Calyptocephalellini. If the clade Batrachophrynus + Calyptocephalellini + Lynchophrys is accepted, the most parsimonious explanation of the ventral position of the mm. flexores teretes in Calyptocephalellini would be a reversal in their ancestor, since the alternative would require independent acquisition of the dorsal position by the ancestor of Batrachophrynus and Lynchophrys, and by the ancestor of the rest of the lower Telmatobiinae. On the basis of these additional data, I propose that Batrachophrynus and Lynchophrys be moved from Telmatobiini and placed in Calyptocephalellini.

The possession of two slips of the mm. flexor teres digitii IV is a uniquely derived condition that arose within Ranidae, and is evidence of a unique common ancestry of the genera Altirana, Aubria, Ceratobatrachus, Conraua, Hildebrandia, Mantella, Manti-dactylus, Petropedetes, Ptychadena, Pyxicephalus, and Rana. Possession of this unique
character is in conflict with the characters on which the current subfamilial classification is based. In each of the ranoid families, some taxa possess the additional medial slip to the m. lumbralis brevis digitii III, whereas other taxa lack the slip. The superficial flexors may present characters useful in determining relationships within these families, but exploration of these relationships lies beyond the scope of this paper.

The relationships of Dendrobatidae are controversial. Ford (1991) presented evidence that supports the hypotheses that the sister group of Dendrobatidae is either (1) Hyloidea or (2) a ranoid, and the presence of a ventral slip to the m. flexor teres digitii IV, as in some ranoids, would have given powerful support for the latter hypothesis. However, the occurrence of this slip varies within the ranoid subfamilies, so the absence of a ventral slip in Dendrobatidae refutes neither hypothesis. However, some support is given to a relationship between Hyloidea and Dendrobatidae from the superficial musculature, as the unusual condition of lacking any fibrous connection to the tendon superficialis or the adjacent aponeurosis is almost restricted to the hyloidine genera *Hyloides* and *Megaelosia*, and Dendrobatidae. This condition is found also in *Hemisus*, *Zachaenus parvulus* (not *Z. stejnegeri*), and Sooglossidae.

The occurrence of the same rare combination of characters of the superficial flexors in all Limnodynastinae and Myobatrachinae is interesting, because there are no apomorphies to support the Myobatrachidae (Ford and Cannatella, 1993). The myobatrachid condition occurs elsewhere only in unrelated genera in variable taxa (*Asterostylus* and *Xenopus*).

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APPENDIX 1: SPECIMENS EXAMINED

The specimens examined are deposited in the following institutions: American Museum of Natural History (AMNH); Department of Zoology, University of Adelaide (AUZ); Department of Biology, East Tennessee State University (ETSU); Natural History Museum, University of Kansas (KU); National Museum of the Federal University of Rio de Janeiro (MNURJ); Museum of Victoria, Australia (NMV), University of Michigan Museum of Zoology (UMMZ). Specimens marked “a” were used in the study of the superficial muscles of Digit III; specimens marked “b” were used in the study of both the superficial muscles of Digit III and the transversus—flexor teres system; unmarked specimens were used in the study of the transversus—flexor teres system only.

Caudata — Aeneides lugubris UMMZ 72635; Ambystoma maculata ETSUb; A. mexicanum ETSUb; Dicamptodon ensatus UMMZ 134829 (3746); Hynobius nigrecens UMMZ 131038; Necturus maculosus UMMZ 118845; Siren lacertina UMMZ 106373(3882).

Anura — Allophrynidae: Allophryne ruthveni AMNH A139265b; KU 166730. Arthroleptidae: Arthroleptis adelfifriederii AMNH A72759b; A. poecilinotus AMNH A3140; A. stenodactylus AMNH A12640b; A. variabilis KU 171792; A. wahlbergi AMNH A73374; Astylostenus diae- matus AMNH A23618b; Cardioglossus leu- comystax AMNH A9311a, AMNH A9312a, AMNH A9313b; Leptodactylodon albiven- tris AMNH A23609b; Schoutedenella xenochirus AMNH A73864; S. xenodactyla AMNH A68686a; Scotobleps japonicus AMNH A65671a; Trichobatrachus robustus AMNH A129866a. Ascaphidae: Ascaphus truei AMNH A20648a, AMNH A36532a, KU 153191, UMMZ 133050 (7392)b. Bombinateridae: Bombina bombina AMNH 64934a: B. orientalis AMNH A58771, KU 38614; B. variegata AMNH A65114a, AMNH A72535; Barbourula busuangensis AMNH A57552. Brachycephalidae: Brachycephalus ephippium AMNH A77353, UMMZ (untagged)b, UMMZ 38256b. Bufonidae: Ansonia longidigita AMNH A22919b; A. muelleri AMNH A69963b; Atele- lupus cruciger AMNH A70794b; A. ignascena AMNH A17486b. AMNH A17493b; Bufo americanus AMNH A78324b, AMNH A124634b; B. bufo AMNH A134236b; B. brauni AMNH A70129b; B. haematiticus AMNH A54640b, AMNH A55493b, AMNH A89454b; B. marinus AMNH 101876b, AMNH A11483b; KU 181621b; B. valliceps AMNH A7018b, AMNH A89127b, AMNH A119666b; B. woodhousei AMNH A32417a; Capensibufo rosei AMNH A144948b; Dendrophryniscus minutus AMNH A114908, AMNH A114910b; Melanophryniscus moreirae AMNH A16998, AMNH A17029b, AMNH A74413; M. stelzneri AMNH A50645; Nectophryne afra AMNH A9451b; Nectophrynoides tornieri AMNH A72718b; N. viviparus AMNH A33213b; Nimbaphrynoides liberiensis AMNH A83261b; Oreophrynella quichii AMNH A99620b, AMNH A9624b; Pedos- tibes hosii AMNH A23815b; Peltophryne guentheri KU 264090; P. longinasus AMNH A101828; P. peltcephala AMNH A61200, AMNH A61205a. Centrolenidae: Centrole-
ne buckleyi KU 178047, KU 178079; C. geckoideum KU 178015; C. prosoblepon UMMZ 117672 (7643)b, UMMZ 167399b; Cochranella albomaculata UMMZ 131878 (4440)b; C. cochranae UMMZ 92098b; Hyalinobatrachium colymbiphyllum KU 65238; H. eurygnathum AMNH A104094b; H. fleischmanni AMNH A51846a, UMMZ 131879b. Dendrobatidae: Aromobates nocturnus AMNH A130032–33, AMNH A130036–38b; Colostethus inguinalis AMNH (uncataloged skinned carcases, 11 specimens)b; C. olmonae AMNH (uncataloged skinned carcases, 12 specimens)b; C. pratti AMNH (uncataloged skinned carcases, 12 specimens)a; C. riveroi KU 133049; C. talamancae AMNH (uncataloged skinned carcases, 3 specimens)a; C. trinitatus AMNH (uncataloged skinned carcases, 12 specimens)b; Dendrobates auratus AMNH (uncataloged skinned carcases, 10 specimens)b, KU 116994, KU 116997; D. histricionicus AMNH (uncataloged skinned carcases, 12 specimens)a; D. lehmanni AMNH (uncataloged skinned carcases, 10 specimens)b; D. pumilio AMNH (uncataloged skinned carcases, 10 specimens)a; D. speciosus AMNH (uncataloged skinned carcases, 11 specimens)b; D. truncatus (uncataloged skinned carcases, 7 specimens)a; Epipedobates espinosai AMNH (uncataloged skinned carcases, 11 specimens)a; E. pictus AMNH (uncataloged skinned carcases, 5 specimens)a; E. tricolor AMNH (uncataloged skinned carcases, 10 specimens)a; E. trivittatus KU 172042; Minyobates minusculus AMNH (uncataloged skinned carcases, 10 specimens)a; M. steyermarki (AMNH (uncataloged skinned carcases, 11 specimens)a; Phyllobates aurotaeniata AMNH (uncataloged skinned carcases, 10 specimens)a; P. lugubris AMNH (uncataloged skinned carcases, 10 specimens)b; P. vittatus AMNH (uncataloged skinned carcases, 10 specimens)b. Discoglossidae: Alytes muletensis AMNH A146044b; A. obstetricians AMNH A41326b, AMNH A145205a, KU 14185; Discoglossus pictus AMNH A50715a, AMNH A51167b; D. sardus AMNH A652b. Heleophrynidae: Heleophryne natalensis AMNH A74139b; KU 105925b; H. purcelli UMMZ 94139b (2 specimens). Hemisotidae: Hemisus guttatus KU 195800; H. mar-
L. rubella AM R88659b; L. subglandulosa AM R51739b; L. thesaurenensis AM R121621b, AM R121629b; L. tornieri AUZb; L. verrauxi AUZb; L. wotjulumensis AUZb; L. xanthomera AUZb; Nycitymystes dayi SAM R12304b; N. daymani AM R18026b; N. dispersa AM R16363b; N. foricula AM R22206, AM R22226b, AM R22229b; N. humeralis AM R132334b, AM R132335b; N. kubori AM R22311b; N. pulchra AM R140613b, AM R140622b; Ostéopilus dominicensis AMNH A31261b; O. taurinus KU 175208; Pachymedusa dacnicolor KU 87138; Pelodyas caerulea SAM R33435b; P. splendida AUZb; Phrynophyas venulosa KU 17136; Phyllomedusa burmeisteri KU 92319; P. sauvgii AMNH A144518b; Pseudacris brachyphona KU 156154; Pternohyla dentata AMNH A107018; P. fodiens UMMZ 117350 (3569)b; Scinax nasica SAM R10522; Triprion spatulata AMNH A13840, UMMZ 104418b. **Hyperoliidae:** Afrixylus aosorioi AMNH A9415, AMNH A9425a, AMNH A9428a, AMNH A9437a, AMNH A9442a; Cryptothy lax greshoffi AMNH A63547b; Heterixalus betsilio AMNH A50429a, AMNH A50431; Hyperolius cystocandicans UMMZ 137253 (3 specimens); H. kivuensis AMNH A73295b; AMNH A73296a; H. marmoratus AMNH A99740a, AMNH A99743a, AMNH A99744a; KU 195822; H. viridiflavus UMMZ 150122b; Kassoa cochranae AMNH A83535b, AMNH A83546; K. senegalensis AMNH A68534, AMNH A68535b, AMNH A68537b; Leptopolis bagacii AMNH A74108b, AMNH A74109a; L. calcaratus AMNH A59472; L. christyi KU 155139; Phlyctimantis leonardi AMNH A83569a, AMNH A83564a, P. verrucosus AMNH A8665; Tachynemis seychellensis UMMZ 175476b. **Leiopelmatidae:** Leiopelma hochstetteri AMNH A51311b, AMNH A51314, UMMZ 177463a; **Leptodactylidae:** Adenomera andreae KU 149367b, KU 152401b; Alsodes nodosus AMNH A23944; A. vanzolini KU 160568b, KU 162208b; Atelognathus patagonicus KU 160428b; A. praebasalticus KU 180999b; A. reverberi KU 180997b; Barycholos pulcher KU 142177b, KU 142187b, KU 142192b; Batrachophrynus macrostomus AMNH A6737, AMNH A6738, KU 173106b; Batrachyla taeniata KU 161482b, KU 161482b, KU 161483b; Caudicoverba caudicoverba AMNH A23915b, KU 159941b, KU 164189b, UMMZ 56620b; Ceratophrys calcarata KU 144966b, KU 207528b; C. cor- nuta KU 196428b, UMMZ 66529b; C. ornata KU 175560b; Chalcerophys pietorri KU 191928b; Crossodactylus dispers KU 92750b, KU 92751b; C. gaudichaud KU 74190b; C. sp. AMNH A103788–91a; Cyclorhampus asper KU 71493b, KU 84715b, KU 92770b; C. eleutherodactylus KU 92781b; C. fuliginosus KU 92786b; Dischidodactylus duidensis AMNH A23194, AMNH A23195; Edalorhina perezi KU 177448b, KU 215452b; Eleutherodactylus augusti KU 39827b, KU 39832b, KU 39833b; E. bransfordi KU 113683b; E. fitzingeri KU 65870b, KU 172268b, KU 172278b; E. fleischmanni KU 30918b, KU 65837b, KU 65850b; E. rani- forms KU 114529b, KU 114548b, KU 145003b; E. achatinus KU 165100b, KU 202280b, KU 202282b, KU 217824b; E. coqui KU 180639b; E. martiniensis KU 282501b, KU 282517b, KU 282544b; E. octavius KU 92827b, KU 113684b; E. phoxocephalus KU 131427b, KU 166060b; E. wni- grum KU 202560b, KU 202580b; E. karlschmidtii KU 281335b; E. schmidtii KU 286267b, KU 286267b, KU 286277b, KU 286280b; E. inoptatus KU 280115b, KU 280411b, KU 280413b, KU 280414b; E. le- prus KU 137517b; E. pipilans KU 58905b, KU 58908b; Eusophus miguelini KU 162234b; E. roseus KU 162151b; E. vertebralis KU 162237b; Holoand bradei KU 92865b; Hydrolaetra schmidtii KU 220360b; Hylyodes asper AMNH A103830a, AMNH A103835– 42a, KU 74214b, KU 92873b; H. glaber AMNH A103881a; H. laterostrigatus AMNH A103898a, AMNH A103903–8a, KU 92876b, KU 92880b; H. nasus AMNH A72456a; H. ornatus AMNH A103913a; H. perplicatus AMNH A15527a; H. pulcher AMNH A103927a, AMNH A103941–3a; Hylorina sylvatica KU 161391b; Insueto- phrynus acaricus KU 161414b; Ischnocne- ma quinxensis KU 123245b; Lepidobatrachus asper KU 80782b; L. llanensis KU 128856b; Leptodactylus fuscus KU 115338b, KU 166429b, KU 166430b; L. pentadactylus KU 25713b, KU 35928b, KU 65715b, KU 65717b; L. rhodomystax KU 122581b; L.
Phrynus poweri AMNH A103947–53, KU 92963b; Odontophrynus americanus AMNH 100439b; O. occidentalis AMNH 160696b; Paratelmatobius lutzii KU 92977b, KU 92978b; Phrynopus biligoniger KU 72865b; P. flavomaculata KU 119738b; P. parkeri KU 181294b, KU 181348b; P. peruvianus KU 138938b; Physalaemus petersi KU 120286b; P. pustulosus KU 58916b, KU 65625b, KU 125037b; Pleurodema brachyops KU 104363b, KU 166659b, KU 166665b; P. cinerea KU 135599b; P. marmorata KU 135773b; P. tucumana KU 160828b; Proceratophrys cristiceps KU 220085b; Somuncuria sumuncurienis KU 180987b; Telmatobius brevipes KU 181491b; T. culeus KU 174962b; T. marmorata KU 162916b; T. peruvianus KU 162058b, KU 162064b; T. schreiteri KU 160884b; T. truebae KU 212454b, KU 280413b; Telmatobufo bullocki MCZ A78829b; T. venustus KU 159811b; Thoropa miliaris KU 74202b, KU 74203b, KU 92855b; Vanzolinus discodactylus KU 119307b, KU 149295b, KU 178270b; Zacaenus parvulus KU 93078b, KU 93081b, MCZ A64356b, UMMZ 127921 (38676–7a); Z. stejnegeri MCZ A100258a. Megophryidae: Megophrys boettgeri AMNH A30323b, AMNH A30389; M. montana AMNH A2993; M. monticola UMMZ 83072b. Microhylidae: Albericus variegatus AMNH (untagged); Aphantophryne pansa AMNH A58131; Breviceps adspersus AMNH A12176; B. gibbosus AMNH A3053b; B. poweri AMNH A73850b; Calluella yunnanensis AMNH A5450a; Callulops persona- tus AMNH A78096b; C. robustus AMNH A72555; C. stictogaster AMNH A13339, KU 93707; Cophialus biroi AMNH A78105, AMNH A78111; C. ornatus AMNH A65443; C. riparius AMNH A130402; C. verrucosus AMNH A113230b; Copiula oxyrhina AMNH A59895 AMNH A140627b; Dermatonetus mulleri AMNH A56111; Dyscophus gueneti AMNH A23935b; Gastrophryne carolinensis AMNH A113324a; G. olivacea AMNH AM62736; Hamptophryne boliviana AMNH A115780; Hylophorus rufescens AMNH A78215, AMNH A113450; Hypopachus barberi KU190404; Kaloula verrucosa AMNH A5298; Mantophrynidae lateralis AMNH A76007; Microhyla heymonsi AMNH A28395; M. ornata AMNH A6727a; Nelsonophryne aequitoriala AMNH A17556; Oreophrynine anthonyi AMNH A58038; O. flava AMNH A58152b; O. idenburgenis AMNH A49665; O. sp. AMNH A98149; Phrynornantis annectens AMNH 97899b; P. bifasciata AMNH A22433; Phrynomerus bifasciatus UMMZ 61377b; Platypelis grandis AMNH A22376, AMNH A23750b; Plethodontylaea ocellata AMNH A23839, AMNH A50407a; Pseudohemisus obscurus AMNH A50480; Reticulotorpero pearsei AMNH A69883b; Scaphio- phryne marmoratus AMNH A133700b, AMNH A133701a; Sphenophryne brevipes AMNH A130533; Uperodon systoma AMNH A75125; Xenobatrachus obesus AMNH A78193. Myobatrachidae: Adelotus brevis AMNH A59096a; Crinia georgiana AMNH A62271b, AUZ; C. riparia AUZ; C. signifera AMNH A40298a; KU 186927; Geocrinia victoriana AMNH A67160b; Helioiopus albopunctatus AMNH A104689a; Lechrionodes melanopyga AMNH A81226a; Limnodynastes dumerili AMNH A59128a, AMNH A59129a, AMNH A63395b; NMV 24884, KU 179927, UMMZ 83395b; L. fletcheri AUZ, KU186887; L. tasmaniensis KU 57062, KU 57067; Mixophyes balbus AUZ; M. iteratus KU179961; M. schevilli AMNH A19942a; Notaden nichollsi AMNH A87221a; Pseudophryne bibroni AMNH A111053a. Pelobatidae: Leptobatrachium hasseltii AMNH A90490; Pelobates varaldi AMNH A62934b; Scaphiopus couchi UMMZ 114279 (2829b); S. holbrooki AMNH A38305b, AMNH A51747; S. hurteri KU 11329, UMMZ 107147 (6445); S. intermontanus AMNH A62652. Pelodytidae: Pelodytes caucasicus AMNH A108329a; KU 203791; P. punctatus UMMZ 111900b. Pipidae: Hymenochirus boettgeri AMNH A23962a, AMNH A65661a; H. camerunensis AMNH A65660; Pipa arrabali AMNH A52820a, AMNH A52831b; Silurana tropicalis AMNH A145948; Xenopus laevis AMNH A37567a; AMNH A37572a; AMNH A45054; X. muel-
leri AMNH A53852b. Pseudidae: Lysapsus lamellus AMNH A98150; L. mantidactylus KU 93212; Pseudis paradoxa AMNH A55685, AMNH A146264b, MNUFJR 14049. Ranidae: Altirana parkeri AMNH A53178; Aubria subsigillata AMNH A129925; Batrachylodes vertebralis AMNH A71744b; B. wolfi AMNH A71777, AMNH A71779; Cacosternum boettgeri AMNH A72776a; C. capense AMNH A97904; Ceratobatrachus guentheri AMNH A84299b; Conraua alleni AMNH A83301; Discodega bufoiformis AMNH A71851b; D. guppyi AMNH A64278b; Hildebrandtia ornata AMNH A10880a, AMNH A10881; Mantella aurantia AMNH A73447a, AMNH A133612a, AMNH A133621a, AMNH A133624a, AMNH A133628–30a, AMNH A133633a, AMNH A133635a, AMNH A133637a, AMNH A133639b, M. baronii AMNH A133657b, AMNH A133659–61b, AMNH A133663a, AMNH A133671a, AMNH A133675–8a, AMNH A136887a; M. betsilio AMNH A140567; M. laevigata AMNH A140561a, AMNH A140564a; M. viridis AMNH A133638b; Mantidactylus albofrenatus AMNH A23901a, AMNH A23904b; M. curtis UMMZ 212708b; M. femoralis AMNH A133690b; M. guttulatus AMNH A50359a; M. luteus AMNH A50251a; AMNH A50255; M. pliciferus AMNH A50504b; Meristogenys jerboa AMNH A90566a, KU 155607, KU 155609; Micrixalus tenassermensis AMNH A97869; Nannophrys ceylonensis AMNH A77467b; Nanorana pleskei AMNH A48771b; Natalobatrachus bonebergi AMNH A73899b; Nyctibatrachus deccanensis AMNH A23827b; Occidogyza cyanophlyctis KU 200413; O. laevis AMNH A72679a, AMNH A102928, AMNH A102939; Palmatorrappia solomonis AMNH A71866b; Petropedetes natator AMNH A84604b, AMNH A84615; P. palmipes AMNH A23936a; Phrynobatrachus dendrobates AMNH A9119; P. graueri AMNH A68760; P. natalensis AMNH A129776; Playmantys boulengeri AMNH A64252; P. corrugatus AMNH A68164; P. guppyi KU 98164; P. papeuni AMNH A59972; P. solomonis AMNH A69320; Pychodena aquiliplicata AMNH A41878; P. anchietae KU 196067; P. mascariensis AMNH A11143; Pyxicephalus adspersus KU 195804; Rana areolata KU 200979; R. berlandieri KU 195391; R. sylvatica UMMZ 138685 (02174); Staurois natator AMNH A136068; Strongylopus grayi AMNH A13558; Tomopterna labrosa AMNH A23752. Rhacophoridae: Aglyptodactylus madagascarensis AMNH A50349a, AMNH A50536b, UMMZ 213640b; Boophis albilabris UMMZ 201442b, UMMZ 201443b; B. goudoti AMNH A23916b; B. luteus AMNH A23896b; B. periegetes UMMZ 198707; B. tephraemystax UMMZ 213947; Buergeria buergeri AMNH A53106, AMNH A112693; B. japonicus AMNH A82494b, AMNH A82496b; Chirixalus doriae AMNH A26758, AMNH A26771a; Chiromantis ru-fescens AMNH A9391b; Polypedates dennysi AMNH A30530b; P. leucomystax AMNH A30069, AMNH A68170; P. megacephalus UMMZ 182716b, UMMZ 189970b; Rhacophorus maculata KU 193643; R. moltrechti UMMZ 182217b, UMMZ 199814b, UMMZ 199849b; R. oxy-cephalus AMNH A26845b. Rhinodermati-da: Rhinoderma darwini AMNH 57314a; KU 161506, KU 161544. Rhinophrynidae: Rhinophrynus dorsalis AMNH A6214b, AMNH A6223a, AMNH A6226a, UMMZ 82134b. Sooglossidae: Nesosan timothy se-ssetii UMMZ 145679b; Sooglossus gardineri UMMZ 23506b; UMMZ 183084b; S. se-chellensis AMNH A26792b, UMMZ 150830b.
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