

Development and variation of the anuran webbed feet (Amphibia, Anura)

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Webbed feet evolved convergently in most groups of aquatic tetrapods. However, extensive webbing is not always limited to an aquatic life style. In Anurans, hind limbs display great variation, including absence, of interdigital membranes, which is explained by differential growth rates of digital and interdigital tissues during early limb development. In order to explore web diversification in anurans, this paper presents analyses of: (1) hind limb early development and its relationship to the expression of interdigital membranes; (2) intraordinal variation of interdigital membranes in adult feet; and (3) intraordinal variation of metatarsal and digit lengths, including comments on metatarsal development. Study of limb development is carried out in larval series of 12 anuran species. Analysis of intraordinal variation comprises a sample of adults of 111 species. We recognize two configurations in the autopodium bud: (1) paddle-like shape with digits differentiated within the confines of interdigital tissues, and (2) pointed autopodium with digits differentiated beyond interdigital tissues. These early differences are conserved in adult morphology, in which allometry and isometry of digit IV (and metatarsal IV) with respect to other digits (and metatarsals) result in asymmetrical and paddle-like autopodium, respectively. The paddle-like autopodium is restricted to fossil and extant pipids and the hylids *Pseudis* and *Lysapsus*, whereas the asymmetrical one is present in most anurans. Both configurations seem to represent an early divergence of the autopodium shape. The paddle-like configuration observed in hylids appears as a reversion to an ancient condition that results from a conserved program of limb development. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **152**, 39–58.

ADDITIONAL KEYWORDS: amphibians – heterochrony – hind limbs – interdigital membranes – Pipidae – *Pseudis* – toes.

INTRODUCTION

Anura is a major group whose origin appears related to the transformation of its locomotor system for saltation (Emerson, 1979). The anuran hind limbs are a consequence of important changes in the developmental program of the tetrapod limb, which involve fusion of the tibia and fibula, elongation and fusion of the tibiale and fibulare, and absence of postaxial distal tarsals (Shubin & Alberch, 1986; Fabrezi, 1993).

Morphological specialization of the vertebral column and pelvis (e.g. the ilia articulate ventral to the sacrum), differences in relative hind limb length,

joints and muscles were studied to determine correlations with jump performance, different life styles (aquatic, terrestrial, arboreal), and specialized habits (swimmer, jumper, walker, burrower, climber, flyer) (Emerson, 1976, 1978, 1979, 1982, 1988; Emerson & de Jongh, 1980; Emerson & Koehl, 1990). Muscles, intercalary elements, adhesive digit pads, interdigital membranes and keratinization of prehallux are structures associated with the anuran limbs that appear in specific locomotor patterns (e.g. adhesive toes pad and intercalary elements in climbers, interdigital membranes in swimmers, keratinized spade in burrowers) (Pough *et al.*, 2001).

The presence of interdigital membranes is observed to be a result of convergence in other groups of tetrapods, occurring in aquatic species but also in

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some non-aquatic ones (e.g. geckos, bats). The interdigital membranes may occur in manus, pes or both. Differentiation, reduction and/or disappearance of interdigital membranes take place during early digit development. In amniotes, the loss of interdigital tissue progresses disto-proximally by apoptosis at the paddle-like stage of the limb buds (Kimura & Shiota, 1996). In those taxa that retain interdigital membranes, such as ducks, there is minimal cell death in the distal borders of interdigital tissues (Gilbert, 1997). Apoptosis in amphibians has only been studied in seven species (Cameron & Fallon, 1977; Vlaskalin, Wong & Tsilfidis, 2004; Franssen *et al.*, 2005). The absence of cell death has been reported for two anurans and four urodeles, but has been detected in one urodele in the presumptive interdigital tissues in both the forelimbs and the hind limbs (Franssen *et al.*, 2005).

Anuran hind limbs display great variation, including absence, of interdigital membranes; the developmental explanation for this could be extrapolated from the study of Cameron & Fallon (1977), who proposed differential growth of digital and interdigital tissues.

The degree of foot webbing has been included in the diagnosis of many anuran species. It has been estimated by considering the number of phalanges outside the membrane (Savage & Heyer, 1997), in a more ambiguous way ('reduced foot webbing', 'foot completely webbed', 'absence of webbing') (Laurent, 1986) or based on web developed between particular digits (Liem, 1970). Despite the extensive and abundant employment of the form of interdigital membranes in taxonomic descriptions of anurans, there is little phylogenetically based information about its morphological variation and development.

Here we integrate information from comparative ontogeny and phylogeny in an analysis of interdigital membranes and their variation in anuran hind limbs to address: (1) morphological and developmental patterns, (2) the type and direction of changes, and (3) the significance of webbed feet in the evolution of anurans.

MATERIAL AND METHODS

Data in this study were analysed in various ways: (1) description of external hind limb development in larval series; (2) documentation of intraordinal variation of interdigital membranes among adult specimens; and (3) quantitative examination of intraordinal variation of digits and metatarsal lengths based on skeletal preparations. Most taxon nomenclature follows Frost *et al.* (2006).

External morphology of hind limb development was examined in larval specimens, the adults of which: (1)

lack interdigital webs – *Dermatonotus muelleri*, *Elachistocleis bicolor*, *Phyllomedusa sauvagii* and *Physalaemus biligonigerus*; and (2) have interdigital membranes – *Bombina variegata*, *Ceratophrys cranwelli*, *Lepidobatrachus laevis*, *Pseudis paradoxa*, *Scinax fuscovarius* and *Xenopus laevis*. Larvae were staged according to the developmental table of Gosner (1960).

We also studied metatarsal/digit differentiation in larval series of species with adults both lacking (*Dermatonotus muelleri*, *Elachistocleis bicolor*, *Phyllomedusa sauvagii*, *Physalaemus biligonigerus*) and possessing (*Chacophrys pierottii*, *Ceratophrys cranwelli*, *Lepidobatrachus laevis*, *Pseudis paradoxa*, *Scinax acuminatus*, *Xenopus laevis*) interdigital membranes. Specimen numbers, collection data and species authority names are listed in Appendix 1.

Adults specimens of 111 anuran species preserved in 70% ethanol were examined in order to describe presence or absence of interdigital membranes (Appendix 2). Skeletal whole-mounts of these 111 anuran species were considered to study qualitative and quantitative variation of limb elements (Appendix 2). Measures of metatarsal and digit lengths were considered in right hind limbs. Total digit length was measured from the proximal epiphysis of the metatarsal to the distal tip of the terminal phalange, except for few a specimens where phalanges were disconnected. We used dial calipers accurate to 0.02 mm, and measurements are given throughout in millimetres. Authority names, collection data, presence of interdigital membrane, and metatarsal and digit lengths of species are listed in Appendix 2.

Studies of the skeleton of larval and adult specimens were made on cleared and stained skeletal whole-mounts prepared following the method of Wassersug (1976). All observations, illustrations and photographs were made using a Nikon SMZ1000 stereo dissection microscope equipped with a digital camera and camera lucida.

RESULTS

EXTERNAL HIND LIMB DEVELOPMENT IN LARVAL SERIES

In tetrapods, early limb development is characterized by three axes along which differentiation progresses (proximal–distal, dorsal–ventral and postaxial–preaxial) (Shubin & Alberch, 1986; Gilbert, 1997). Proximal–distal differentiation occurs first in the limb bud. Subsequent interaction of the three axes of growth characterizes the autopodium, which in most tetrapods is first observed in the paddle-like stage. In most anurans the autopodium is not paddle-like because proximo-distal differentiation involves rapid

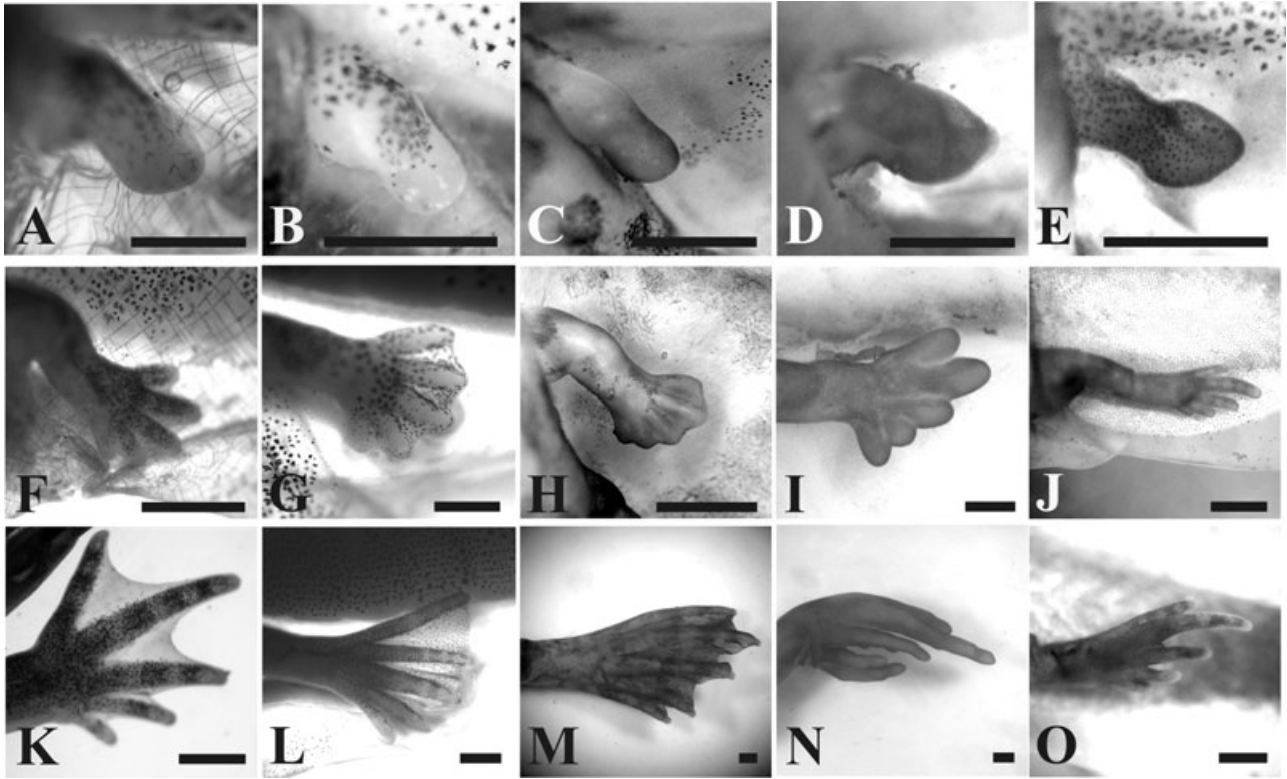


Figure 1. External hind limb morphology in anuran larvae. A–E, larval stage 31, a preaxial constriction delimits the distal autopodium; F–J, larval stage 36, digit differentiation is advanced; K–O, larval stage 40. A, *Bombina variegata*: the autopodium is almost cylindrical with an incipient postaxial elongation (the primary axis). B, *Xenopus laevis* and C, *Pseudis paradoxa*: the autopodium is almost cylindrical without an evident distal tip denoting digit IV. D, *Phyllomedusa sauvagii* and E, *Elachistocleis bicolor*: the pointed autopodium is clearly defined by the elongation of primary axis. F, *B. variegata*: elongation of digit IV is scarcely noticeable, and interdigital membranes are shorter than the digits. G, *X. laevis* and H, *P. paradoxa*: the autopodium is paddle-like, and interdigital tissues, which are extended up to digit tips, separate digits. Digits V, IV and III show similar degrees of growth. I, *Phyllomedusa sauvagii* and J, *E. bicolor*: digit differentiation progresses as outgrowths in the proximo-distal direction and elongation of digit IV is more extensive than that of the other digits. Interdigital membranes are absent. K, *B. variegata*: well-developed interdigital membrane and the elongated digit IV become defined before metamorphosis. L, *X. laevis* and M, *P. paradoxa*: later stages display extensive interdigital membranes reaching to the toe tips, with digits V and III as long as digit IV. M, *Phyllomedusa sauvagii* and O, *E. bicolor*: digits are completely free. Scale bar = 1 mm.

elongation of the primary axis, which represents digit IV. Digit differentiation occurs by way of distal lengthening from the autopodium bud, with the digits being separated by interdigital grooves.

Interspecific variation in the external morphology of hind limb buds is expressed as two well-differentiated types at larval stage 31, at which point the limb bud is divided into proximal and distal segments by a preaxial constriction (Fig. 1). An intermediate configuration between these types is observed in *B. variegata*, which has a quite rounded rather than pointed distal segment (autopodium) (Fig. 1A). The other species exhibit a limb bud in which the autopodium is pointed and flat (Fig. 1D, E), or a straight, cylindrical autopodium, with a rounded distal end, as in *P. paradoxa* and *X. laevis* (Fig. 1B,

C). Differences between these two limb buds types become more evident as development progresses, as the second type preserves its distal rounded end, even after flattening and the commencement of digit differentiation, whereas in the first type the elongation of toe IV is noticeable. In contrast to *P. paradoxa* and *X. laevis*, which conserve the paddle-like configuration of the autopodium, *B. variegata* displays a paddle-like configuration up to the stage in which five digits are differentiated and elongation of digit IV becomes evident. At later stages, toe differentiation progresses distally without evidence of retraction of interdigital tissues. Species with interdigital membranes (*B. variegata*, *S. fuscovarius*, *Lepidobatrachus laevis*, *C. cranwelli*) exhibit interdigital tissue (Fig. 1F, K) when the toes are totally

differentiated, whereas in other species (*Phyllomedusa sauvagii*, *D. muelleri*, *E. bicolor*, *Physalaemus biligonigerus*) digital separation progresses without interdigital tissue (Fig. 1I, J, N, O). In contrast, in *P. paradoxa* and *X. laevis*, digit IV elongation is modestly noticeable. The autopodium conserves the paddle-like morphology and digit differentiation occurs within the confines of the autopodium (Fig. 1G, H, L, M). In these species, growth of the digits and the interdigital tissues seems to be synchronous.

Our observations allow us to recognize two early developmental pathways that involve interdigital membranes among anurans: (1) hind limb bud with an evident proximal–distal differentiation of the primary axis in which digits grow out of the paddle and interdigital tissues seem to progress at a slower developmental rate or show no development, as observed in most anuran species; and (2) hind limb buds with a paddle-like morphology in which the primary axis is scarcely evident, and interdigital tissues grow synchronously with toe elongation, as recorded in *X. laevis* and *P. paradoxa*.

INTRAOORDINAL VARIATION OF INTERDIGITAL MEMBRANES AMONG ADULT SPECIMENS

Intraordinal variation observed among a sample of 111 anuran species allowed us to define two states for the character relative to the presence of interdigital membranes:

State 0, in which all phalanges are free, which means interdigital membranes are totally absent (Fig. 2A–C). Absence of interdigital membranes was recorded in those terrestrial species (listed in Appendix 2) of Arthroleptidae, Brachycephalidae, Brevicipitidae, Dendrobatidae, Hemisotidae, Myobatrachidae, Hylidae, Leptodactylidae, Leiuperidae, Mantellidae and Microhylidae.

State 1, representing feet with interdigital membranes of different degrees of development (some or all phalanges have membranes, Fig. 2D–L). This condition was observed in species (listed in Appendix 2) of Alytidae, Amphignatodontidae, Arthroleptidae, Bombinatoridae, Bufonidae, Centrolenidae, Ceratophryidae, Cycloramphidae, Dicroglossidae, Hylidae, Hyperoliidae, Limnodynastidae, Pelobatidae, Pelodytidae, Petropedetidae, Phrynobatrachidae, Pipidae, Ptychadenidae, Pyxicephalidae, Ranidae, Rhacophoridae, and Scaphiropodidae.

VARIATION OF TOE LENGTHS

Early stages of limb development start with proximal–distal differentiation, which results in differentiation of primary axis cartilages. The primary axis is formed by the fibula, fibulare and digit IV in

anuran hind limbs (Shubin & Alberch, 1986). Observation of primary cartilage condensations in selected anuran species revealed variation, which is related to rates of differentiation of digit IV. Most species have a fourth metatarsal that is dominant, and this is the first metatarsal and digital element to differentiate (Fig. 3A). Digit development progresses with differentiation of the postaxial digit V, and the preaxial digits III, II and I (Fig. 3A–C). In contrast, in *X. laevis* and *P. paradoxa* metatarsals IV and III appear almost at the same time and develop at synchronic rates (Fig. 3D–I).

In adults, intraordinal variation of toe IV length seems to be related to metatarsal IV length (Fig. 4).

There is variation among species in the length of the metatarsal, and thus the phalangeal segments for each digit (Fig. 5). For most species, metatarsals II and I represent more than half the total length of the correspondent digit, and metatarsals III, IV and V are quite the half. Those species with complete webbing (*P. paradoxa*, *Lysapsus limellum*, *Hymenochirus boettgeri*, *Pipa carvalhoi*, *Pipa parva*, and *Xenopus* spp.) exhibit a pattern where all digits have elongated metatarsals (Fig. 5).

Consequently, comparisons between metatarsal and digit IV lengths relative to the other metatarsals and digits reveal also variation. Metatarsal IV is quite isometric with metatarsals I, II, III, and V in *P. paradoxa*, *L. limellum* and Pipidae (Fig. 6). Meanwhile in the other species, metatarsal IV is always longer (Fig. 6). Total length of digit IV also appears quite similar to the other digits in *P. paradoxa*, *L. limellum* and Pipidae. By contrast, for most anurans digit IV is always the longest (Fig. 7), as expected given that it has the highest number of phalanges.

These quantitative analyses reveal the following: (1) the feet of some species with complete webbing have elongated metatarsals and short distal segments, the five metatarsals are quite isometric, and digit IV is not predominately the longest. These features determinate a paddle-like autopodium configuration, as observed in *Hymenochirus boettgeri*, *Pipa carvalhoi*, *Pipa parva*, *Xenopus victorianus*, *X. fraseri*, *X. muelleri*, *P. paradoxa* and *L. limellum*. (Fig. 4); and (2) the foot in most anurans is characterized by having digit IV longest, with metatarsal IV always longer, and preaxial digits and metatarsals decreasing preaxially. These features define an asymmetrical configuration of the autopodium denoting a postaxial dominance in the skeletal elements (Fig. 4).

DISCUSSION

Anurans constitute a monophyletic group with more than 40 extant terminal taxa at familial level (Frost

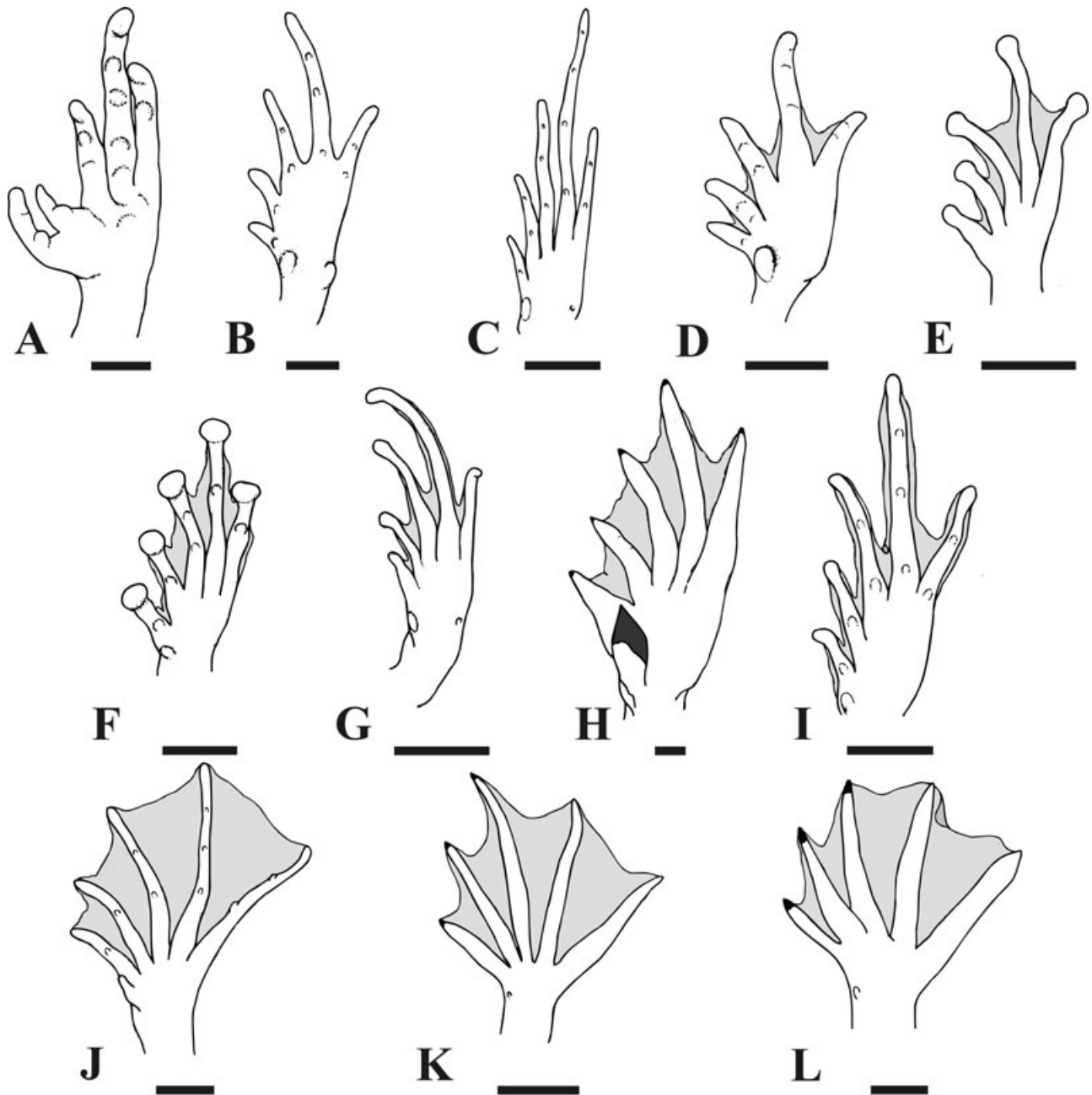


Figure 2. Intraordinal variation of interdigital membranes among adult anurans. A, *Phyllomedusa sauvagii*. B, *Pleurodema borellii*. C, *Leptodactylus bufonius*. D, *Melanophryniscus rubriventris*. E, *Hyperolius castaneus*. F, *Scinax acuminatus*. G, *Phrynobatrachus versicolor*. H, *Lepidobatrachus laevis*. I, *Telmatobius oxycephalus*. J, *Pseudis paradoxa*. K, *Hymenochirus boettgeri*. L, *Xenopus victorianus*. Grey areas represent presence of interdigital membrane. Scale bar = 5 mm.

et al., 2006). From this hypothesis, basal anurans (leiopelmatids, rhinophrynids, pipids, alytids, bombinatorids, pelodytids, scaphiopodids, pelobatids, megophryids) have webbed feet, a condition that is conserved in most derived groups (neobatrachians). The absence of interdigital membranes seems to be

the derived condition, which has appeared independently in several groups of terrestrial frogs and some treefrogs (hylids, leptodactylids, dendrobatids, microhylids, brevicipitids, hemisotids, arthroleptids). The derived condition has not been reported for anuran taxa included among non-neobatrachians (basal

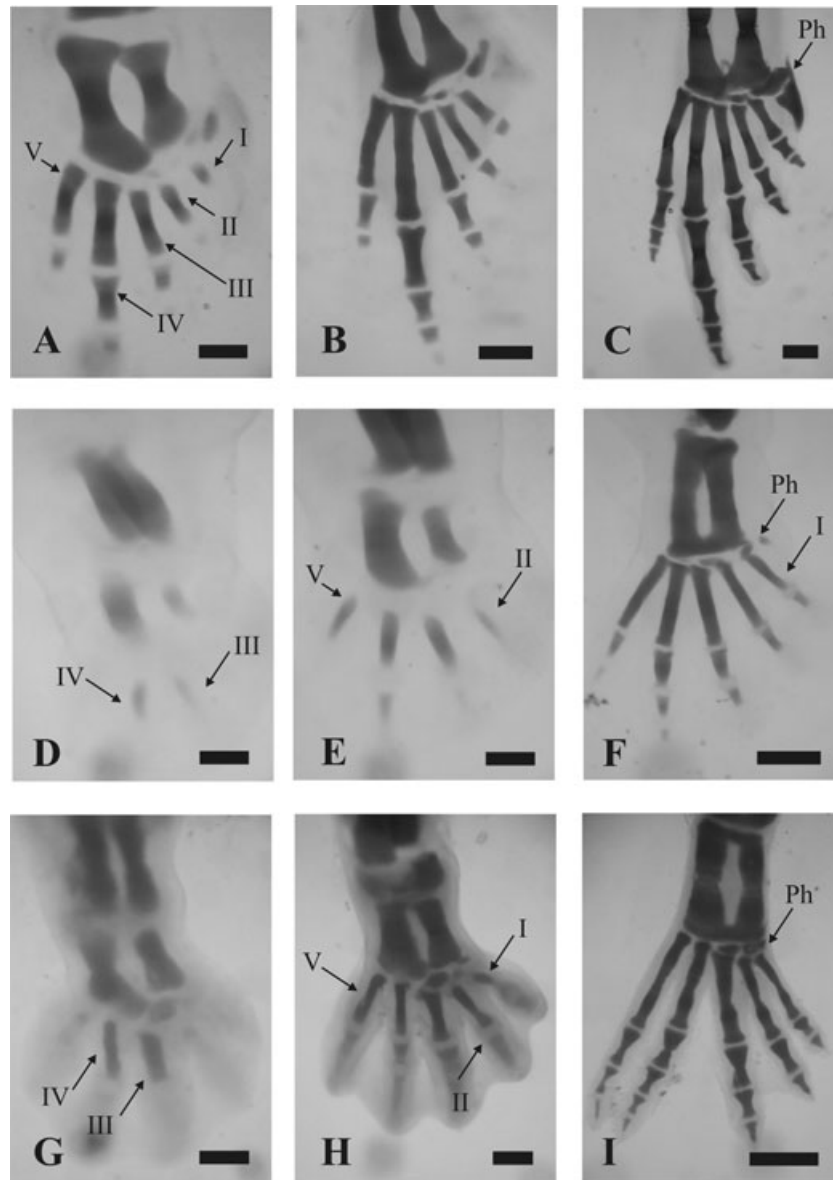
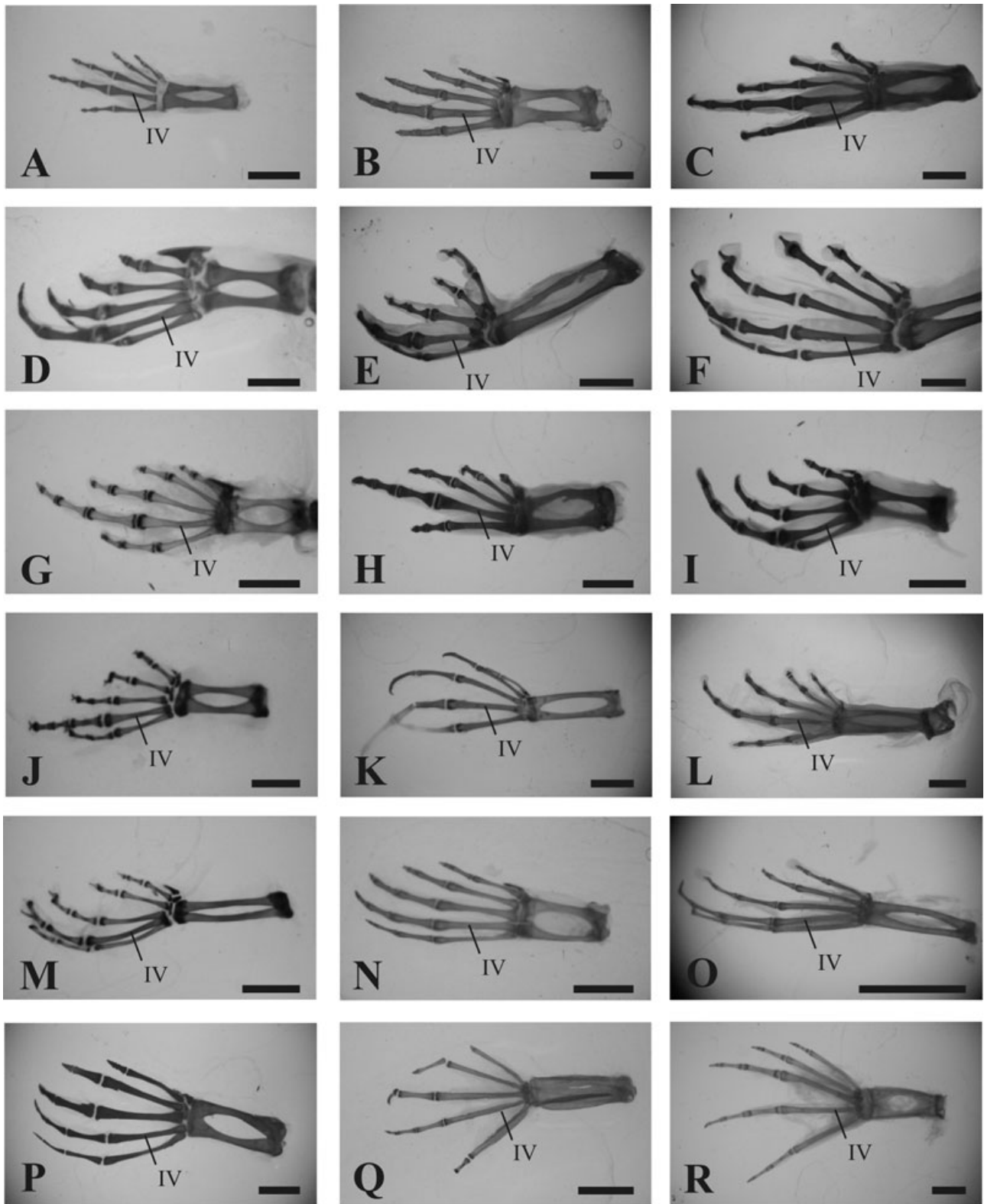


Figure 3. Early differentiation of the primary cartilaginous condensations of metatarsals among selected anurans. A–C, *Chacophrys pierottii*, larval stages 35, 37 and 39. Proximo-distal elongation of digit IV (metatarsal and phalanges) is always advanced with respect to development of the others digits. D–F, *Pseudis paradoxa*, larval stages 32, 35 and 37. Differentiation of metatarsal IV and that of metatarsal III occur simultaneously. Metatarsals are quite similar in length. G–I, *Xenopus laevis*, larval stages 34, 36 and 40. Primary cartilages of metatarsals IV and III are the first to differentiate but are as long as metatarsals V and II, which appear subsequently. Scale bar = 0.2 mm in A, D–I, and 0.5 mm in B, C, F. Abbreviations: V, metatarsal V; IV, metatarsal IV; III, metatarsal III; II, metatarsal II; I, metatarsal I; Ph, prehallux.

Figure 4. Variation of metatarsal IV length in adult specimens. A, *Bombina variegata*. B, *Leptodactylus bufonius*. C, *Telmatobius oxycephalus*. D, *Lepidobatrachus llanensis*. E, *Phyllomedusa sauvagii*. F, *Trachycephalus venulosus*. G, *Opisthodon spenceri*. H, *Chaunus granulatus*. I, *Dermatonotus muelleri*. J, *Phrynomantis bifasciatus*. K, *Ptychadena guibei*. L, *Hydrophylax albolabris*. M, *Leptopelis christyi*. N, *Pseudis paradoxa*. O, *Lysapsus limellum*. P, *Xenopus victorianus*. Q, *Hymenochirus boettgeri*. R, *Pipa carvalhoi*. Most species display metatarsal IV as the longest. In contrast, the last five species display similar lengths of metatarsals III, IV and V. Arrow indicates metatarsal IV. Scale bar = 5 mm.



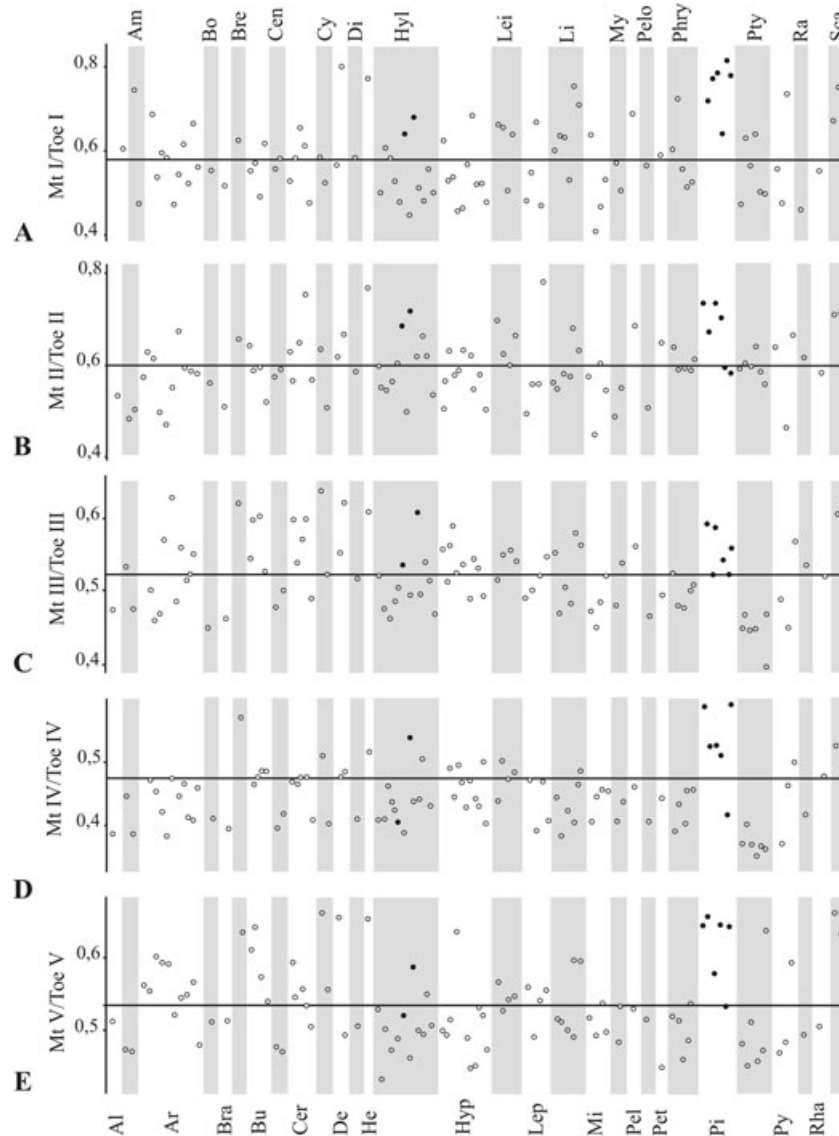


Figure 5. Variation of metatarsal length with respect to total toe length. Vertical axis indicates the coefficient of metatarsal length/total toe length. Horizontal axis crosses vertical axis at the mean value. Higher values of the coefficient suggest relatively shorter phalangeal segment. Black circles represent anurans with complete webbing (the hylids *Pseudis paradoxa* and *Lysapsus limellum*, and the pipids *Xenopus* spp., *Hymenochirus boettgeri* and *Pipa* spp.). A, metatarsal I length/toe I length. B, metatarsal II length/toe II length. C, metatarsal III length/toe III length. D, metatarsal IV length/toe IV length. E, metatarsal V length/toe V length. There is intraspecific variation in the relative length of the phalangeal segment with respect to metatarsal length among digits. The species marked with black circles display metatarsals relatively longer in the five digits. Abbreviations of analysed taxa: Al, Alytidae; Am, Amphignatodontidae; Ar, Arthroleptidae; Bo, Bombinatoridae; Bra, Brachycephalidae; Bre, Brevicipitidae; Bu, Bufonidae; Cen, Centrolenidae; Cer, Ceratophryidae; Cy, Cycloramphidae; De, Dendrobatidae; Di, Dicroglossidae; He, Hemisotidae; Hyl, Hylidae; Hyp, Hyperoliidae; Lei, Leiuperidae; Lep, Leptodactylidae; Li, Limnodynastidae; Mi, Microhylidae; My, Myobatrachidae; Pel, Pelobatidae; Pelo, Pelodytidae; Pet, Petropedetidae; Phry, Phrynobatrachidae; Pi, Pipidae; Pty, Ptychadenidae; Py, Pyxicephalidae; Ra, Ranidae; Rha, Rhacophoridae; Sca, Scaphiopodidae.

anurans) and those taxa with aquatic habits. The plesiomorphic condition includes variation in expression from extensive to rudimentary interdigital membranes. Extensively webbed feet are typical of aquatic

species of hylids, pipids, bombinatorids, ceratophryids, cycloramphids, dicroglossids, ranids and treefrogs such as some rhacophorids and mantellids illustrated by Guibé (1978).

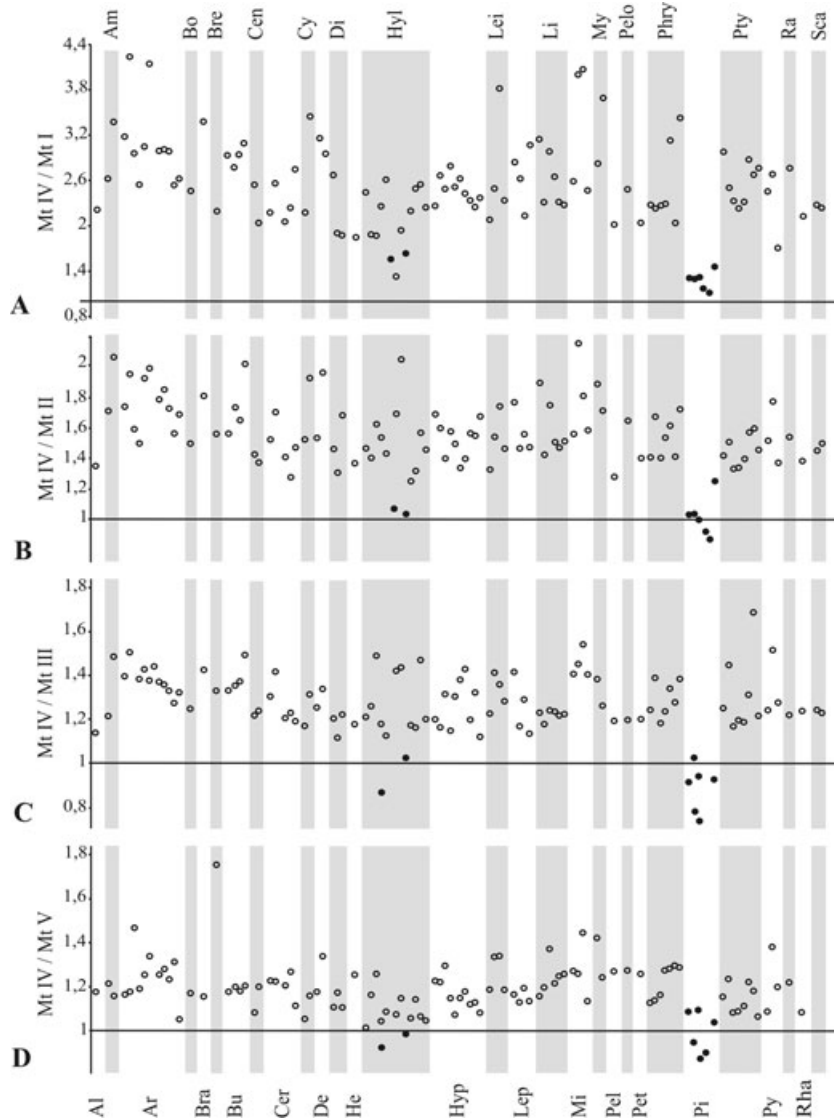


Figure 6. Length relationships between metatarsal IV and metatarsals I, II, III and V. Vertical axis indicates metatarsal length relationship. Horizontal axis intercepts vertical axis where the relationship is equal to one. Black circles represent anurans with complete webbing (the hylids *Pseudis paradoxa* and *Lysapsus limellum*, and the pipids *Xenopus* spp., *Hymenochirus boettgeri* and *Pipa* spp.), which share a same pattern with metatarsal IV almost equal to or shorter than the others. A, metatarsal IV vs. metatarsal I. B, metatarsal IV vs. metatarsal II. C, metatarsal IV vs. metatarsal III. D, metatarsal IV vs. metatarsal V. Abbreviations of analysed taxa: Al, Alytidae; Am, Amphignatodontidae; Ar, Arthroleptidae; Bo, Bombinatoridae; Bra, Brachycephalidae; Bre, Brevicipitidae; Bu, Bufonidae; Cen, Centrolenidae; Cer, Ceratophryidae; Cy, Cycloramphidae; De, Dendrobatidae; Di, Dicroglossidae; He, Hemisotidae; Hyl, Hylidae; Hyp, Hyperoliidae; Lei, Leiuperidae; Lep, Leptodactylidae; Li, Limnodynastidae; Mi, Microhylidae; My, Myobatrachidae; Pel, Pelobatidae; Pelo, Pelodytidae; Pet, Petropedetidae; Phry, Phrynobatrachidae; Pi, Pipidae; Pty, Ptychadenidae; Py, Pyxicephalidae; Ra, Ranidae; Rha, Rhacophoridae; Sca, Scaphiopodidae.

Intraordinal variation in the relative length of metatarsals and digits exhibits two character states correlated with differences in developmental patterns. In *X. laevis* and *P. paradoxa*, differentiation of metatarsals IV and III is almost simultaneous, and differentiation in length of distal elements is accompanied

by growth of interdigital tissues (Figs 1, 3). Similar development of skeletal elements was described for *Pipa pipa* (Trueb, Pügener & Maglia, 2000). The heterochronic change, with respect to most anurans, results in isometric metatarsals in pipids, *P. paradoxa* and *Lysapsus limellum*, also described for *Rhinophry-*

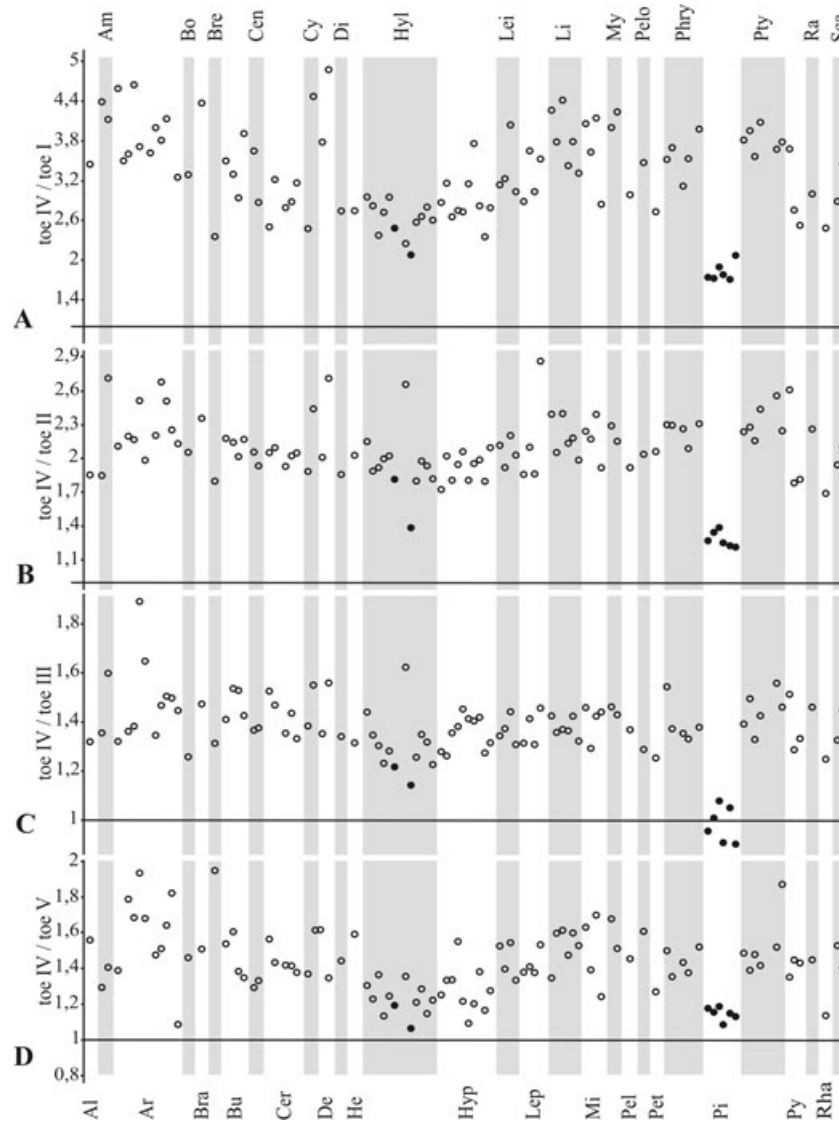


Figure 7. Length relationships between toe IV and toes I, II, III and V. Vertical axis indicates toe length relationship. Horizontal axis intercepts vertical axis where the relationship is equal to one. Black circles represent anurans with complete webbing (the hylids *Pseudis paradoxa* and *Lysapsus limellum*, and the pipids *Xenopus* spp., *Hymenochirus boettgeri* and *Pipa* spp.) that share similar toe lengths. A, toe IV vs. toe I. B, toe IV vs. toe II. C, toe IV vs. toe III. D, toe IV vs. toe V. Abbreviations of analysed taxa: Al, Alytidae; Am, Amphignatodontidae; Ar, Arthroleptidae; Bo, Bombinatoridae; Bra, Brachycephalidae; Bre, Brevicipitidae; Bu, Bufonidae; Cen, Centrolenidae; Cer, Ceratophryidae; Cy, Cycloramphidae; De, Dendrobatidae; Di, Dicroglossidae; He, Hemisotidae; Hyl, Hylidae; Hyp, Hyperoliidae; Lei, Leiuperidae; Lep, Leptodactylidae; Li, Limnodynastidae; Mi, Microhylidae; My, Myobatrachidae; Pel, Pelobatidae; Pelo, Pelodytidae; Pet, Petropedetidae; Phry, Phrynobatrachidae; Pi, Pipidae; Pty, Ptychadenidae; Py, Pyxicephalidae; Ra, Ranidae; Rha, Rhacophoridae; Sca, Scaphiropodidae.

nus dorsalis by Andersen (1978). Furthermore, the relative length of phalangeal segments of digits seems to be shorter than in most anurans.

Early developmental differences that are seen as two configurations of limb buds are conserved in the adult configurations, in which allometry and isometry of digit IV (and metatarsal IV) with respect to other

digits (and metatarsals) result in asymmetrical and a paddle-like autopodium, respectively. The paddle-like autopodium is only observed in the aquatic pipids, *L. limellum*, and *P. paradoxa*, and is also related to extensive webbing.

Cameron & Fallon (1977) described distinctive patterns of digit formation between amphibians and

amniotes, noting that in amphibians there are no zones of differential cell death during digit formation, and digits appear to be patterned by differential proliferation of interdigital and digital cells, rather than by massive cell death as in amniotes. This statement was based on observations of digit formation using vital staining and histological and autoradiographic techniques in the anurans *X. laevis*, and *Bufo americanus*, and the urodeles *Ambystoma maculatum*, *Ambystoma mexicanum* and *Taricha torosa*. Recently, Vlaskalin *et al.* (2004) confirmed by TUNEL analyses the absence of cell death during digit formation in the urodele *Notophthalmus viridescens*, although Franssen *et al.* (2005) found apoptotic cells in the urodele *Desmognathus aeneus*, with the suggestion that the latter exhibits a pattern different from that described for amniotes. At present, for anurans the only argument able to explain digit formation and the persistence of interdigital membranes in anurans was put forward by Cameron & Fallon (1977), but more amphibian species must be investigated to enhance our understanding of the cellular mechanisms involved in digit formation and its relationship to interdigital tissues.

Following the hypothesis proposed by Cameron & Fallon (1977), we note in *X. laevis* and *P. paradoxa* a synchronous growth of digital and interdigital areas, which could be interpreted as representing a delayed developmental rate of digits (especially digit IV) and/or an accelerated developmental rate of interdigital tissues. Alberch & Alberch (1981) described paedomorphosis in digit formation (affecting the differentiation of distal phalanges) that results in fully webbed hands and feet in *Bolitoglossa occidentalis*, which is associated with developmental peculiarities of this species (Alberch & Alberch, 1981).

The similitude in length of metatarsals seems to be characteristic of fossil taxa. In the Jurassic frogs *Notobatrachus* and *Eodiscoglossus*, metatarsal IV is not the longest but digit IV is strongly elongated (Estes & Reig, 1973; Roček, 2000). This configuration suggests an asymmetrical shape of the autopodium with postaxial dominance.

The Cretaceous frogs are well represented by pipids and palaeobatrachids that have fossil records in lacustrine environments (Estes & Reig, 1973; Báez, 1996; Báez & Trueb, 1997). The extant pipids are placed among the basal anurans in some phylogenies (Haas, 2003; Frost *et al.*, 2006) but have been advocated as the most basal anuran group in other hypotheses (Púgner, Maglia & Trueb, 2003). Most of the well-preserved specimens in the fossil record of pipids have elongated and quite isometric metatarsals, and a scarcely elongated digit IV (Estes & Reig, 1973; Báez, 1981, 1996). Records of Palaeobatra-

chidae (fossil taxon related to Pipidae) have autopodia like pipids (Jarošová, 1974).

The fossil evidence suggests there was an early divergence in the configuration of the anuran foot related to habit; the paddle-like configuration of pipid frogs might represent an ancient condition.

The aquatic life style of pipids has been related to a set of morphological characters: depressed bodies with broad, flat and triangular heads; terminal nostrils; limbs orientated laterally; lateral line system; and extensive webbing (Laurent, 1986; Frittsch, Drewes & Ruibal, 1987; Trueb *et al.*, 2000). This set of features is unique for pipids. Non-pipid anurans may have some of them – e.g. the aquatic *Lepidobatrachus laevis* (Ceratophryidae) and *Occidozyga lima* (Dicroglossidae) have adults with complete lateral line system (Frittsch *et al.*, 1987); *P. paradoxa* has a general morphology like *Xenopus* (Laurent, 1986) and the traits here presented – but not the whole set.

The hind limbs of pipids and *Pseudis* + *Lysapsus*, two phylogenetically distant groups specialized for aquatic locomotion, share well-developed interdigital membranes and almost isometrically expressed metatarsals and digits. The morphological similarities they share are due to changes in the early stages of their hind limb development in comparison with that of most anurans. Our findings indicate that the anuran hind limb morphology displays heterochronic variation during digit formation that has consequences for metatarsal and digit lengths and interdigital membrane development that have resulted in similar modes of locomotion. However, an aquatic life style is a necessary condition but not a sufficient explanation for the reappearance of the paddle-like configuration observed in *P. paradoxa* and *L. limellum*. Because pipids are basal anurans (Haas, 2003; Púgner *et al.*, 2003; Frost *et al.*, 2006), a similar developmental pattern within some neobatrachians is a clear example that the genetic basis for this pattern is conserved in the anuran limb morphogenesis program.

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APPENDIX 1

LARVAL SERIES EXAMINED FOR
HIND LIMB DEVELOPMENT

Bombinatoridae: MCN 1002 *Bombina variegata* (Linnaeus, 1758): 15 specimens at larval stages 31, 34, 36–46.

Ceratophryidae: MCN 670 *Ceratophrys cranwelli* Barrio, 1980: 35 specimens at larval stages 29–46 and seven osteological whole-mounts at larval stages 34, 37, 39. MCN 1027, 1028, 1029 *Chacophrys pierottii* (Vellard, 1948) 63 specimens at larval stages 26–46 and six osteological whole-mounts at larval stages 35, 37, 39. MCN 663 *Lepidobatrachus laevis* Budgett, 1899: 43 specimens at larval stages 31–40 and six osteological whole-mounts at larval stages 33, 37, 39.

Leiuperidae: MCN 076 *Physalaemus biligonigerus* (Cope, 1861): 58 specimens at larval stages 27–46 and 20 osteological whole mounts at larval stages 32–46.

Microhylidae: MCN 603 *Dermatonotus muelleri* (Boettger, 1885): 70 specimens at larval stages 30–42 and six osteological whole-mounts at larval stages 33, 37, 39. MCN 602 *Elachistocleis bicolor* (Guérin-Méneville, 1838): 60 specimens at larval stages 26–42 and eight osteological whole-mounts at larval stages 33, 35–39.

Hylidae: MCN 599 *Phyllomedusa sauvagii* Boulenger, 1882: 61 specimens at larval stages 29–43 and 28 osteological whole mounts at larval stages 31–42; MCN 683, 597. *Pseudis paradoxa* (Linnaeus, 1758): 77 specimens at larval stages 26–43 and 15 osteological whole mounts at larval stages 28–39; MCN 983 *Scinax acuminatus* (Cope, 1862): 46 specimens at larval stages 26–46 and 12 osteological whole mounts at larval stages 30–41.

Pipidae: MCN 490 *Xenopus laevis* (Daudin, 1802): 20 specimens larval stages 29–46 and 12 osteological whole mounts at larval stages 30, 33–39, 42–46.

APPENDIX 2

Taxon nomenclature follows Frost *et al.* (2006), except for the genus *Schoutedenella*, which keeps its assignation as a different genus based on Laurent & Fabrezi (1985).

Institutional abbreviations: FML, Instituto de Herpetología, Fundación Miguel Lillo, Tucumán, Argentina; MCN, Museo de Ciencias Naturales, Universidad Nacional de Salta, Argentina; MNHN (Montevideo), Museo Nacional de Historia Natural, Montevideo, Uruguay; MNHN (Paris), Muséum National d'histoire Naturelle, Paris, France; RFL, Dr Raymond F. Laurent, personal collection in Museo de Ciencias Naturales, Universidad Nacional de Salta, Argentina; UIS, Colección Herpetológica y Laboratorio de Biología Reproductiva de Vertebrados, Escuela de Biología, Universidad Industrial de Santander, Bucaramanga, Colombia.

Family	Species	Catalogue number	Webbing	Metatarsal I length	Toe I length	Metatarsal II length	Toe II length	Metatarsal III length	Toe III length	Metatarsal IV length	Toe IV length	Metatarsal V length	Toe V length
Alytidae	<i>Discoglossus pictus</i> Oth, 1837	FML 3945	Present	4.16	6.88	6.80	12.80	8.48	17.94	9.20	23.74	7.82	15.26
Amphignatodontidae	<i>Flectonotus fitzgeraldi</i> (Parker, 1934)	MCN 017	Present	1.46	1.96	2.24	4.64	3.38	6.36	3.84	8.60	3.16	6.68
Amphignatodontidae	<i>Gastrotheca gracilis</i> Laurent, 1969	FML 2965	Present	1.82	3.84	2.96	5.88	4.70	9.94	6.14	15.88	5.30	11.28
Arthroleptidae	<i>Arthroleptis adolfi-friederici</i> Nieden, 1911	MCN 822	Absent	2.00	–	4.34	–	6.40	–	8.44	–	7.14	–
Arthroleptidae	<i>Arthroleptis poecilonotus</i> Peters, 1863	MCN 950	Absent	2.14	3.60	3.66	5.96	4.38	9.36	5.44	12.90	4.60	7.64
Arthroleptidae	<i>Arthroleptis variabilis</i> Matschie, 1893	MCN 840	Present	2.46	4.00	4.04	6.00	6.08	10.86	7.46	16.00	5.84	10.72
Arthroleptidae	<i>Asstylosternus diadematus</i> Werner, 1898	FML 3215	Absent	1.88	2.74	3.44	6.00	4.78	9.54	5.98	12.66	5.14	9.14
Arthroleptidae	<i>Cardioglossa cyaneospila</i> Laurent, 1950	MCN 821	Absent	1.90	3.64	3.28	5.52	4.70	9.14	5.68	13.76	4.60	8.38
Arthroleptidae	<i>Cardioglossa leucomystax</i> (Boulenger, 1903)	RFL 170	Absent	2.26	3.40	3.66	6.24	4.88	9.34	5.72	14.00	4.34	7.66
Arthroleptidae	<i>Leptopeltis chrystyi</i> (Boulenger, 1912)	MCN 829	Present	2.66	4.74	4.16	7.16	5.82	10.56	7.00	15.22	6.68	13.94
Arthroleptidae	<i>Schoutedenella lameerei</i> (Witte, 1921)	MCN 941	Absent	1.16	2.16	2.16	3.44	2.56	5.58	3.44	7.58	2.36	4.26
Arthroleptidae	<i>Schoutedenella pyrrhoscelis</i> (Laurent, 1952)	MCN 827	Absent	0.98	1.68	1.56	3.14	2.36	4.14	3.00	7.84	2.40	4.04

Arthroleptidae	<i>Schoutedenella schubotzi</i> (Nieden, 1911)	MCN 942	Absent	0.86	2.00	1.76	3.74	2.86	4.54	3.54	7.46	2.64	4.46
Arthroleptidae	<i>Schoutedenella sylvatica</i> Laurent, 1954	MCN 945	Absent	1.24	2.28	2.06	3.74	3.00	6.18	3.70	8.28	2.94	5.64
Bombinatoridae	<i>Bombina variegata</i> (Linnaeus, 1758)	MCN 810	Present	1.88	3.40	3.06	5.46	3.98	8.88	4.60	11.18	3.92	7.66
Brachycephalidae	<i>Eleutherodactylus discoidalis</i> (Peracca, 1895)	MCN 462	Absent	1.92	3.72	3.56	7.00	5.10	11.06	6.46	16.34	5.58	10.88
Brevicipitidae	<i>Breviceps poweri</i> Parker, 1934	FML 3165	Absent	2.34	3.76	3.28	5.00	4.26	6.86	5.14	9.00	2.94	4.62
Bufo	<i>Amitophrynus funereus</i> (Bocage, 1866)	RFL 302	Present	3.06	5.54	5.74	8.94	7.44	13.66	9.00	19.34	7.68	12.56
Bufo	<i>Chaunus granulatus</i> (Spix, 1824)	MCN 796	Present	2.82	4.94	4.46	7.58	6.34	10.60	7.76	16.28	6.52	10.14
Bufo	<i>Melanophryniscus rubriventris</i> (Vellard, 1947)	MCN 071	Present	2.04	4.16	3.64	6.12	4.86	8.06	6.00	12.34	5.14	8.96
Bufo	<i>Nannophryne variegata</i> Günther, 1870	MCN 018	Present	2.06	3.34	3.16	6.08	4.86	9.22	6.38	13.14	5.26	9.74
Centrolenidae	<i>Allophryne ruthveni</i> Gaige, 1926	MNHN (Montevideo) 00539	Present	1.27	2.28	2.29	4.00	2.87	6.02	3.26	8.24	3.03	6.36
Centrolenidae	<i>Centrolene notostictum</i> Ruiz-Carranza & Lynch, 1991	UIS 410	Present	2.00	3.44	3.00	5.08	3.58	7.16	4.12	9.84	3.46	7.36
Ceratophryidae	<i>Ceratophrys cranwelli</i> Barrio, 1980	MCN 819	Present	7.80	14.44	11.10	17.70	14.20	23.7	16.92	36.10	13.76	23.16
Ceratophryidae	<i>Chacophrys pieratii</i> (Vellard, 1948)	FML 2651	Present	1.98	3.40	3.00	5.30	4.04	7.50	5.10	10.96	4.18	7.66
Ceratophryidae	<i>Lepidobatrachus laevis</i> Budgett, 1899	MCN 109, MCN 695	Present	7.28	11.12	10.52	16.22	13.10	22.92	14.80	31.08	12.24	21.96
Ceratophryidae	<i>Lepidobatrachus llanensis</i> Reig & Cei, 1963	MCN 667	Present	4.50	7.36	7.88	10.46	8.84	14.74	10.10	21.16	8.00	14.98
Ceratophryidae	<i>Telmatobius oxycephalus</i> Vellard, 1946	MCN 438	Present	3.54	7.44	6.56	11.56	8.64	17.66	9.68	23.66	8.66	17.16
Cycloramphidae	<i>Odontophrynus americanus</i> (Duméril & Bibron, 1841)	MCN 105	Present	4.30	7.36	6.16	9.72	8.46	13.24	9.36	18.34	8.84	13.34

Family	Species	Catalogue number	Webbing	Metatarsal I length	Toe I length	Metatarsal II length	Toe II length	Metatarsal III length	Toe III length	Metatarsal IV length	Toe IV length	Metatarsal V length	Toe V length
Cyclorhynchidae	<i>Rhinoderma darwini</i> Duméril & Bibron, 1841	MCN 020	Present	1.28	2.44	2.26	4.46	3.66	7.00	4.38	10.88	3.76	6.76
Dendrobatidae	<i>Dendrobates truncatus</i> (Cope, 1861)	UIS 243	Absent	1.46	2.58	3.00	4.86	4.00	7.24	4.64	9.74	3.94	6.00
Dendrobatidae	<i>Ranitomeya violacea</i> (Ruiz-Carranza & Ramirez Pinilla, 1992)	UIS 132	Absent	0.96	1.20	1.44	2.16	2.34	3.76	2.84	5.86	2.14	4.34
Dicroglossidae	<i>Fejervarya limncharis</i> (Gravenhorst, 1829)	MNHN (Paris) 1987-2367	Present	1.33	–	2.45	–	3.19	–	3.59	–	3.28	–
Dicroglossidae	<i>Hoplobatrachus occipitalis</i> (Günther, 1858)	MCN 807	Present	10.22	17.52	15.06	25.72	18.38	35.56	19.70	48.00	16.74	33.12
Dicroglossidae	<i>Occidozyga laevis</i> (Günther, 1858)	MNHN (Paris) 1987-8698	Present	1.73	–	1.95	–	2.90	–	3.30	–	2.99	–
Hemistidae	<i>Hemistis guineensis</i> Cope 1865	FML 1244	Absent	3.60	4.66	4.82	6.28	5.94	9.74	6.6	12.78	5.26	8.04
Hylidae	<i>Argenteohyla siemersi</i> (Mertens, 1937)	FML 3954	Present	3.94	7.88	6.56	10.98	8.46	16.26	9.58	23.4	9.52	18.00
Hylidae	<i>Dendropsophus nanus</i> (Boulenger, 1889)	MCN 791	Present	2.56	4.22	3.46	6.28	4.16	8.76	4.84	11.80	4.16	9.64
Hylidae	<i>Hylomantis lemur</i> (Boulenger, 1882)	MCN 012	Absent	2.54	4.36	2.92	5.36	3.62	7.86	4.74	10.26	3.76	7.50
Hylidae	<i>Hypoxobas andinus</i> (Müller, 1926)	MCN 937	Present	3.88	7.36	5.64	10.00	7.86	16.20	8.74	20.00	8.36	17.70
Hylidae	<i>Isthmohyla rivularis</i> (Taylor, 1952)	MCN 013	Present	1.88	3.94	3.48	5.78	4.60	9.12	4.96	11.68	4.58	9.38
Hylidae	<i>Lysapsus limellum</i> Cope, 1862	FML 716	Present	2.56	4.00	3.74	5.46	4.36	8.14	4.00	9.86	4.34	8.34
Hylidae	<i>Phyllomedusa hypochondrialis</i> (Daudin, 1800)	FML 452	Absent	3.41	–	2.73	–	3.64	–	4.61	–	4.32	–
Hylidae	<i>Phyllomedusa sauuagii</i> Boulenger, 1882	MCN 795	Absent	4.18	9.36	3.96	7.94	6.40	12.96	8.16	21.00	7.16	15.52
Hylidae	<i>Pseudis paradoxa</i> (Linnaeus, 1758)	MCN 812	Present	5.16	7.58	8.00	11.16	8.26	13.56	8.38	15.56	8.56	14.56

Hylidae	<i>Scinax acuminatus</i> (Cope, 1862)	MCN 800	Present	2.76	5.40	4.86	7.86	5.50	11.12	6.10	13.92	5.76	11.52
Hylidae	<i>Scinax fuscovarius</i> (Lutz, 1925)	MCN 813	Present	1.92	4.00	3.62	5.46	4.32	8.00	4.76	10.78	4.14	8.38
Hylidae	<i>Scinax nasicus</i> (Cope, 1862)	MCN 156	Present	2.48	4.46	4.00	6.46	4.86	9.46	6.30	12.46	5.96	10.84
Hylidae	<i>Trachycephalus venulosus</i> (Laurenti, 1768)	FML 2712	Present	5.66	11.32	8.72	16.30	11.26	24.08	12.68	29.40	12.18	24.06
Hyperoliidae	<i>Afraxalus laevis</i> (Ahl, 1930)	RFL 16 g	Present	1.66	2.66	2.24	4.46	3.34	6.00	3.76	7.66	3.06	6.14
Hyperoliidae	<i>Afraxalus osorioi</i> (Ferreira, 1906)	MCN 994	Present	2.26	4.28	3.74	6.64	5.44	10.64	6.00	13.46	4.94	10.04
Hyperoliidae	<i>Afraxalus quadrivittatus</i> (Cope, 1861)	MCN 943	Present	2.00	3.72	3.52	5.58	4.14	7.36	4.96	10.00	3.84	7.46
Hyperoliidae	<i>Hyperolius castaneus</i> Ahl, 1931	MCN 833	Present	1.66	3.64	2.96	5.12	4.28	7.26	4.68	10.00	4.10	6.44
Hyperoliidae	<i>Hyperolius kiuuensis</i> Ahl, 1931	MCN 804	Present	2.26	4.88	3.80	6.46	4.80	9.16	5.72	13.34	5.34	11.00
Hyperoliidae	<i>Hyperolius marmoratus</i> Rapp, 1942	RFL 101fg	Present	1.62	2.86	3.16	5.00	3.42	6.38	4.24	9.00	3.68	8.24
Hyperoliidae	<i>Hyperolius viridiflavus</i> (Duméril & Bibron, 1841)	FML 3942	Present	2.16	3.16	3.76	6.06	4.14	8.48	5.26	11.88	4.46	9.90
Hyperoliidae	<i>Kassina senegalensis</i> (Duméril & Bibron, 1841)	MCN 823	Present	2.08	4.00	3.14	5.74	4.34	8.00	4.88	11.34	4.38	8.24
Hyperoliidae	<i>Opisthoxylax immaculatus</i> (Boulenger, 1903)	MCN 825	Present	2.16	4.14	3.16	5.46	4.06	7.66	4.88	9.74	4.32	8.30
Hyperoliidae	<i>Phlyctinantis verrucosus</i> (Boulenger, 1912)	MCN 832	Present	3.94	8.26	5.56	11.06	8.70	17.70	9.36	23.20	8.64	18.28
Leiuperidae	<i>Physalaemus biligonigerus</i> (Cope, 1861)	MCN 802	Absent	2.94	4.44	4.60	6.60	5.36	10.42	6.12	13.94	5.14	9.08
Leiuperidae	<i>Physalaemus santafecinus</i> Barrio, 1965	FML 937	Absent	2.62	4.00	4.20	6.74	5.16	9.40	6.50	12.94	4.88	9.28
Leiuperidae	<i>Pleurodema borellii</i> (Peracca, 1895)	MCN 379	Absent	2.16	4.28	4.76	7.94	6.74	12.14	8.26	17.44	6.16	11.36
Leiuperidae	<i>Pleurodema bufoninum</i> Bell, 1843	MCN s/n	Absent	3.54	5.54	5.60	8.44	7.00	12.96	8.24	17.00	6.98	12.76

Family	Species	Catalogue number	Webbing	Metatarsal I length	Toe I length	Metatarsal II length	Toe II length	Metatarsal III length	Toe III length	Metatarsal IV length	Toe IV length	Metatarsal V length	Toe V length
Leptodactylidae	<i>Leptodactylus bufonius</i> Boulenger, 1894	MCN 074	Absent	2.98	6.20	4.80	9.72	6.70	13.68	8.46	17.92	7.24	12.96
Leptodactylidae	<i>Leptodactylus chaquensis</i> Cei, 1950	MCN 039	Absent	5.60	10.22	9.88	17.70	13.22	26.42	14.62	37.28	13.00	26.52
Leptodactylidae	<i>Leptodactylus laticeps</i> Boulenger, 1918	FML 2187	Absent	4.64	6.94	6.28	11.24	8.34	16.00	9.86	21.00	8.24	15.24
Leptodactylidae	<i>Leptodactylus latinasus</i> Jiménez de la Espada, 1875	MCN 086	Absent	2.00	4.26	4.12	5.28	5.66	10.34	6.14	15.06	5.46	9.84
Limnodynastidae	<i>Lechriodus fletcheri</i> (Boulenger, 1890)	FML 03775	Present	3.00	5.00	5.00	8.90	8.26	14.94	9.46	21.34	8.16	15.84
Limnodynastidae	<i>Limnodynastes dumerilli</i> Peters, 1863	FML 3772	Present	2.58	4.06	4.14	7.56	5.34	11.4	5.94	15.48	4.94	9.66
Limnodynastidae	<i>Limnodynastes lignarius</i> Tyler, Martin & Davies, 1979	FML 3776	Present	1.68	2.66	2.86	4.92	4.34	8.6	5.00	11.80	3.66	7.32
Limnodynastidae	<i>Limnodynastes tasmaniensis</i> Günther, 1858	FML 3773	Present	3.18	6.00	5.58	9.70	7.30	15.14	8.38	20.68	6.92	14.10
Limnodynastidae	<i>Neobatrachus pictus</i> Peters, 1863	FML 3777	Present	3.92	5.20	6.14	9.04	8.00	13.78	9.10	19.60	7.32	12.26
Limnodynastidae	<i>Opisthodon spenceri</i> Parker, 1940	FML 3771	Present	3.22	4.54	4.80	7.60	6.40	11.36	7.30	15.00	5.84	9.80
Microhylidae	<i>Dermatonotus muelleri</i> (Boettger, 1885)	MCN 997	Absent	2.80	4.40	4.60	8.00	5.76	12.24	7.24	17.86	5.68	10.98
Microhylidae	<i>Elachistocleis bicolor</i> (Guérin-Méneville, 1838)	MCN 996	Absent	1.00	2.46	1.86	4.14	3.12	6.98	4.00	9.00	3.18	6.46
Microhylidae	<i>Gastrophryne carolinensis</i> (Holbrook, 1835)	FML 3365	Absent	1.06	2.28	2.38	3.94	3.22	6.66	4.32	9.48	3.00	5.58
Microhylidae	<i>Phrynomantis bifasciatus</i> (Smith, 1847)	MCN 880	Absent	2.84	5.36	4.36	8.00	5.54	10.66	6.96	15.36	6.14	12.34
Myobatrachidae	<i>Crinia signifera</i> (Girard, 1853)	FML 3778	Absent	1.38	2.42	2.06	4.22	3.16	6.60	3.92	9.64	2.78	5.76

Myobatrachidae	<i>Taudactylus diurnus</i> Straughan & Lee, 1966	FML 3774	Absent	1.04	2.06	2.24	4.06	3.28	6.10	3.82	8.72	3.08	5.78
Pelobatidae	<i>Pelobates cultripes</i> (Cuvier, 1829)	FML 3982	Present	5.76	8.38	8.94	13.06	10.28	18.3	11.53	25.00	9.12	17.22
Pelodytidae	<i>Pelodytes punctatus</i> (Daudin, 1802)	FML 3940	Present	2.46	4.36	3.74	7.36	5.46	11.76	6.14	15.10	4.84	9.40
Petropedetidae	<i>Conraua crassipes</i> (Buchholz and Peters <i>In</i> Peters, 1875)	MCN 834	Present	2.44	4.14	3.54	5.46	4.44	9.00	5.00	11.28	4.00	8.92
Phrynobatrachidae	<i>Phrynobatrachus acutirostris</i> Nieden, 1913	MCN 951	Present	4.22	7.00	6.86	10.74	8.40	16.04	9.68	24.72	8.60	16.58
Phrynobatrachidae	<i>Phrynobatrachus asper</i> Laurent, 1951	MCN 995	Present	1.78	2.46	2.36	4.00	3.18	6.64	3.96	9.14	3.48	6.78
Phrynobatrachidae	<i>Phrynobatrachus dendrobates</i> (Boulenger, 1919)	MCN 826	Present	2.46	–	4.00	–	5.00	–	5.58	–	4.84	–
Phrynobatrachidae	<i>Phrynobatrachus natalensis</i> (Smith, 1849)	MCN 824	Present	2.58	4.64	3.84	6.48	5.14	10.80	5.90	14.64	4.66	10.14
Phrynobatrachidae	<i>Phrynobatrachus petropedetoides</i> Ahl, 1924	MCN 948	Present	1.98	3.86	3.86	6.56	5.14	10.28	6.24	13.70	4.86	10.00
Phrynobatrachidae	<i>Phrynobatrachus sulfureogularis</i> Laurent, 1951	MCN 949	Present	3.18	–	4.60	–	5.52	–	6.48	–	5.00	–
Phrynobatrachidae	<i>Phrynobatrachus versicolor</i> Ahl, 1924	MCN 828	Present	2.08	3.96	4.14	6.76	5.76	11.34	7.16	15.68	5.54	10.32
Pipidae	<i>Hymenochirus boettgeri</i> (Tornier, 1896)	MCN 811	Present	5.28	6.78	6.78	9.24	7.38	12.46	6.98	11.86	6.48	10.04
Pipidae	<i>Pipa carvalhoi</i> Ruthven & Gaige, 1923	FML 2307	Present	9.00	12.52	11.00	16.38	11.24	21.54	11.42	21.72	12.00	18.74
Pipidae	<i>Pipa parva</i> (Miranda-Ribeiro, 1937)	FML 2856	Present	7.16	9.28	9.50	12.96	9.74	16.58	9.38	17.8	8.68	15.00
Pipidae	<i>Xenopus fraseri</i> Boulenger, 1905	RFL 186	Present	3.88	4.94	4.96	7.06	5.28	9.74	4.54	8.88	5.26	8.14
Pipidae	<i>Xenopus muelleri</i> (Peters, 1844)	RFL 242/2	Present	8.86	13.84	11.28	19.00	11.80	22.60	9.84	23.64	10.96	20.56
Pipidae	<i>Xenopus victorianus</i> Ahl, 1924	RFL 343	Present	4.84	5.94	5.78	9.94	7.60	13.60	7.24	12.24	7.00	10.88

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Ptychadenidae	<i>Ptychadena bibroni</i> (Hallowell, 1845)	MCN 999	Present	3.76	5.96	6.28	10.40	7.36	15.80	9.44	23.60	7.66	17.00
Ptychadenidae	<i>Ptychadena chrysogaster</i> Laurent, 1954	MCN 1000	Present	2.76	5.84	5.84	9.86	7.12	15.94	8.24	22.16	7.16	14.88
Ptychadenidae	<i>Ptychadena christyi</i> (Boulenger, 1919)	MCN 1001	Present	3.80	6.74	6.66	11.16	8.00	18.04	8.84	24.00	8.26	16.16
Ptychadenidae	<i>Ptychadena guibei</i> Laurent, 1954	RFL 163	Present	4.00	6.26	6.68	10.46	7.96	17.86	8.94	25.46	8.22	18.00
Ptychadenidae	<i>Ptychadena mascareniensis</i> (Duméril & Bibron, 1841)	MCN 820	Present	3.46	–	5.74	–	7.16	–	8.00	–	7.16	–
Ptychadenidae	<i>Ptychadena perreti</i> Guibé & Lamotte, 1958	MCN 837	Present	3.26	–	5.96	–	7.86	–	9.40	–	7.78	–
Ptychadenidae	<i>Ptychadena porosissima</i> (Steindachner, 1867)	MCN 838	Present	3.00	5.98	5.00	8.54	5.58	14.00	8.00	21.86	6.76	14.34
Ptychadenidae	<i>Ptychadena uzunguensis</i> (Loveridge, 1932)	MCN 839	Present	3.00	6.04	5.66	10.14	7.26	15.56	8.24	22.76	7.76	12.16
Pyxicephalidae	<i>Amietia angolensis</i> (Bocage, 1866)	MCN 803	Present	6.52	11.72	10.58	16.56	13.92	28.52	16.04	43.18	15.00	32.00
Pyxicephalidae	<i>Aubria subsigillata</i> (Duméril, 1856)	MCN 835	Present	1.36	2.86	2.06	4.44	2.76	6.16	3.66	7.90	2.64	5.46
Pyxicephalidae	<i>Pyxicephalus adspersus</i> Tschudi, 1838	MCN 806	Present	12.98	17.66	16.26	24.46	18.92	33.28	22.22	44.42	18.52	31.18
Ranidae	<i>Hydrophylax albolabris</i> (Hallowell, 1856)	MCN 805	Present	3.10	6.74	5.56	9.02	7.50	14.00	8.54	20.44	7.00	14.18
Rhacophoridae	<i>Chiromantis rufescens</i> (Günther, 1869)	MCN 831	Present	4.34	7.86	6.68	11.46	8.04	15.46	9.24	19.34	8.56	16.96
Scaphiropodidae	<i>Scaphiopus couchii</i> Baird, 1854	MCN 808	Present	4.82	7.18	7.62	10.74	9.56	15.76	11.02	20.94	9.12	13.76
Scaphiropodidae	<i>Spea bombifrons</i> (Cope, 1863)	MCN 809	Present	9.72	12.96	14.52	20.38	19.12	30.86	21.88	44.68	20.12	31.76