



A survey of prepollex and prehallux variation in anuran limbs

MARISSA FABREZI

Museo de Ciencias Naturales, Universidad Nacional de Salta, Mendoza 2, 4400-Salta, Argentina

Received October 1999; accepted for publication February 2000

This paper reviews skeletal variation of the prepollex and prehallux among anurans and analyses their ontogeny in neotropical species. Morphological diversity is related to the number and features of distal elements. In some groups, clear phylogenetic trends may be interpreted from prepollical and/or prehallux reduction. However, specialized patterns converge from similar habit or behaviour. Developmental data are considered for discussing homology hypotheses and also to interpret evolutionary changes of anuran prepollex and prehallux morphologies. There is an apparent invariance in the presence of these structures that suggests the prepollex and prehallux were integrated, conserved and evolved in the plan of anuran limbs. © 2001 The Linnean Society of London

ADDITIONAL KEY WORDS: limb plan – homology – limb development.

INTRODUCTION

The prepollex and prehallux are preaxial structures of the autopodium characteristic of anuran limbs and are reported in Devonian tetrapods (Coates & Clack, 1990; Levedev & Coates, 1995), temnospondyls (Gregory, Minner & Noble, 1923; Schaeffer, 1941), urodeles (Holmgren, 1933; Vorobyeva & Hinchliffe, 1996a), and some mammals (Gillies & Hopkins, 1922; Holmgren, 1933; Stafford & Thorington, 1998), although in this last group these structures were considered as sesamoids (Gillies & Hopkins, 1922). In spite of this range of occurrence, the prepollex and prehallux have received scant attention from morphologists and systematists, and have not been considered important in the ground plan of the tetrapod limb.

There are some hypotheses about prepollex and prehallux homologies based on analyses of anuran limbs. Howes & Ridewood (1888) believed that the anuran prepollex represented the first vestigial digit and the prehallux also represented a vestigial and supernumerary digit. These authors considered the prehallux segmented structure as a primitive condition among anurans. Gillies & Hopkins (1922) proposed that the prepollical and prehallux skeletal elements were non-homologous with those present in some mammal groups, and identified the prepollex and prehallux

elements as homologous with metacarpals/metatarsals and phalanges of true digits. They supported the hypothesis of ancestral heptadactyly and hexadactyly in tetrapods by these arguments. Andersen (1978) compared the musculature of different anuran limbs and emphasized that the differences between the muscles of the prepollex and prehallux refute the serial homology hypothesis. He concluded that the prepollex represents the reduced digit I and the prehallux is not a true digit. Shubin & Alberch (1986) described the differentiation of digits from a series of morphogenetic events involving condensation, branching, and segmentation in the postaxial axis of the limb; while in the preaxial axis, condensation and segmentation events produce a discrete proximal autopodium element (radiale/tibiale). They described in urodele and anuran limbs, the development of other preaxial elements distal to the radiale/tibiale, identifying them as Element Y and prepollex/prehallux. In anurans, prepollex and prehallux primary cartilages arise from the preaxial axis in proximodistal sequence after the differentiation of Element Y, and before digital arch formation has concluded (Schmalhausen, 1907; Holmgren, 1933; Saint-Aubain, 1981; Fabrezi & Alberch, 1996). Currently, the interpretation of autopodium elements is in agreement with the morphogenetic approach proposed by Shubin & Alberch (1986) and in these terms prepollex and prehallux would not be homologous with digit or digit elements.

E-mail: museo@ciunsa.edu.ar

Prepollical or prehallical cartilages were not observed during the limb development of urodeles (Saint-Aubain, 1981; Dinsmore & Hanken, 1986; Blanco & Alberch, 1992; Vorobyeva & Hinchliffe, 1996a) but a prehallical element or a well developed prehallux appear among variants of the adult tarsus of *Salamandrella keyserlingii* (Vorobyeva & Hinchliffe, 1996a) and *Triturus* sp. (Rienesl & Wagner, unpublished observations). In contrast to urodeles, anurans always have a prepollex and prehallux. The only exceptions to this generalization are the absence of a prepollex reported in *Crinia signifera* and *Osornophryne bufoniformis* (Andersen, 1978) and the absence of a prehallux observed in some pipids (Howes & Ridewood, 1888). The widespread presence of prepollex and prehallux among anurans is an important reason for studying these structures from several perspectives.

Some hypotheses about phylogenetic and taxonomic aspects, and morphological considerations of prepollex and prehallux among anurans were developed some time ago; however, these analyses considered limited samples of intraordinal variability (Andersen, 1978; Gillies & Hopkins, 1922; Howes & Ridewood, 1888). Phylogenetic changes have been proposed for a few anuran taxa (Graybeal & Cannatella, 1995; Lobo, 1995; Lynch & Ruiz-Carranza, 1996) but there are no studies focused on morphological diversity at the suprageneric level because most of morphological features of the prepollex and/or prehallux included in taxonomic descriptions are irrelevant without a general approach to the diversity of these structures among the anurans.

In the last 20 years, the tetrapod limb has been one of the most important subjects of evolutionary biology with new evidence from phylogenetic, morphological, morphogenetic, and genetic perspectives that contribute to interpreting the fin to limb transition and limb evolution (Vorobyeva & Hinchliffe, 1996b). On this basis, the prepollex and prehallux, as components of some tetrapod limbs, should be analysed again. Here I undertake a comparative study of anuran limbs as a first step to interpreting evolutionary trends in the prepollex and prehallux. I survey prepollex and prehallux diversity among anurans, and in addition, I include information on their development in some taxa. The primary aim of this paper is an understanding of prepollex and prehallux patterns of diversification and developmental changes involved in the basic plan of anuran limbs.

MATERIAL AND METHODS

Most of the specimens—adults and tadpoles—were cleared and double stained with Alcian blue and Alizarin red (Wassersug, 1976). Some specimens—dry skeletons, X-ray films or whole mounts stained only

with Alizarin red—are deposited in the Laboratoire des Reptiles et Amphibiens (Museum National d'histoire Naturelle, Paris) and were provided by Dr Alain Du-bois.

Larval specimens examined here were between stages 37 and 46 (Gosner, 1960) when differentiation of preaxial cartilages occurs (Fabrezi & Alberch, 1996).

Specimens of 110 species of Pipanura (Ford & Cannatella, 1993) were analysed. The species, specimen numbers, and collection data are listed in Appendix I. Where no reference is cited, the observations are based on the present study.

Chondrification was attributed to those structures stained with Alcian Blue while mineralization and ossification were confirmed with Alizarin Red S. In some cases it is possible to see the difference between mineralization and ossification because mineralization is observed as diffuse spots in a cartilaginous matrix whereas ossification appears as uniform coloration in the whole structure.

The organization of descriptions and literature data follows the phylogenetic classification proposed by Ford & Cannatella (1993) and the taxonomic status of different taxa to the genus level agrees with Frost (1985) and Duellman (1993).

Abbreviations of museums

FML: Instituto de Herpetología, Fundación Miguel Lillo, Tucumán (Argentina); MCN: Museo de Ciencias Naturales, Universidad Nacional de Salta (Argentina); MNHN: Museum National d'histoire Naturelle, Paris (France); RFL: Dr Raymond F. Laurent personal collection.

RESULTS

PREPOLLEX AND PREHALLUX VARIATION AMONG ADULT SPECIMENS

Anura

Vieraella herbstii (Báez & Basso, 1996): prepollex and prehallux were not preserved.

Notobatrachus degiustoi (Báez & Basso, 1996): prepollex formed by two elements, the distal one large.

Ascaphus truei (Andersen, 1978; Ritland, 1955): prepollex formed by two elements, the proximal element similar in size to other carpal elements and the distal one larger and pointed. Prehallux formed by two elements, the proximal one small, and the distal one large and pointed.

Leiopelmatanura (*Leiopelma* + *Bombinanura*)

Leiopelma hochstetteri (Cannatella & Trueb, 1988): prepollex formed by two large elements, the distal one pointed.

Bombinanura (Bombinatoridae + Discoglossanura)

Eodiscoglossus santojae (Estes & Reig, 1973): prepollex formed by four short pieces, the second one more developed. Prehallux formed by two small bones.

Bombinatoridae

Bombina bombina (Howes & Ridewood, 1888): prepollex formed by three elements. Prehallux formed by two elements, the distal one smaller. *Bombina orientalis* (Maglia & Púgener, 1998): prepollex formed by four elements that decrease in size distally, the terminal one diminutive. Prehallux with three elements, the two distal ones smaller. Schmalhausen (1907) drew the prepollex of *Bombina variegata* tadpole with a pointed distal cartilage.

Discoglossanura

(Discoglossidae + Mesobatrachia + Neobatrachia)
Discoglossidae

Discoglossus pictus (Andersen, 1978; Howes & Ridewood, 1888; Jarosova, 1973, 1974): prepollex formed by two elements, the distal one expanded. Prehallux formed by two elements, the distal one smaller. *Discoglossus sardus* (Pugener & Maglia, 1997): prepollex formed by two elements and the prehallux of three small elements. Prepollex ossification occurs after metamorphosis, and prehallux ossification and mineralization begin in proximal and distal elements respectively before metamorphosis.

Alytes cisternasii, *A. muletensis* and *A. obstetricans* (Sanchiz, 1984): prepollex formed by two elements, the distal one smaller. The proximal element is ossified in *A. cisternasii* and *A. obstetricans* and cartilaginous in *A. muletensis*. Prehallux formed by two cartilaginous elements in *A. muletensis*.

Pipanura (Mesobatrachia + Neobatrachia)
Mesobatrachia (Pelobatoidea + Pipoidea)
Pelobatoidea
(Megophryidae + Pelobatidae + *Pelodytes*)

Megophryidae

Megophrys montana (Howes & Ridewood, 1888): prepollex formed by two elements, the distal one very small and thin. Prehallux is a small element.

Pelobatidae

Pelobates cultripes, *P. fuscus* and *P. syriacus* (Andersen, 1978; Howes & Ridewood, 1888): prepollex formed by two elements, the distal one small and thin. Prehallux formed by two small elements.

Scaphiopus intermontana (Trueb, 1996: 368): prepollex formed by two elements, the distal one pointed. Prehallux formed by two elements, the distal one axehead-shaped.

Spea bombifrons (Wiens, 1989): prepollex formed by three elements, the two distal ones elongated. The

prepollex is the last structure to ossify in the forelimb, and its distal element is not ossified. Prehallux formed by two elements, the distal one large, flattened, and axehead-shaped. The prehallux distal element supports the keratinized spade typical of pelobatids and is the first to ossify, but its tip remains cartilaginous.

Pelodytidae

Pelodytes punctatus (Howes & Ridewood, 1888; Fabrezi, 1992, 1993): prepollex formed by two elements, the distal one large and expanded, with evidence of segmentation. Prehallux formed by two elements that form a hammer-shaped structure; the distal element with a dorsal process.

Pipoidea (Pipidae + Rhinophrynidae)
Rhinophrynidae

Rhinophrynus dorsalis (Trueb, 1996): prepollex formed by two elements, the distal one reduced. Prehallux present and formed by two elements, the distal one large and axehead-shaped. These prehallux features were mentioned among synapomorphies of fossil and extant Rhinophrynidae (Ford & Cannatella, 1993).

Pipimorpha
'Pipid' fossils

Saltenia ibanezi (Báez, 1981): prepollex formed by one element and prehallux formed by two elements, the distal one elongated and pointed.

Cordicephalus gracilis (Estes & Reig, 1973): prepollex formed by a single element and prehallux with two elements.

Paleobatrachidae

Paleobatrachus sp. (Jarosova, 1973; 1974): prepollex absent (but could have been present or not present). Prehallux formed by three elements, the proximal one narrowed in its middle part (hourglass-shaped), and in its distal end forming a plane or convex head attached to the second element. The latter is elongated and moderately widened in its proximal part. The terminal element is a minute, triangular ossicle.

Pipidae

Pipa pipa (Howes & Ridewood, 1888), *Pipa carvalhoi* and *P. parva*: prepollex formed by a single element. Prehallux absent.

Xenopus vestitus (Trueb, 1996: 368): prepollex formed by a single element. Prehallux formed by two elements, the distal one conical and elongated.

The key for species identification of members of the genus *Xenopus* (Kobel, Loumont & Tinsley, 1996) points out that the prehallux is not evident externally in *X. largeni* and *X. gilli*. Saint-Aubain (1981) analysed forelimb development in *X. laevis* and described the prepollical distal element as a preaxial free chondrification. She suggested that the prepollical proximal

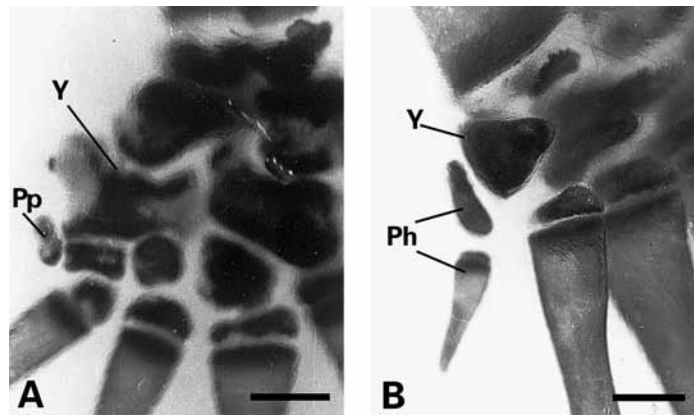


Figure 1. *Xenopus wittei*. A, ventral view of carpal bones (right hand). B, ventral view of preaxial tarsal bones (right foot). Scale bar=0.5 mm. Abbreviations: Ph, prehallal elements; Pp, prepollical elements. Y, Element Y.

element could be incorporated into Element Y. In the same species, Holmgren (1933) described a single prehallal element. In *X. fraseri* and *X. wittei* (Fig. 1A, B) the prepollex is formed by a single element lateral to the Element Y and not related to metacarpale II. The prehallux is formed by two elements, the distal one conical and elongated.

Hymenochirus boettgeri: prepollex formed by a single small element. Apparently, the prehallux is absent; although two ventral elements—associated with the articulation tibiale and metatarsals I and II and hidden by plantar sesamoids—could be prehallal elements.

Neobatrachia
 Bufonoidea
 'Myobatrachidae'

Limnodynastes tasmaniensis (Howes & Ridewood, 1888): prepollex formed by two elements, the distal one pointed. Prehallux formed by two elements, the distal one with a conspicuous dorsal process. *Limnodynastes fletcheri* (Andersen, 1978): prepollex formed by two elements, the distal one pointed.

Neobatrachus pictus: prehallux formed by two elements, the distal one elongated and axehead-shaped.

Pseudophryne bibroni (Howes & Ridewood, 1888): prepollex formed by two elements, the distal one pointed. Prehallux formed by two elements.

Crinia signifera (Andersen, 1978): prepollex absent. Prehallux formed by two elements, the distal one pointed. In this study, the prehallux is regarded as similar to Andersen's description.

Geocrinia laevis and *G. victoriana* (Gollman, 1991): prepollex formed by two elements, the distal one smaller and pointed. Prehallux formed by two elements, the distal one smaller. Skeletal variations affecting the number of prehallal elements and their ossifications were described in hybrid populations of these two species (Gollman, 1991).

Sooglossidae

Sooglossus sechellensis and *Nesomantis thomasseti* (Laurent, unpublished observations): prepollex formed by two elements, the distal one elongated and pointed. 'Leptodactylidae'

Batrachyla nibaldoi (Formas, 1997: 11): prepollex formed by two elements, the distal one longer. Prehallux formed by two elements, the distal one expanded laterally.

Hylorina sylvatica (Lavilla & Lobo, 1992): prepollex formed by three elements that decrease in size distally, the distal one cartilaginous. Prehallux formed by four segments incompletely ossified.

Telmatobius schreichteri (Andersen, 1978): prepollex formed by three small elements. Prehallux formed by a single element. *Telmatobius yuracare* (de la Riva, 1994): sexually dimorphic prepollical structures were described. The prepollex of the male is formed by six segments (the distal one remains cartilaginous) and the prepollex of female is formed by two or three cartilaginous elements. The prehallux is cartilaginous at its end.

Ceratophrys ornata and *Odontophrynus americanus* (Howes & Ridewood, 1888): prepollex formed by three well-defined and ossified elements that join to form a stout structure. Prehallux formed by two elements, the proximal one is spherical and the distal one is axehead-shaped and has a pronounced dorsal process. Wild (1997) described limb ossification processes of *Ceratophrys cornuta*. Prepollical elements are ossified in the adult. The prehallux is the last hind limb structure to ossify and the distal prehallal element retains its ventral part, cartilaginous or mineralized. *Ceratophrys cranwelli*, *Lepidobatrachus laevis*, *Odontophrynus americanus* (Fig. 2A,B) and *O. lavillai*: prepollex formed by three short elements that decrease in size distally. Prehallux formed by two elements, the

proximal one is large and articulated with the distal axehead-shaped bone.

Leptodactylus albilabris and *L. pentadactylus* (Howes & Ridewood, 1888): prepollex formed by three elements. Prehallux formed by four small elements. *Leptodactylus bufonius* (Fig. 2C), *L. chaquensis* and *L. latinus* (Fig. 2D): prepollex formed by three or four ossified or mineralized elements of similar size. They have irregular shapes, present constrictions, and are joined by connective tissue in a strong structure. Mineralized spots are found in this mass of connective tissue. Prehallux formed by three mineralized segments; sometimes the distal ones are cartilaginous.

Physalaemus pustulosus (Andersen, 1978): prepollex formed by two elements. Prehallux formed by two elements, the distal one small and spheroid. *Physalaemus fernandezae*, *P. biligonigerus*, *P. maculiventris*, *P. cuvieri*, *P. nattereri*, *P. henseli*, *P. gracilis*, *P. riograndensis* (Lobo, 1995): prepollex formed by two elements in most species; in *P. maculiventris* three prepollical elements were observed. Prehallux formed by three elements in *P. henseli* and *P. riograndensis*, and two elements in the other species. *Physalaemus biligonigerus* (Fig. 2E,F) and *P. cuqui*: prepollex formed by three segments of similar size. The distal element is short and pointed. A mineralized piece is attached to the intermediate element. Prehallux formed by two elements, the distal one enlarged and pointed. The prehallux distal element is more developed and ossified in *P. biligonigerus*.

Pseudopaludicola boliviana, *P. ceratophyes*, *P. falcipes*, *P. llanera*, *P. mineira*, *P. mystacalis*, *P. pusilla*, *P. ternetzi*, and *P. saltica* (Lobo, 1995): prepollex formed by three elements in *P. ceratophyes*, *P. falcipes*, *P. mineira*, *P. ternetzi* and *P. saltica*, and two elements in the others. Prehallux formed by three elements in *P. falcipes*, *P. ternetzi* and *P. saltica*, and two in most of other species (prehallux is not described in *P. ceratophyes*).

Pleurodema borellii (Fig. 2G) and *P. cinerea* (Fig. 2H): prepollex formed by three short elements, the distal one pointed. In *P. cinerea*, the prepollex is cartilaginous. Prehallux formed by four short segments, the distal one smaller and pointed. Prehallux is mineralized in *P. borellii* and is cartilaginous in *P. cinerea*.

Brachycephalidae

Brachycephalus ephippium (Andersen, 1978): prepollex minute, formed by two elements. Prehallux absent. Alberch & Gale (1985: 10, 11) illustrated one prehallux element in *Psyllophryne didactyla* and *Brachycephalus ephippium*.

Bufonidae

Atelopus farci (Lynch, 1993: 83): prepollex formed by two elements, the distal one as long as metacarpal

II. *Atelopus ignescens* (Andersen, 1978): prepollex formed by two small elements. Prehallux formed by a single element.

Osornophryne bufoniformis (Andersen, 1978): prepollex absent. Prehallux formed by three elements.

Truebella skoptes and *T. tothastes* (Graybeal & Cannatella, 1995): prepollex formed by a spherical element. Prehallux formed by two elements in *T. skoptes* and three in *T. tothastes*.

Bufo calamita (Howes & Ridewood, 1888): prehallux formed by three small elements. *Bufo arenarum*, *B. funereus*, *B. granulatus* (Fig. 3A,B), and *B. paracnemis*: prepollex stout, formed by two elements. The distal prepollical element is pointed in *B. arenarum*, *B. granulatus*, and *B. paracnemis*, blunter in *B. funereus*. Prehallux formed by two or three short elements joined by a half moon of dense connective tissue on its external border.

Melanophryniscus rubriventris: prepollex formed by two small elements, the distal one small and blunt. Prehallux formed by two elements, the distal one smaller.

Rhinodermatidae

Rhinoderma darwinii (Howes & Ridewood, 1888): prepollex formed by one element. Prehallux formed by two elements. Andersen (1978) described the prepollex of this species as formed by two elements, the distal one smaller, and the prehallux formed by a single element. Fabrezi (1992, 1993) described two prepollical elements, and two prehallux elements, the distal one almost vestigial.

Centrolenidae

Centrolene prosoblepon (Andersen, 1978): prepollex formed by three segments, the distal one flattened. Centrolenids (Lynch & Ruiz-Carranza, 1996): ossified prepollex that is usually composed of a single element, but sometimes three elements, with nuptial excrescence externally. These authors illustrated the skeleton of the hands of *Centrolene notostictum* and *Cochranella ruizi* and showed that distal elements conform to a long and pointed structure. The prepollex in this group forms a prepollical spine that may or not may be concealed. In *Cochranella spinosa* the tip of the prepollical spine protrudes through the skin.

Hylidae

Hyla albopunctata, *H. arborea*, *Calyptahyla echinata*, *Gastrotheca marsupiata* (Howes & Ridewood, 1888): prepollex formed by two elements, the proximal one has a medial constriction, and the distal one is only a single piece (although it may appear segmented or constricted into two segments); in *H. albopunctata* which belongs to the group with an 'external prepollex', the distal element is very expanded and pointed at the end. Prehallux formed by four segments, the proximal

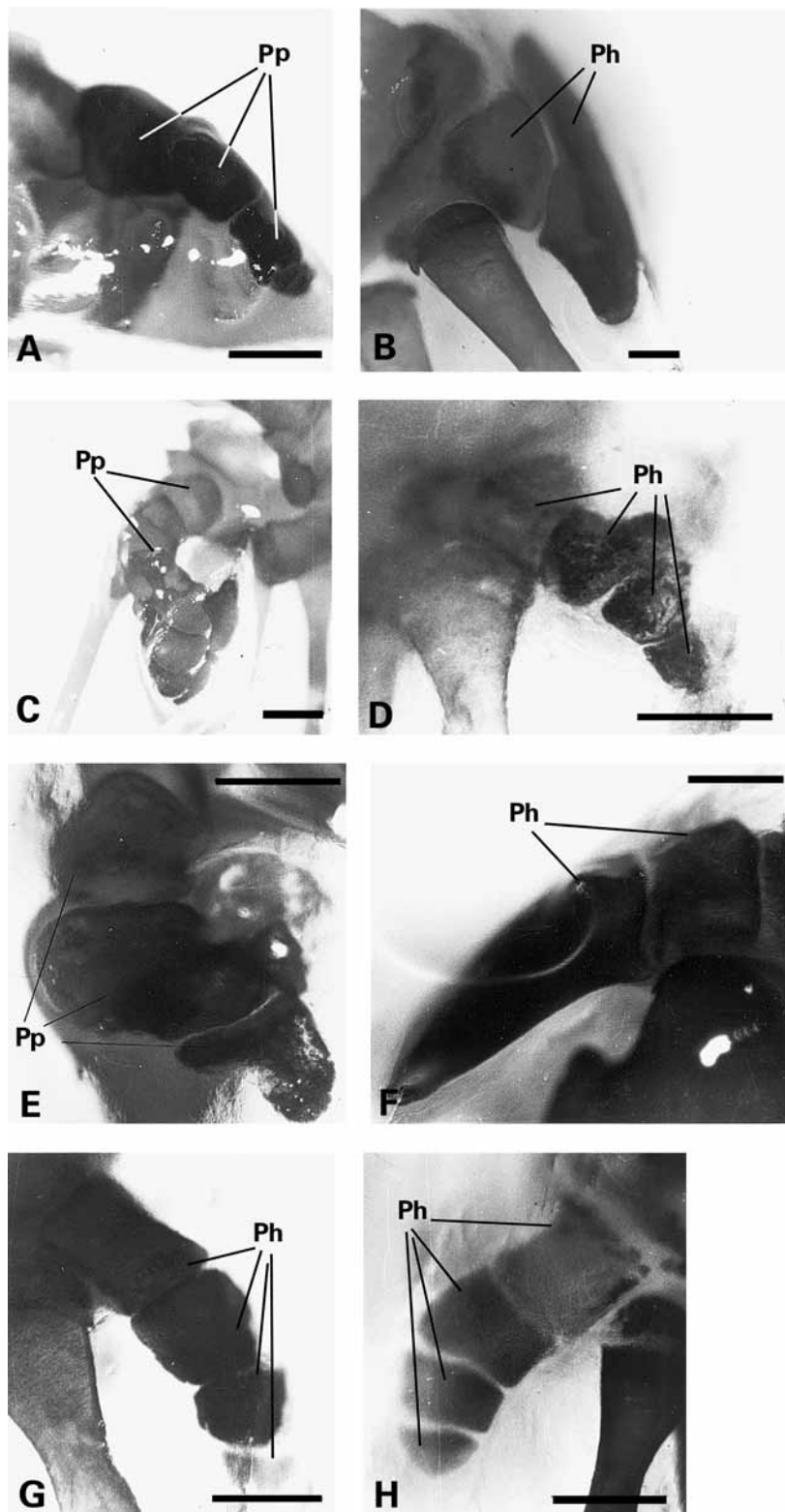


Figure 2. A, *Odontophrynus americanus* prepollex (left hand). B, *O. americanus* prehallux (left foot). C, *Leptodactylus bufonius* prepollex (right hand). D, *Leptodactylus latinasus* prehallux (left foot). E, *Physalaemus biligonigerus* prepollex (right hand). F, *P. biligonigerus* prehallux (right foot). G, *Pleurodema borelii* prepollex (left hand). H, *Pleurodema cinerea* prehallux (right foot). Scale bar=0.5 mm. Abbreviations as in Figure 1.

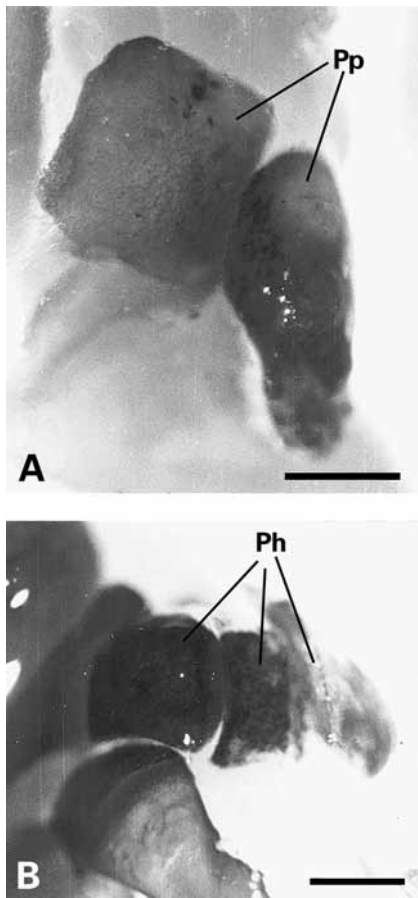


Figure 3. *Bufo granulosis*. A, prepollex (left hand). B, prehallux (left foot). Scale bar = 0.5 mm. Abbreviations as in Figure 1.

one is large and the distal ones are minute. *Hyla rosebergi* (Kluge, 1981): prepollex formed by two articulated bones, the distal one elongated and curved with a terminal spine that protrudes through the skin in males. *Hyla andina* (Fig. 4A,B), *H. minuta*, *H. nana*, *H. raniceps* and *Phrynohyas venulosa*: prepollex formed by two articulated bones. The proximal one is spheroid the distal element has a well-developed dorsal process and its base is expanded. Distally, this prepollical element narrows and forms a pointed tip well developed as a spine in *H. andina* and *H. raniceps*. In *H. andina* the distal prepollical element is as long as metacarpal II and the terminal spine protrudes through the skin. Prehallux formed by two elements, the proximal one is cubic, and the distal one is short, cartilaginous and has a small dorsal process. The prehallux in these species is formed by two elements, the distal one is small.

Pachymedusa dacnicolor and *Phyllomedusa hypochondrialis* (Howes & Ridewood, 1888): prepollex formed by two elements, the proximal one has a medial

constriction, and the distal one is a single piece. Prehallux formed by three elements. *Phyllomedusa savagii* (Fig. 4C): prepollex formed by two elements, the proximal one is articulated with the distal one, which is knife-shaped with a narrow base and has a cartilaginous external border. Prehallux formed by three small elements, the distal ones cartilaginous.

Scinax x-signatus (Howes & Ridewood, 1888): prepollex formed by two articulated elements. Prehallux formed by four elements. *Scinax fuscovarius* (Fig. 4D, E) and *S. nasicus*: prepollex formed by four pieces; the second one is longer and slender, the distal piece is small and spheroid and only the proximal element is ossified. Prehallux formed by four short elements, the proximal one is ossified.

Pseudidae

Pseudis paradoxa (Howes & Ridewood, 1888, this study): prepollex formed by two elements, the distal one elongated. Prehallux formed by two elements, the distal one enlarged.

Lysapsus limellus: prepollex formed by two elements, the distal element is not as developed as in *Pseudis paradoxa*. Prehallux formed by two small bones.

Ranoidea 'Ranidae'

Rana temporaria and *R. pipiens* (Howes & Ridewood, 1888): prepollex formed by two elements. Prehallux formed by up to five elements. The proximal one may be ossified in *R. pipiens*. Distal elements (2 to 4) are small, the third may bear a small dorsal process. They are joined by a mass of connective or cartilaginous tissue. Even when the prehallux is ossified, the elements remain distinct.

Nannophrys ceylonensis and *N. guentheri* (Clarke, 1983: 386): prepollex and prehallux formed by two elements.

Micrixalus fuscus, *Rana cubitalis*, *R. lateralis*, *R. humeralis*, *R. sierramadrensis*, *R. warszewitschii*, *Chaparana aenea*, *Paa fasciculispina*, and *P. feae*: prepollex formed by two elements, the distal one is pointed except in *P. fasciculispina* and *P. feae*, in which it is expanded, strong and curved.

Ingerana sp. (Fig. 5A,B): prepollex formed by two ossified elements, the proximal one is spheroid and the distal one has an expanded base and slender blunt tip. The distal prepollical element has an external cartilaginous edge. Prehallux formed by only one cuboid element.

Conraua crassipes (Fig. 5C,D): prepollex and prehallux cartilaginous. Prepollex formed by three elements forming a conical structure. The prehallux is hammer-shaped, with evidence of joints between its elements. The elements are: proximal, intermediate (with three pieces, one of which has a dorsal process) and two distal cartilages at the tip.

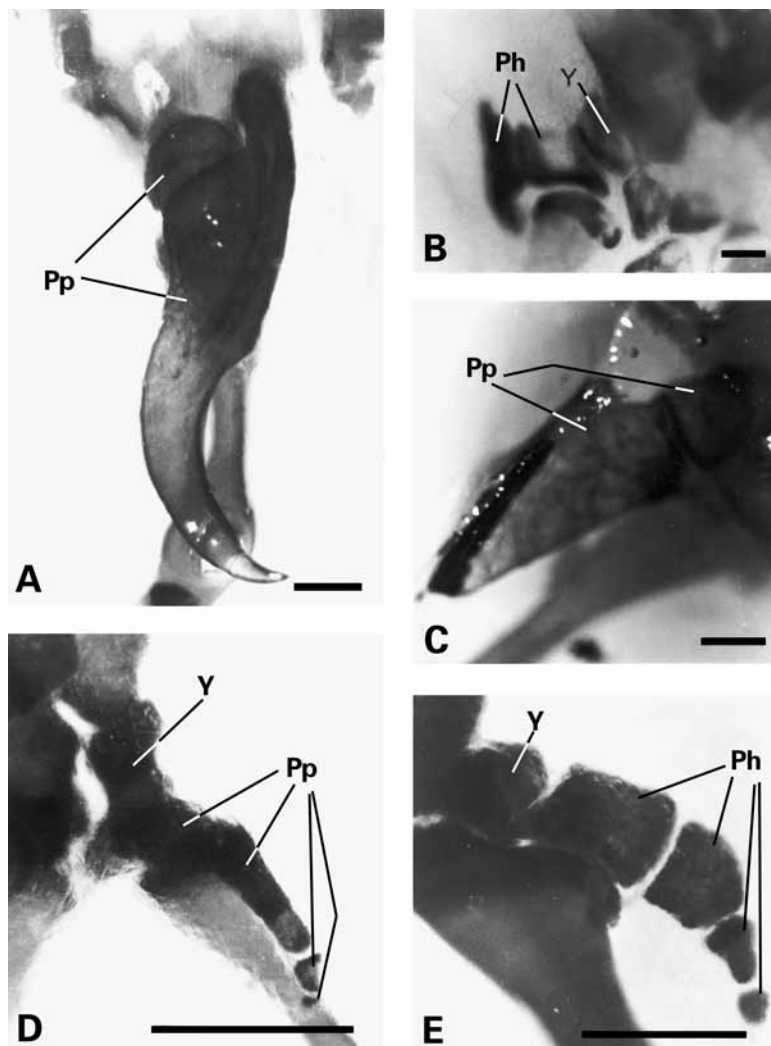


Figure 4. A, *Hyla andina* prepollex (left hand). B, *H. andina* prehallux (right foot). C, *Phyllomedusa sawagii* prepollex (right hand). D, *Scinax fuscovarius* prepollex (left hand). E, *S. fuscovarius* prehallux (left foot). Scale bar = 0.5 mm. Abbreviations as in Figure 1.

Phrynoglossus laevis: prepollex formed by two osseous elements, the distal one is elongated, flat and has a blunt tip. Prehallux formed by four osseous pieces. They are joined in a hammer-shaped structure with a cartilaginous external edge.

Hoplobatrachus occipitalis (juvenile): prepollex formed by two cartilaginous pieces, the distal one pointed. Prehallux formed by four short cartilaginous elements, the distal one pointed and the second cartilage bears a small dorsal process. The elements are united by a mass of connective tissue.

Limnonectes limnocharis: prepollex formed by two ossified pieces, the proximal one is spheroid and the distal one is large and flattened, with a cartilaginous edge. Prehallux formed by four ossified elements joined in a hammer-shaped structure with a cartilaginous external edge.

Aubria subsigillata (juvenile) (Fig. 5E,F): prepollex formed by two elements, the distal one conical. Prehallux formed by four short segments, the second has a dorsal process. Prepollex and prehallux are cartilaginous and present spots of mineralization.

Ptychadena aequiplicata, *P. christyi*, *P. chrysogaster*, *P. guibei*, *P. mascareniensis*, *P. perreti*, *P. porosissima*, and *P. uzungwensis* (Fig. 6A,B): prepollex formed by two elements, the proximal one is spherical and the distal one is elongated and expanded. Prehallux formed by three short elements, the intermediate one has an incipient dorsal process, and the distal one is very small and may be cartilaginous.

Phrynobatrachus acutirostris, *P. asper* (Fig. 6D), *P. dendrobates*, *P. natalensis*, *P. petropedoides*, *P. sulfureogularis* (Fig. 6C), and *P. versicolor*: prepollex formed by three elements, the two distal ones form a

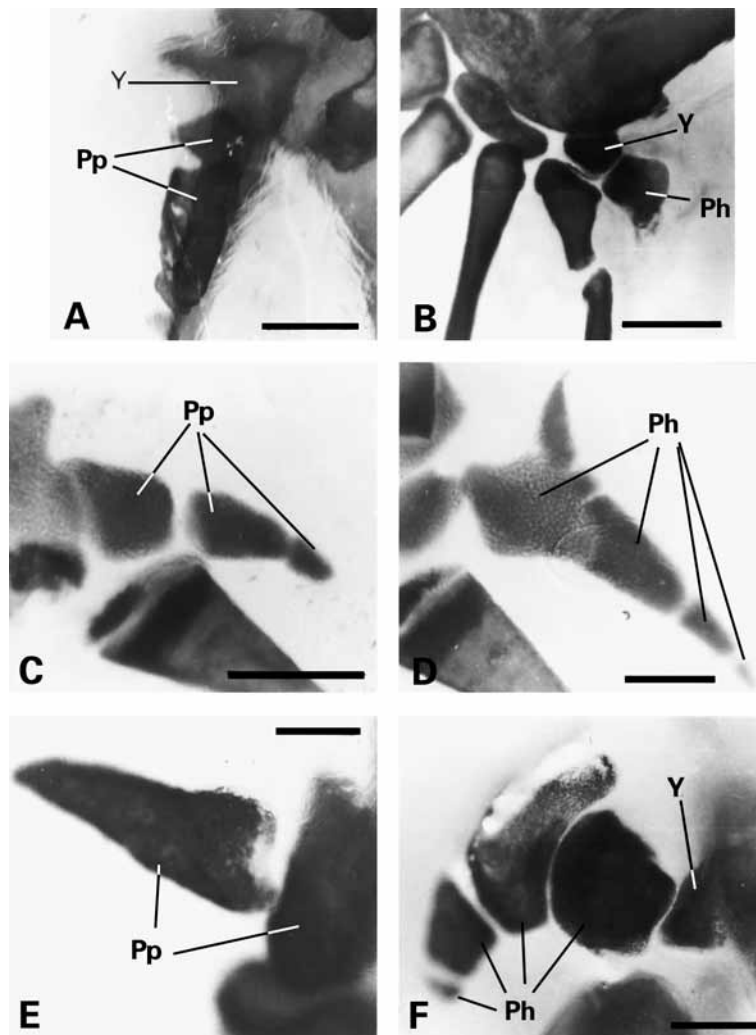


Figure 5. A, *Ingerana* sp. prepollex (right hand). B, *Ingerana* sp. prehallux (left foot). C, *Conraua crassipes* prepollex (left hand). D, *C. crassipes* prehallux (left foot). E, *Aubria subsigillata* prepollex (right hand). F, *A. subsigillata* prehallux (right foot). Scale bar=0.5 mm. Abbreviations as in Figure 1.

slender and conical structure. Prehallux formed by three elements, the distal one is very small and spheroid, the larger middle one has an incipient dorsal process. In *P. asper*, a small and free cartilage seems to be an incipient dorsal process. Both prepollex and prehallux are cartilaginous and present spots of mineralization.

Mantellidae

Mantella cowani, *M. betsileo*, *Mantidactylus betsileanus*, *M. biporus*, *M. boulengeri*, *M. curtus*, *M. elegans*, *M. femoralis*, *M. madecassus*, and *M. pulcher*: prepollex formed by two elements, the distal one short and conical. Prehallux formed by three small elements except in *Mantidactylus betsileanus* and *M. femoralis*, in which there are four small pieces.

Arthroleptidae

Astylosternus diadematus (Fig. 7A,B): prepollex formed by three cartilaginous elements. The middle element is long and conical, and the distal one is a small and oval cartilage. Prehallux formed by two joined cartilages, the distal one is axehead-shaped.

Arthroleptis adolfifriederici (Fig. 7C,D), *A. poecilonotus* (Fig. 7G), *A. stenodactylus* and *A. variabilis*: prepollex formed by a single element in *A. stenodactylus*. In the other species, the prepollex is formed by two elements, the distal one is short and pointed. Prehallux formed by a hammer-shaped structure (with an incipient dorsal process) in *A. adolfifriederici* and the prehallux is developed and axehead-shaped in *A. poecilonotus*.

Arthroleptis hematogaster, *A. pyrrhoscelis* (Fig. 7E),

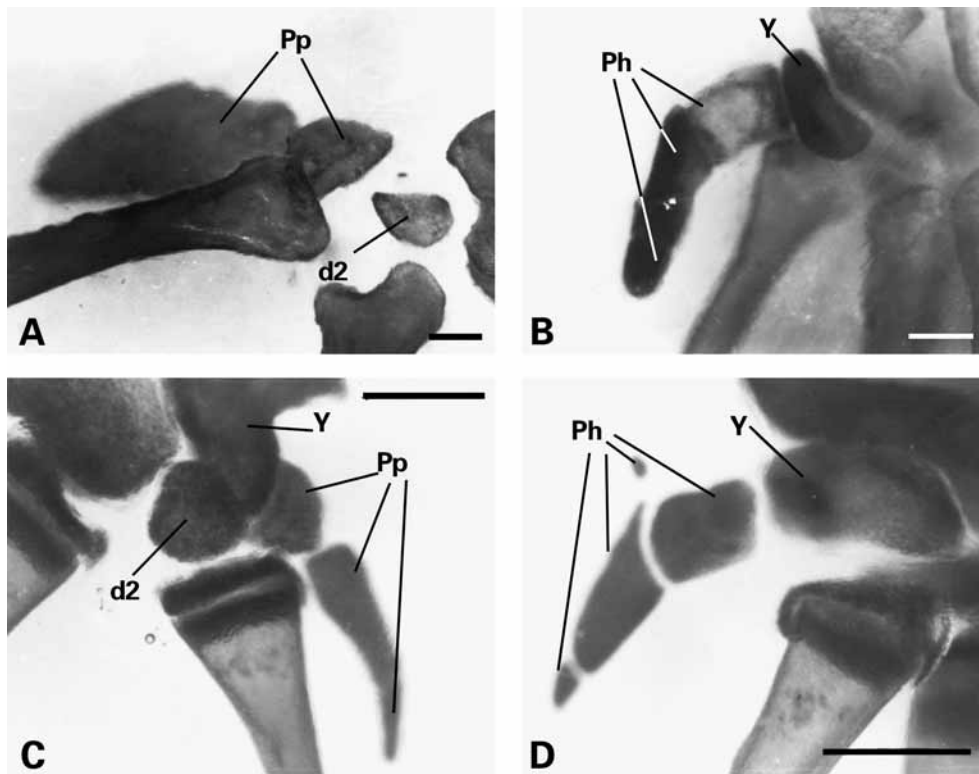


Figure 6. A, *Ptychadena uzungwensis* prepollex (right hand). B, *P. uzungwensis* prehallux (right foot). C, *Phrynobatrachus sulfureogularis* prepollex (left hand). D, *P. asper* prehallux (right foot). Scale bar = 0.5 mm. Abbreviation: d2, distal carpal 2: Other abbreviations as in Figure 1.

A. schubotzi, *A. sylvaticus*, *Cardioglossa cyaneospila* (Fig. 7F) and *C. leucomystax*: prepollex formed by a single, minute and spherical element. Prehallux formed by a single and rectangular element in *Arthroleptis* spp. that shows more development in its distal portion in *C. cyaneospila*. In *C. leucomystax*, the prehallux has three elements. Prepollex and prehallux are cartilaginous or partially mineralized.

Hyperoliidae

Afrixalus fulvovittatus, *A. laevis*, *A. osorioi*, *Hyperolius castaneus* (Fig. 8C), *H. marmoratus*, *Kassina angeli*, *K. senegalensis*, *Leptopelis christyi* (Fig. 8A,B), *Opisthohylax immaculatus*, and *Phlyctimantis verrucosus*: prepollex and prehallux are cartilaginous. Prepollex formed by two elements, the proximal one spherical and the distal one conical and elongated. Prehallux formed by two very closely joined elements; in *Afrixalus* spp. the distal prehallux element has a dorsal process that is not well developed.

Rhacophoridae

Aglyptodactylus madagascariensis, *Boophis luteus*, *B. tephraeomystax*, and *Chiromantis rufescens*: prepollex formed by two elements, the distal one very long (as long as metacarpal II in *B. luteus*) and pointed. Prehallux

formed by four small pieces in *A. madagascariensis* and *B. luteus* and two elements in the others.

Dendrobatidae

Colostethus subpunctatus, *Dendrobates auratus* (Fig. 9A,B), and *Epipedobates pictus*: prepollex formed by two elements, the proximal one is spherical and the distal one is smaller, short and conical. Prehallux formed by two small elements joined by a cartilaginous edge; the distal one has a small dorsal process.

Hemisotidae

Hemisis guineensis: prehallux formed by two elements, the distal one longer, expanded proximally and axehead-shaped.

Microhloidea

Scaphiophrynidae

Scaphiophryne calacarata and *S. marmorata*: prepollex formed by two short elements. Prehallux formed by two pieces, the well developed distal one is axehead-shaped.

Microhylidae

Breviceps mossambicus and *B. poweri* (Laurent, 1942; and this study): prepollex formed by a single

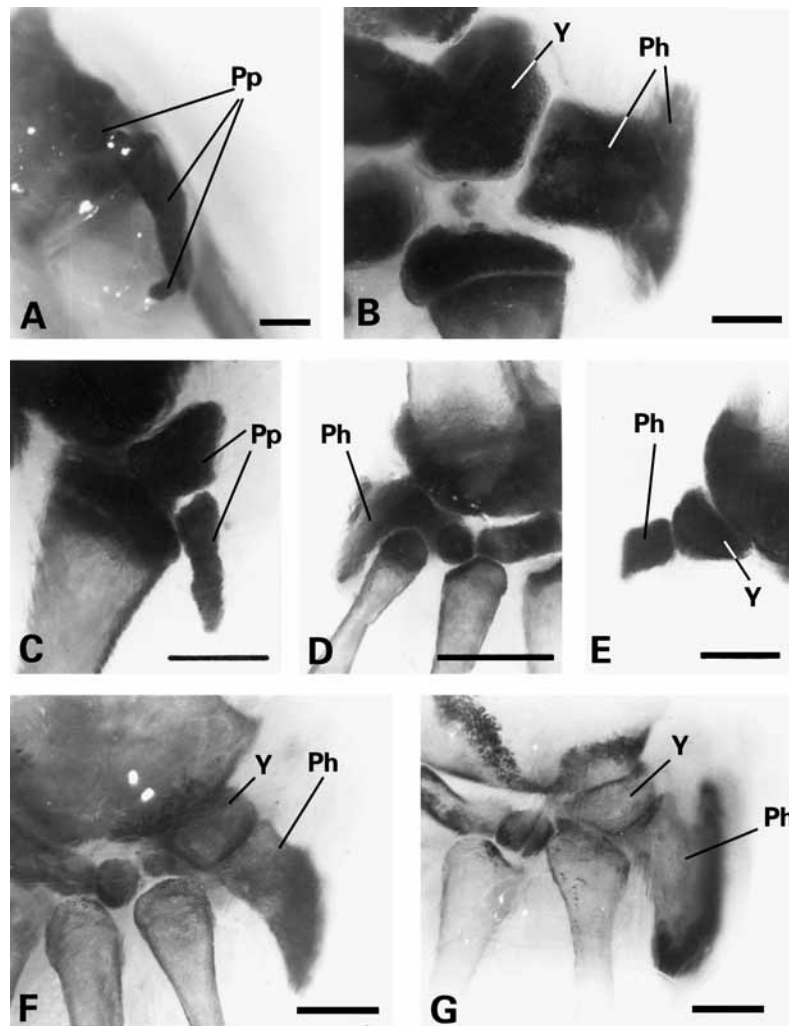


Figure 7. A, *Astylosternus diadematus* prepollex (left hand). B, *A. diadematus* prehallux (left foot). C, *Arthroleptis adolfriederici* prepollex (left hand). D, *A. adolfriederici* prehallux (right foot). E, *A. pyrrhoscelis* prehallux (right foot). F, *Cardioglossa cyaneospila* prehallux (left foot). G, *Arthroleptis poecilnotus* prehallux (left foot). Scale bar = 0.5 mm. Abbreviations as in Figure 1.

element. Prehallux formed by two elements, the distal one axehead-shaped.

Phynomantis bifasciatus (Fig. 10A,B): prepollex formed by two elements, the proximal one quadrangular and the distal one conical, with a wide base. Prehallux formed by three pieces, the terminal one stout and attached to the intermediate element.

Dermatonotus muelleri, *Elachistocleis bicolor*, *Gastrophryne carolinensis*, *G. olivacea*, and *Hypopachus variolosus*: prepollex formed by two elements, the proximal one spheroid and larger than the distal one, which is short and truncated.

Tables 1 and 2 show a taxonomic synthesis of prepollex and prehallux variation among anuran taxa.

PREPOLLEX AND PREHALLUX DEVELOPMENT

The differentiation of prepollical and prehallucal cartilages in the species analysed occurs in larval stages distal to Element Y, and in a proximodistal sequence. In the species in which the Element Y of the forelimb displays a complex origin (three condensations, Fabrezi & Alberch, 1996), such as hylids, bufonids, and leptodactylids; the proximal prepollical element appears after the condensations differentiate but before they fuse. Ossification or mineralization of prepollical and prehallucal cartilages were not observed during larval stages; they occur in juvenile or adult stages.

In *Xenopus laevis* the prepollical element appears during metamorphic larval stages, after the os-

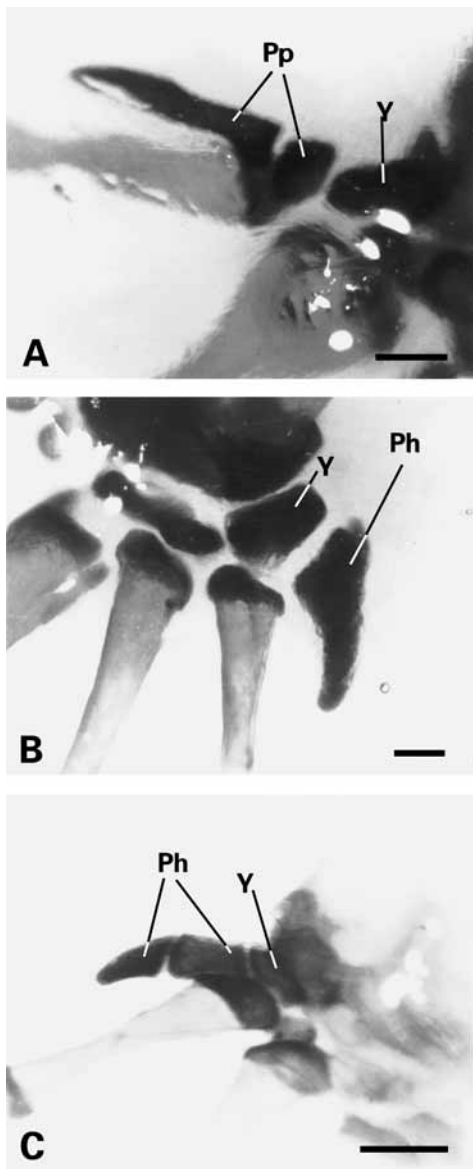


Figure 8. A, *Leptopelis christyi* prepollex (right hand). B, *L. christyi* prehallux (left foot). C, *Hyperolius castaneus* prehallux (right foot). Scale bar=0.5 mm. Abbreviations as in Figure 1.

sification of the radioulna and metacarpals. The prehallical proximal element is evident in pre-metamorphic stages, before the differentiation of metatarsal I and distal tarsal 1; the distal prehallical element arises in metamorphic stages when the ossification in the proximal tarsalia and metatarsalia is advanced.

In *Ceratophrys cranwelli*, *Lepidobatrachus laevis* (Fig. 11E), *Odontophrynus americanus*, and *O. lavillai* (Fig. 11F) the proximal prepollical cartilage differentiates at larval stage 36, when distal carpal 2 and metatarsal II have just developed; distal prepollical

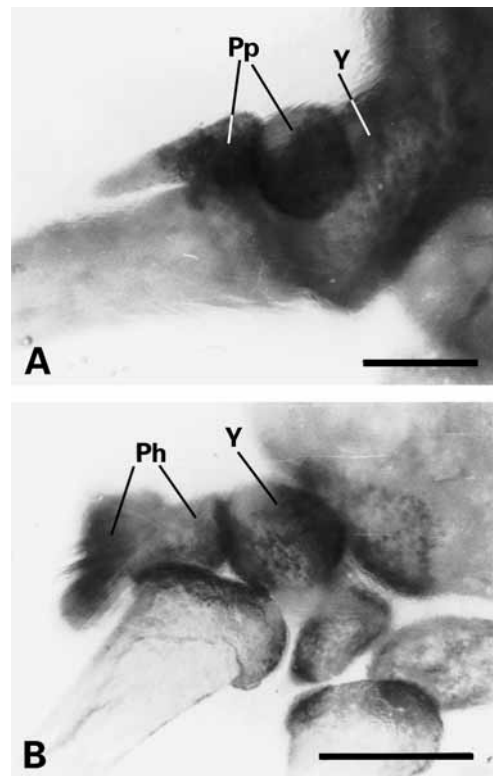


Figure 9. *Dendrobates auratus*. A, prepollex (right hand). B, prehallux (right foot). Scale bar=0.5 mm. Abbreviations as in Figure 1.

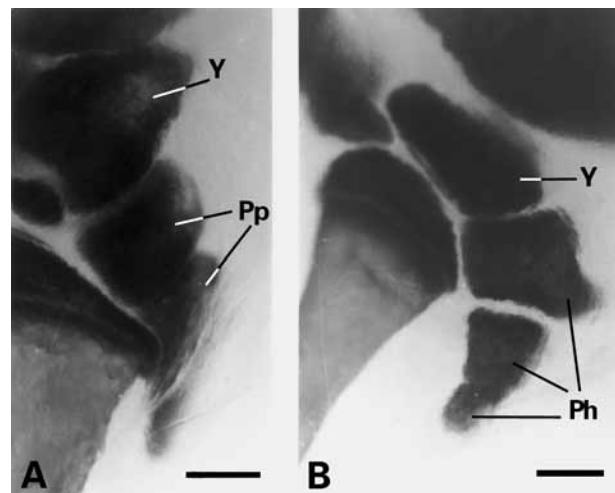


Figure 10. *Phrynomantis bifasciatus*. A, prepollex (left hand). B, prehallux (left foot). Scale bar=0.5 mm. Abbreviations as in Figure 1.

cartilages arise between larval stages 38 and 41. The proximal prehallical cartilage develops at larval stage 38 and the distal one at larval stage 39, growing quickly and becoming axehead-shaped immediately.

In *Bufo paracnemis*, *Leptodactylus bufonius* (Fig.

Table 1. Summary of taxonomic distribution of different prepollex patterns among anurans

Prepollex	Taxa examined in this study	Taxa examined in other studies
Absent		Bufonidae (Andersen, 1978) Myobatrachidae (Andersen, 1978)
Two elements; the distal one more or less developed	Bufonidae Dendrobatidae Hyperoliidae Mantellidae Microhylidae Myobatrachidae Pseudidae Ranidae	<i>Ascaphus truei</i> (Andersen, 1978, Ritland, 1955) Bufonidae (Andersen, 1978) Discoglossidae (Andersen, 1978; Howes & Ridewood, 1888; Jarosova, 1973; Pügener & Maglia, 1997) <i>Leiopelma hochstetteri</i> (Cannatella & Trueb, 1988) Leptodactylidae (Andersen, 1978; Formas, 1997; Lobo, 1995) Myobatrachidae (Andersen, 1978; Gollman, 1991; Howes & Ridewood, 1888) Pelobatoidea (Andersen, 1978; Fabrezi, 1992; Howes & Ridewood, 1888; Trueb, 1996) Pseudidae (Howes & Ridewood, 1888) Ranidae (Clarke, 1983; Howes & Ridewood, 1888) Rhinodermatidae (Andersen, 1978; Fabrezi, 1992) Rhinophrynidae (Trueb, 1996) Sooglossidae (Laurent, unpublished observations)
One proximal element	Arthroleptidae Microhylidae Pipidae	Brachycephalidae (Andersen, 1978) Bufonidae (Graybeal & Cannatella, 1995) Microhylidae (Laurent, 1942) Pipimorpha (Báez, 1981; Estes & Reig, 1973; Howes & Ridewood, 1888; Saint-Aubain, 1981; Trueb, 1996)
Three or more elements; the distal ones decrease in size distally and are not articulated	Arthroleptidae Hylidae Leptodactylidae	Bombinatoridae (Howes & Ridewood, 1888; Maglia & Pügener, 1998) Centrolenidae (Andersen, 1978) <i>Eodiscoglossus santojae</i> (Estes & Reig, 1973) Leptodactylidae (Andersen, 1978; De la Riva, 1994; Howes & Ridewood, 1888; Lavilla & Lobo, 1992; Lobo, 1995) Pelobatidae (Wiens, 1989)
Two elements; the distal one hypermorphic	Hylidae Ranidae Rhacophoridae	Bufonidae (Lynch, 1993) Centrolenidae (Lynch & Ruiz-Carranza, 1996) Hylidae (Andersen, 1978; Howes & Ridewood, 1888; Kluge, 1981)

11A), *L. chaquensis* and *L. latinasus*, *Physalaemus biligonigerus* prepollical and prehallal cartilages are differentiated between larval stages 38 and 42.

In hylids, proximal prepollical cartilage develops before the differentiation of distal carpal 2 takes place. In *Hyla andina* the prepollical proximal cartilage is developed at larval stage 36. The distal prepollical cartilage arises at larval stage 38 and grows quickly; at larval stage 40 it is as long as metacarpal II and has a dorsal process and terminal spine well developed (Fig. 11B). In *Phrynohyas venulosa*, prepollex development begins at larval stage 37 and ends during metamorphosis (stage 43). It involves three elements (Fig. 11C); the intermediate one is expanded and the distal one is a small spherical cartilage that fuses with the intermediate to form a pointed prepollical distal

element as is found in the adult. In *Scinax nasicus* and *S. fuscovarius* the prepollical cartilages differentiate between larval stages 37 and 42. In the hylid species analyzed, prehallal cartilages are differentiated between larval stages 38 and 42.

In *D. muelleri*, prepollical and prehallal cartilages differentiate between larval stages 37 and 42. The proximal cartilage of prepollex arises before the differentiation of distal carpal 2 and metacarpal II.

DISCUSSION

PREPOLLEX AND PREHALLUX HOMOLOGY

Digit development from condensation, branching and segmentation in the postaxial axis is an argument

Table 2. Summary of taxonomic distribution of different prehallux patterns among anurans

Prehallux	Taxa examined in this study	Taxa examined in other studies
Absent	Pipidae	Pipidae (Howes & Ridewood, 1888)
Two elements; the distal one more or less developed	Arthroleptidae Bufonidae Dendrobatidae Hylidae Hyperoliidae Leptodactylidae Microhylidae Myobatrachidae Pipidae Pseudidae Rhacophoridae	<i>Ascaphus truei</i> (Andersen, 1978; Ritland, 1955) Bombinatoridae (Howes & Ridewood, 1888) Bufonidae (Graybeal & Cannatella, 1995) Discoglossidae (Andersen, 1978; Howes & Ridewood, 1888; Jarosova, 1974; Sanchiz, 1984) <i>Eodiscoglossus santोजae</i> (Estes & Reig, 1973) Hylidae (Howes & Ridewood, 1888) Leptodactylidae (Andersen, 1978; Formas, 1997; Lobo, 1995) Myobatrachidae (Andersen, 1978; Gollman, 1991; Howes & Ridewood, 1888) Pelobatidae (Andersen, 1978; Howes & Ridewood, 1888) Pelodytidae (Fabrezi, 1993; Howes & Ridewood, 1888) Pipidae (Trueb 1996) Pseudidae (Howes & Ridewood, 1888) Ranidae (Clarke, 1983) Rhinodermatidae (Fabrezi, 1993; Howes & Ridewood, 1888)
One proximal element	Arthroleptidae Ranidae	Brachycephalidae (Alberch & Gale, 1985) Bufonidae (Andersen, 1978) Leptodactylidae (Andersen, 1978) Megophryidae (Howes & Ridewood, 1888)
Three or more elements; sometimes the distal ones are joined by connective or cartilaginous tissue in a hammer-shaped structure	Arthroleptidae Bufonidae Hylidae Leptodactylidae Mantellidae Microhylidae Ranidae Rhacophoridae	Bombinatoridae (Maglia & Pügener, 1998) Bufonidae (Andersen, 1978; Graybeal & Cannatella 1995; Howes & Ridewood, 1888) Discolossidae (Pügener & Maglia, 1997) Hylidae (Howes & Ridewood, 1888) Leptodactylidae (Howes & Ridewood, 1888; Lavilla & Lobo, 1992; Lobo, 1995) Paleobatrachidae (Jarosova, 1974) Ranidae (Howes & Ridewood, 1888)
Two elements; the distal one hypermorphic and related to a keratinized structure	Arthroleptidae Hemisotidae Leptodactylidae Microhylidae Myobatrachidae	Leptodactylidae (Howes & Ridewood, 1888; Wild, 1997) Microhylidae (Laurent, 1942) Pelobatidae (Trueb, 1996; Wiens, 1989) Rhinophrynidae (Ford & Cannatella, 1993; Trueb, 1996)

for interpreting the prepollex and prehallux as non-homologous with true digits or phalanges because these structures develop from the preaxial axis without branching (Shubin & Alberch, 1986). Further evidence includes the following:

(1) Sequence of digital development is posterior to anterior. The most anterior digit is the last to differentiate (Hinchliffe, 1991; Shubin & Alberch, 1986). In some taxa, such as hylids and microhylids, prepollical and prehallal primary cartilages differentiate before the end of digit development in

premetamorphic tadpoles. If the prepollex or prehallux are the most anterior digits they should develop always at the end.

(2) Digital reduction in anurans affects anterior digits (Alberch & Gale, 1985). In *Atelopus farcii* (Lynch, 1993) the distal prepollical element is as long as metacarpal II, but this digit has only one phalanx. Other taxa, with digital reduction in pes illustrated by Alberch & Gale (1985) have one or two prehallal elements and digit I reduced or lost. The widespread occurrence of prepollical and pre-

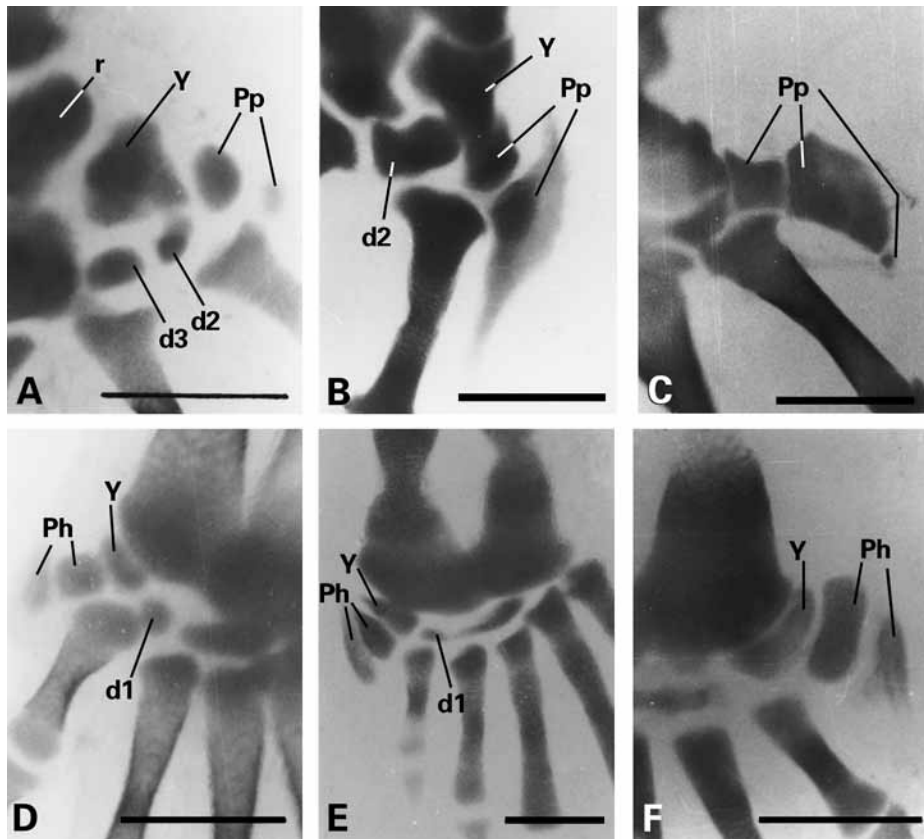


Figure 11. A, *Leptodactylus bufonius*, primary carpal cartilages in a stage 39 tadpole (left hand). B, *Hyla andina*, primary carpal cartilages in a stage 41 tadpole (left hand). C, *Phrynohyas venulosa*, primary carpal cartilages in a stage 42 tadpole (left hand). D, *Scinax fuscovarius*, primary tarsal cartilages in a stage 41 tadpole (right foot). E, *Odontophrynus americanus*, primary tarsal cartilages in a stage 41 tadpole (right foot). F, *Lepidobatrachus laevis*, primary tarsal cartilages in a stage 42 tadpole (left foot). Scale bar=0.5 mm. Abbreviations: d3, distal carpal 3. r, radiale. d1, distal tarsal 1. Other abbreviations as in Figures 1 and 6.

hallical elements—even in anurans with digital reduction—suggests the independence of processes of digit and prepollex/prehallux origin.

Developmental evidence also indicates that these structures share spatial and temporal features implying they are determined by developmental constraints (Wagner, 1994). Therefore, I suggest that the prepollex and prehallux represent biological homology in the terms of Wagner's concept (1994).

PREPOLLEX AND PREHALLUX IN TETRAPOD LIMBS

As noted above, the prepollex and prehallux are present in some non-anuran taxa. Saint-Aubain (1981) compared several traits of lissamphibian limbs and presented a phylogeny showing the prepollex as primitive character; she also proposed that the prepollex reduction represents an independently derived condition in urodeles and some anurans. Fossil taxa closely related to anurans (Rage & Rocek, 1989; Shubin &

Jenkins, 1995) are not helpful because autopodial elements are not preserved. The *Eryops* carpus (Gregory *et al.*, 1923) and the *Trematops* tarsus (Schaeffer, 1941) have well-conserved prepollices and prehallices and an intermediate bone between the radiale/tibiale and the prepollex/prehallux proximal element that could be interpreted as the Element Y present in lissamphibians. Prepollical and prehallical elements have also been described in Devonian tetrapods (Coates & Clack, 1990; Levedev & Coates, 1995).

The early appearance of the prepollex and prehallux in the autopodium is an argument for interpreting them as primitive characters in extant anurans. Even when the fossil record is discontinuous, it suggests that there was an early divergence in the ground plan of limbs, from which amphibians have more elements in the preaxial axis (Element Y, prepollex/prehallux) than amniotes. The prepollex and prehallux could be also considered derived characters evolved independently in several tetrapods. Unfortunately, the

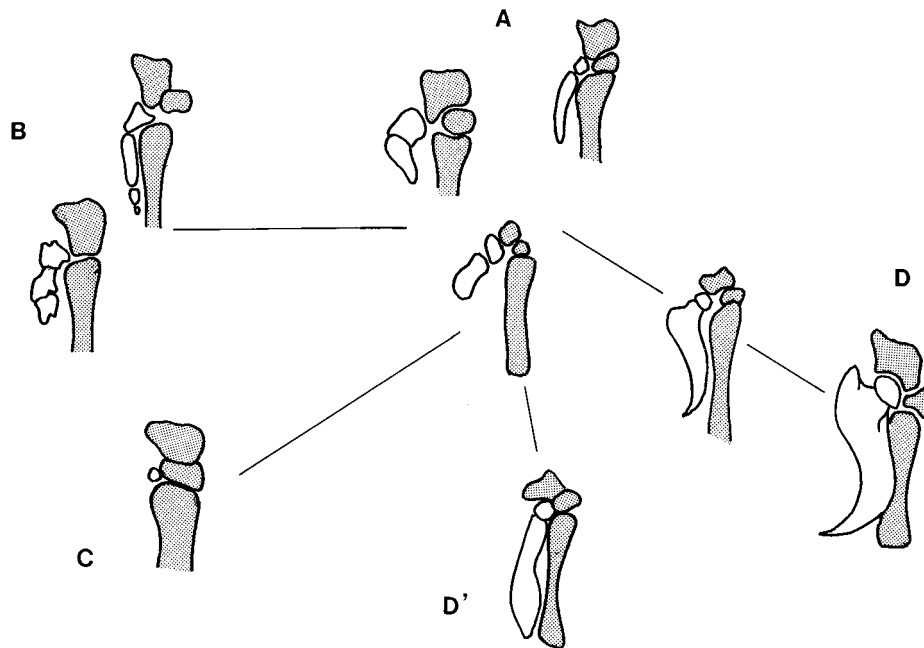


Figure 12. Schematized hypothesis of evolutionary changes of prepollex based on developmental changes. A, prepollex formed by two elements, the distal one more or less developed. B, prepollex formed by three or more cartilaginous or mineralized elements. C, prepollex formed only by the proximal element. D and D', prepollex formed by two elements, the distal one hypermorphic. Gray elements are Element Y, distal carpal 2, and metacarpal II.

incompleteness of the amphibian fossil record makes it difficult to interpret the phylogenetic occurrence of the prepollex and prehallux in extinct taxa. However, phylogenetic analysis of the prepollex and prehallux among tetrapods needs a global reinterpretation of the components of the autopodium of fossil groups.

PREPOLLEX AND PREHALLUX IN ANURANS

The anuran prepollex and prehallux are integrated structures in the limb plan. From the analysis presented, it is possible to propose some generalizations: (1) they are quite constant structures; (2) morphological diversity displays proximal stability and distal variability; (3) morphological diversity of prepollex or prehallux seems to be independent of each other; (4) even when morphological diversity displays clear phylogenetic trends in some groups, convergence resulting from similar habits or behaviour is common. In order to explore these generalizations, I propose that there is a generalized and widespread morphology from which derived or specialized morphologies originated by developmental changes involving absence of prepollex/prehallux, non-differentiation of the distal element, increase in the element numbers, and hypermorphism of the distal element. This hypothesis is schematized in Figures 12 and 13.

Absence of the prepollex was described in two unrelated species (Andersen, 1978) and should be confirmed, while absence of the prehallux is observed in

some pipids. Absence of the prehallux in *Pipa* spp. and *Hymenochirus* spp. may be related to the extreme specialization of the tarsal elements with reduction of distal tarsalia, Element Y, and the presence of extra ossification on the tarsus plantar face (Fabrezi, 1993).

The most widespread morphology has two distinct elements, the distal one more or less developed. Anurans with this prepollical and prehallux pattern have inner metacarpal/metatarsal tubercles well developed. It is possible that the primary roll of the prepollex and prehallux is related to the interaction with skin structures.

Reduction or loss of distal prepollical elements is observed in Pipoidea (fossil and extant taxa) and some Neobatrachia. Among Pipoidea, a reduced distal prepollical element was observed in rhinophrynids (Trueb, 1996), while most pipids present only the proximal prepollical element. Prepollex features could have phylogenetic value in this monophyletic group (Cannatella & Trueb, 1988). In Neobatrachia, the loss of the distal prepollical element occurs in some genera of Bufonidae, Arthroleptidae, and Microhylidae. Graybeal & Cannatella (1995) pointed out that the presence of a single prepollical element is unusual and derived in Bufonidae—they found it in *Truebella*, *Crepidophryne* and *Pedostibes*. Because only *Pedostibes* has a spherical element, as in *Truebella*, they suggested that the prepollex condition represents a synapomorphy of *Truebella*, if the two taxa are not

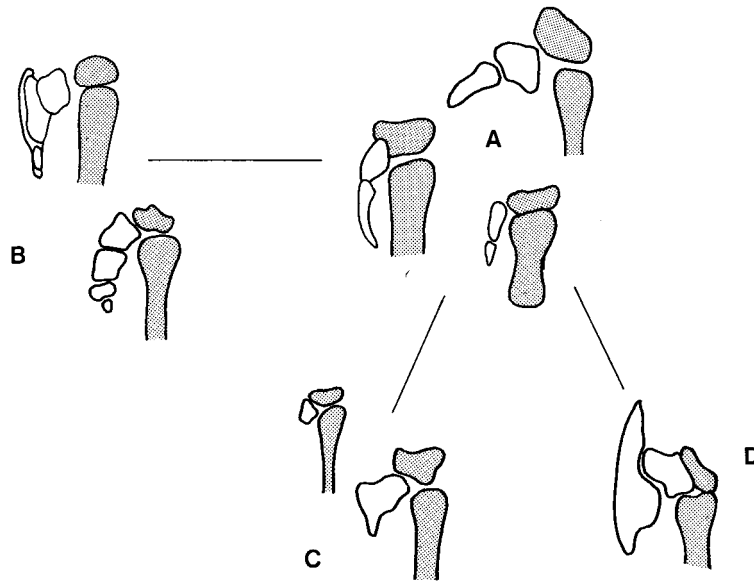


Figure 13. Schematized hypothesis of evolutionary changes of prehallux based on developmental changes. A, prehallux formed by two elements, the distal one more or less developed. B, prehallux formed by three or more cartilaginous or mineralized elements, sometimes forming a hammer-shaped structure. C, prehallux formed only by the proximal element. D, prehallux formed by two elements, the distal one hypermorphic. Grey elements are Element Y and metatarsal II.

closely related. In Arthroleptidae, *Cardioglossa* spp., *Arthroleptis hematogaster*, *A. pyrrhoscelis*, and *A. schubotzi* share the absence of distal element. Curiously, these species of *Arthroleptis* previously were placed in the genus *Schoutedenella*, closely related to *Cardioglossa* (Laurent, 1973).

Reduction or loss of prehallical distal element is found in *Megophrys montana* (Howes & Ridewood, 1888) and some neobatrachians. In brachycephalids, morphological consequences of a miniaturization process affect the last structures formed in development (Alberch & Gale, 1985). In arthroleptids, *Cardioglossa cyaneospila* and the same species of *Arthroleptis* previously mentioned lack of the distal prehallical element. Apparently, among anurans the condition of the prepollex and prehallux are independent each other, but in the case of these species, distal prepollical and prehallical reductions occur simultaneously. Evolutionary explanations for this occurrence should be directed toward the size reduction exhibited in these species. Phylogenetic relationships could merge using prepollical and prehallical traits in the systematic analysis of arthroleptines.

A prepollex and a prehallux with three or more skeletal elements are found in several groups and also are associated with well developed skin tubercles. These patterns could be interpreted as generalized, although they are less frequent than those structures formed by two elements. The increase in the number of skeletal elements does not imply more complexity

in the structure—most of these patterns could be interpreted as not fully developed because they remain cartilaginous or mineralized, seldom ossified. For example, *Scinax* spp. have cartilaginous prepollex formed by four elements; differentiation of these elements ends in metamorphic larval stages while in other hylids, prepollex primary cartilages are developed earlier and are generally ossified. In ranids, the prehallical elements are joined in a hammer-shaped structure with an incipient dorsal process. These data suggest a low developmental rate in these patterns.

The prepollex and prehallux with well-developed distal elements are observed in different and unrelated taxa, and have a defined ecological role. Developmental data imply that they are the result of increase in the developmental rate affecting size and shape of distal elements or hypermorphosis (McKinney & McNamara, 1991). They develop quickly and acquire their particular features immediately. The specialization of the distal prepollical element is observed in some treefrogs. Some species of *Hyla* (Howes & Ridewood, 1888; Kluge, 1981; this study), and *Cochranella* (Lynch & Ruiz-Carranza, 1996) present a prepollex with a spine protruding through the skin. Kluge (1981) pointed out "... prepollical spines became useful in intrasexual aggression after the structures had evolved to a considerable size and stiffness...". Most hylids have a prepollex formed by two articulated elements with a large and pointed distal element; this condition could represent the first step in prepollex specialization. Posterior interactions

with musculature and skin convert the prepollex into a special organ for a particular behaviour. In rhacophorids, prepollex enlargement does not display spine elaboration. However, hypermorphosis of the distal prepollical element is not limited to treefrogs and occurs in other taxa. *Atelopus farcii* (Lynch, 1993) is not arboreal, presenting hypermorphosis of the distal prepollical element and loss of digit II phalanges. An enlarged distal prehallical element is closely related to burrowing or fossorial habits and appears in several taxa. This pattern is characterized as headaxe-shaped and provides the support for a keratinous 'spade'. During development, the distal prehallical element grows quickly and is already defined before metamorphic larval stages. It is also a result of an hypermorphic development because in other taxa such as *Phrynohyas*, *Phyllomedusa*, *Hyla*, *Bufo*, *Leptodactylus*, *Pleurodema*, *Dermatonotus*, differentiation of prehallical elements may terminate later.

In related species, interspecific variability is observed as differences in size or extension of mineralization or ossification. For example, *Pleurodema borellii* and *P. cinerea* are species of similar morphology that inhabit northern Argentina (Cei, 1980); the prepollex and prehallux are ossified in *P. borellii* and cartilaginous in *P. cinerea*. Another example is seen in *Physalaemus biligonigerus* and *P. cuqui*, two sympatric species that differ in size, among other characters. The distal prehallical element of *P. cuqui* (the smaller species) is shorter and retains cartilaginous parts, while the distal element in *P. biligonigerus* is well ossified. Gollman (1991) mentioned variations in the number of prehallical elements in hybrids of two species of *Geocrinia* and described reduction or loss of distal prepollical/prehallical elements among the hybrid characters.

Intraspecific variations in skeletal structures have been pointed out in population studies of *Alytes* (Sanchiz, 1984) and *Geocrinia* (Gollman, 1991) in which differences in cartilage rudiments, ossifications, and mineralizations were described. Perhaps one of the most important aspects related to intraspecific variability refers to sexual dimorphism. This was noticed in *Telmatobius yuracare* (de la Riva, 1994), but it has not been considered in this study.

From comparative data presented here there is an apparent invariance in the presence of the prepollex and prehallux that suggests these structures were conserved and integrated in the anuran limb plan; they evolved independently from each other and were seldom lost. Morphological diversification of these structures displays distal variability associated with developmental process, as seen in intra- and inter-specific analyses. Despite the fact that the number of taxa examined is still limited, phylogenetic interpretations can be proposed from the prepollex and

prehallux traits in some groups. However, the morphological diversity is not easy to explain in terms of phylogenetic trends because derived patterns are largely determined by developmental constraints and converge for similar ecological requirements. They are the result of heterochronic changes, the first step in the modular evolution (Gilbert, 1998; Wagner, 1997). The most extreme specializations of these patterns are found in the prepollical spine and the prehallical 'spade' in which these structures become new organs related to specialized behaviour or habitat.

I have summarized the foregoing data from a comparative analysis taking into consideration the fact that the prepollex and prehallux are morphological evidence of an evolutionary process in anuran limbs. More information about the taxonomic occurrence of a prepollex and prehallux among lissamphibians and extinct groups would be useful for interpreting these structures in the evolution of tetrapod limbs.

ACKNOWLEDGEMENTS

I thank numerous colleagues. Dr Pere Alberch provided inspiration and suggestions for this study. Dr Günther Wagner, an anonymous reviewer and Dr Marvalee Wake added helpful comments on an earlier draft of the manuscript. Dr Richard Wassersug made valuable criticisms for a constructive discussion. Dr Richard Tinsley carefully read to improve the text. Dr Raymond Laurent let me analyse African specimens from personal collections. Dr Alain Dubois allowed the examination of specimens and X-ray films deposited in the Laboratoire des Reptiles et Amphibiens, Museum National d'histoire Naturelle (Paris, France). I also thank the Fundación Miguel Lillo and the Museo de Ciencias Naturales for the loan of specimens. This work was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (PEI 428/97) and Consejo de Investigación of Universidad Nacional de Salta (Grant 633), both from Argentina.

REFERENCES

- Alberch P, Gale EA. 1985. A developmental analysis of an evolutionary trend: digital reduction in amphibians. *Evolution* **39**: 8–23.
- Andersen ML. 1978. The comparative myology and osteology of the carpus and tarsus of selected Anurans. Unpublished D. Phil. Thesis, University of Kansas, Lawrence.
- Báez AM. 1981. Redescription and relationships of *Saltenia ibanezi*, a late Cretaceous pipid frog from Northwestern Argentina. *Ameghiniana* **18**: 127–154.
- Báez AM, Basso NG. 1996. The earliest known frogs of the Jurassic of South America: Review and cladistical appraisal of their relationships. In: Arratia G, ed. *Contributions of*

- Southern South America to Vertebrate Paleontology Abh. (A)* **30**: 131–158. Münchner Geowiss.
- Blanco MJ, Alberch P. 1992.** Caenogenesis, developmental variability and evolution in the carpus and tarsus of the marbled newt *Triturus marmoratus*. *Evolution* **46**: 677–687.
- Cannatella DC, Trueb L. 1988.** Evolution of pipoid frogs: intergeneric relationships of the aquatic family Pipidae (Anura). *Zoological Journal of the Linnean Society* **94**: 1–38.
- Cei JM. 1980.** Amphibians of Argentina. *Monitore Zoologico Italiano N.S. Monographs* **2**: 1–609.
- Clarke BT. 1983.** A morphological re-examination of the genus *Nannophrys* (Anura: Ranidae) with comments on its biology, distribution and relationships. *Zoological Journal of the Linnean Society* **79**: 377–398.
- Coates ML, Clack JL. 1990.** Polydactyly in the earliest known tetrapod limbs. *Nature* **347**: 66–69.
- de la Riva I. 1994.** A new aquatic frog of the genus *Telmatobius* (Anura: Leptodactylidae) from Bolivian cloud forests. *Herpetologica* **50**: 38–45.
- Dinsmore CE, Hanken J. 1986.** Native variant limb skeletal patterns in the red-backed salamander, *Plethodon cinereus*, are not regenerated. *Journal of Morphology* **190**: 191–200.
- Duellman WE. 1993.** *Amphibian species of the world: Additions and corrections*. Special Publication No 21, Museum of Natural History, The University of Kansas.
- Estes R, Reig O. 1973.** The early fossil record of frogs a review of the evidence. In: Vial JL, ed. *Evolutionary Biology of the Anurans: Contemporary Research on major problems*. Columbia: University of Missouri Press, 11–63.
- Fabrezi M. 1992.** El carpo de los Anuros. *Alytes* **10**: 1–29.
- Fabrezi M. 1993.** The anuran tarsus. *Alytes* **11**: 47–63.
- Fabrezi M, Alberch P. 1996.** The carpal elements of anurans. *Herpetologica* **52**: 188–204.
- Ford L, Cannatella DC. 1993.** The major clades of frogs. *Herpetological Monographs* **7**: 94–117.
- Formas JR. 1997.** A new species of *Batrachyla* (Anura: Leptodactylidae) from Southern Chile. *Herpetologica* **53**: 6–13.
- Frost DR. 1985.** *Amphibian Species of the World: a Taxonomic and Geographical Reference*. Lawrence, Kansas: Allen Press.
- Gilbert SF. 1998.** *Developmental Biology*, 5th edition. Sunderland, Massachusetts: Sinauer Associates Inc. Publishers.
- Gillies CD, Hopkins PW. 1922.** The phylogenetic significance of the prehallux and the prepollux: a theory. *Proceedings of the Royal Society of Queensland* **33**: 30–38.
- Gollman G. 1991.** Osteological variation in *Geocrinia laevis*, *Geocrinia victoriana*, and their hybrid populations (Amphibia; Anura; Myobatrachidae). *Zeit Zool. Systematik u. Evolutionsforschung* **29**: 289–303.
- Gosner K. 1960.** A simplified table for staging anuran embryos and larvae, with notes on identification. *Herpetologica* **16**: 183–190.
- Graybeal A, Cannatella DC. 1995.** A new taxon of Bufonidae from Perú, with descriptions of two new species and a review of the phylogenetic status of supraespecific bufonid taxa. *Herpetologica* **51**: 105–131.
- Gregory WK, Minner R, Noble GK. 1923.** The carpus of *Eryops* and the structure of the primitive chiropterygium. *Bulletin American Museum of Natural History* **48**: 279–288.
- Hinchliffe, RJ. 1991.** Developmental approaches to the problem of transformation of limb structure in evolution. In: Hinchliffe JR, Hurle JR, Summerbell D, eds. *Developmental Patterning of the Vertebrate Limb*. New York: Plenum Press, 313–323.
- Holmgren N. 1933.** On the origin of the tetrapod limb. *Acta Zoologica, Stockholm* **14**: 185–295.
- Howes GB, Ridewood W. 1888.** On the carpus and tarsus of the Anura. *Proceedings of the Zoological Society of London* **1888**: 141–180.
- Jarosova J. 1973.** The components of the carpus in *Palaebatrachus* and their development in two related recent species. *Casopis Narodniho Muzea* **142**: 89–106.
- Jarosova J. 1974.** The components of the tarsus in *Palaebatrachus* and their development in two related recent species. *Acta Universitatis Carolinae-Geologica* **1**: 119–144.
- Kluge A. 1981.** The life history, social organization and parental behavior of *Hyla rosemergi* Boulenger, a nest building gladiator frog. *Miscellaneous Publications Museum of Zoology, University of Michigan* **160**: 1–70.
- Kobel HR, Loumont C, Tinsley R. 1996.** The extant species. In: Tinsley RC, Kobel HR, eds. *The Biology of Xenopus*. Clarendon Press, Oxford, 9–33.
- Laurent RF. 1942.** Note sur l'Osteologie des genres *Breviceps* and *Phrynomerus* (Batraciens). *Revue de Zoologie et de Botanique Africaines* **35**: 417–418.
- Laurent RF. 1973.** The natural classification of the Arthrolpetinae. *Revue de Zoologie et de Botanique Africaines* **87**: 666–678.
- Lavilla EO, Lobo F. 1992.** Osteological notes on *Hylorina sylvatica* (Anura: Leptodactylidae). *Bolletino del Museo Regionale di Scienze Naturali - Torino* **10**: 209–216.
- Levedev CA, Coates M. 1995.** The postcranial skeleton of the Devonian tetrapod, *Tulerpeton curtum* Levedev. *Zoological Journal of the Linnean Society* **114**: 307–348.
- Lobo F. 1995.** Análisis filogenético del género *Pseudopaludicola* (Anura: Leptodactylidae). *Cuadernos de Herpetología* **9**: 21–36.
- Lynch JD. 1993.** A new harlequin frog from the Cordillera Oriental of Colombia (Anura, Bufonidae, *Atelopus*). *Alytes* **11**: 77–87.
- Lynch JD, Ruiz-Carranza PM. 1996.** A remarkable new centrolenid frog from Colombia with a review of nuptial excrecences in the family. *Herpetologica* **52**: 525–535.
- Maglia AM, Pugener LA. 1998.** Skeletal development and adult osteology of *Bombina orientalis* (Anura: Bombinatoridae). *Herpetologica* **54**: 344–363.
- McKinney ML, McNamara KJ. 1991.** *Heterochrony. The evolution of ontogeny*. New York: Plenum Press.
- Pugener LA, Maglia AM. 1997.** Osteology and skeletal development of *Discoglossus sardus* (Anura: Discoglossidae). *Journal of Morphology* **233**: 267–286.
- Rage JC, Rocek Z. 1989.** Redescription of *Triadobatrachus*

- massinoti* (Piveteau, 1936) an anuran amphibian from the Early Triassic. *Paleontographica Abt.A.* **206**: 1–16.
- Ritland RM. 1955.** Studies on the post-cranial morphology of *Ascaphus truei*. I. Skeleton and spinal nerves. *Journal of Morphology* **97**: 119–178.
- Saint-Aubain ML de. 1981.** Amphibian limb ontogeny and its bearing on the phylogeny of the group. *Zeit Zool. Systematik u. Evolutionsforschung* **19**: 175–194.
- Sanchíz B. 1984.** Análisis filogenético de la tribu Alytini (Anura: Discoglossidae) mediante el estudio de su morfoestructura ósea. In: Hemmer H, Alcover JA, eds. *Historia Biológica del Ferret (Life history of the Mallorcan midwife toad)*. Editorial Moll, Ciutat de Mallorca, 61–108.
- Schaeffer B. 1941.** The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bulletin American Museum Natural History* **78**: 395–472.
- Schmalhausen JJ. 1907.** Die Entwicklung des Skelettes der vorderen Extremität der Anuren Amphibien. *Anatomischer Anzeiger* **7–8**: 177–187.
- Shubin N, Alberch P. 1986.** A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* **20**: 319–387.
- Shubin N, Jenkins FA. 1995.** An Early Jurassic jumping frog. *Nature* **377**: 49–52.
- Stafford BJ, Thorington RW Jr. 1998.** Carpal development and morphology in archont mammals. *Journal of Morphology* **235**: 135–156.
- Trueb L. 1996.** Historical constraints and morphological novelties in the evolution of the skeletal system of pipid frogs (Anura: Pipidae). In: Tinsley RC, Kobel HR, eds. *The biology of Xenopus*. Oxford: Clarendon Press, 349–377.
- Vorobyeva EI, Hinchliffe JR. 1996a.** Developmental pattern and morphology of *Salamandrella keyserlingii* limbs (Anura, Hynobiidae) including some evolutionary aspects. *Russian Journal of Herpetology* **3**: 68–81.
- Vorobyeva EI, Hinchliffe JR. 1996b.** From fins to limbs. Developmental perspectives on paleontological and morphological evidence. *Evolutionary Biology* **29**: 263–311.
- Wagner GP. 1994.** Homology and the mechanisms of development. In: Hall BK, ed. *Homology. The hierarchical basis of comparative biology*. San Diego: Academic Press, 274–299.
- Wagner GP. 1997.** Homologues, natural kinds and the evolution of modularity. *American Zoologist* **36**: 36–43.
- Wassersug R. 1976.** A procedure for differential staining of cartilage and bone in whole formalin fixed vertebrates. *Stain Technology* **51**: 131–134.
- Wiens JJ. 1989.** Ontogeny of the skeleton of *Spea bombifrons* (Anura: Pelobatidae). *Journal of Morphology* **202**: 29–51.
- Wild ER. 1997.** Description of the adult skeleton and developmental osteology of the hyperossified horned frog, *Ceratophrys cornuta* (Anura: Leptodactylidae). *Journal of Morphology* **232**: 169–206.

APPENDIX

SPECIMENS EXAMINED

- Afrixalus fulvovittatus*, RFL 44b: 2 specimens. Whole mounts stained for bone and cartilage.
- Afrixalus laevis*, RFL 16g: 1 specimen; RFL 92a: 1 specimen. Whole mounts stained for bone and cartilage.
- Afrixalus osorioi*, RFL 4: 2 specimens. Whole mounts stained for bone and cartilage.
- Aglyptodactylus madagascariensis*, MNHN 1978–2972: 1 specimen; MNHN 1978–2958: 1 specimen. Whole mounts stained for bone.
- Arthroleptis adolfriederici*, RFL 90c: 3 specimens (1 male, 1 female and 1 juvenile). Whole mounts stained for bone and cartilage.
- Arthroleptis hematogaster*, RFL 103e: 3 specimens (1 male, 1 female and 1 juvenile). Whole mounts stained for bone and cartilage.
- Arthroleptis poecilonotus*, RFL 232h: 2 female specimens; RFL 251: 2 juvenile specimens. Whole mounts stained for bone and cartilage.
- Arthroleptis pyrrhoscelis*, RFL 121: 4 specimens (2 males and 2 females). Whole mounts stained for bone and cartilage.
- Arthroleptis schubotzi*, RFL 175b: 4 specimens (2 males and 2 females). Whole mounts stained for bone and cartilage.
- Arthroleptis stenodactylus*, RFL 108b: 1 juvenile specimen. Whole mount stained for bone and cartilage.
- Arthroleptis variabilis*, RFL 143: 1 female specimen. Whole mount stained for bone and cartilage.
- Astylosternus diadematus*, FML 3215: 2 specimens (1 adult and 1 juvenile). Whole mounts stained for bone and cartilage.
- Aubria subsigillata*, RFL 209: 2 juvenile specimens; RFL 348: 1 specimen. Whole mounts stained for bone and cartilage.
- Boophis luteus*, MNHN 1978–2971: 1 specimen. Whole mount stained for bone.
- Boophis tephraeomystax*, MNHN 1978–2973: 1 specimen. Whole mount stained for bone.
- Breviceps mossambicus*, FML 3166: 1 specimen. Whole mount stained for bone and cartilage.
- Breviceps poweri*, FML 3165: 1 female specimen. Whole mount stained for bone and cartilage.
- Bufo arenarum*, FML 2298: 1 specimen; MCN 126: 1 specimen. Whole mounts stained for bone and cartilage.
- Bufo funereus*, RFL 302: 3 specimens. Whole mounts stained for bone and cartilage.
- Bufo granulatus*, MCN 036: 6 specimens. Whole mounts stained for bone and cartilage.
- Bufo paracnemis*, FML 4400: 1 specimen; FML 4369: 30 tadpoles. Whole mounts stained for bone and cartilage.
- Cardioglossa cyaneospila*, RFL 66: 2 male specimens. Whole mounts stained for bone and cartilage.
- Cardioglossa leucomystax*, RFL 170: 2 specimens. Whole mounts stained for bone and cartilage.
- Ceratophrys cranwelli*, MCN 260: 2 specimens; MCN 021: 25 tadpoles; MCN 425: 18 tadpoles. Whole mounts stained for bone and cartilage.
- Chaparana aenea*, MNHN 1989.7.2: 1 specimen. Dry skeleton.
- Chiromantis rufescens*, RFL 382: 2 specimens. Whole mounts stained for bone and cartilage.
- Colostethus subpunctatus*, FML 2588: 1 specimen. Whole mounts stained for bone and cartilage.
- Conraua crassipes*, RFL 246: 2 specimens (1 female and 1 juvenile). Whole mounts stained for bone and cartilage.

- Dendrobates auratus*, FML 1722:1 specimen. Whole mount stained for bone and cartilage.
- Dermatonotus muelleri*, MCN122: 1 specimen; MCN 143: 1 specimen; MCN 234: 14 tadpoles; MCN 236: 8 tadpoles; MCN122 Whole mounts stained for bone and cartilage.
- Epipedobates pictus*, FML 3516: 1 female specimen. Whole mount stained for bone and cartilage.
- Gastrophryne carolinensis*, FML 3365: 1 specimen. Whole mount stained for bone and cartilage.
- Gastrophryne olivacea*, FML 2384: 1 specimen. Whole mount stained for bone and cartilage.
- Hemisus guineensis*, FML 1244: 1 specimen. Whole mount stained for bone and cartilage.
- Hoplobatrachus occipitalis*, RFL 348: 1 juvenile specimen. Whole mount stained for bone and cartilage.
- Hyla minuta*, FML 4282: 1 specimen. Whole mount stained for bone and cartilage.
- Hyla nana*, FML 4352: 1 specimen. Whole mount stained for bone and cartilage.
- Hyla andina*, MCN 390: 4 specimens; MCN 024: 25 tadpoles. Whole mounts stained for bone and cartilage.
- Hyla raniceps*, FML 3611:1 specimen. Whole mount stained for bone and cartilage.
- Hymenochirus boettgeri*, RFL 205b: 4 specimens. Whole mounts stained for bone and cartilage.
- Hyperolius castaneus*, RFL 54c: 10 specimens (6 males, 2 females and 2 juveniles). Whole mounts stained for bone and cartilage.
- Hypopachus variolosus*, FML 1723: 1 specimen. Whole forelimb mount stained for bone and cartilage.
- Ingerana* sp., MNHN 1985-604: 1 specimen. Whole mount stained for bone and cartilage.
- Kassina angeli*, RFL 158g: 1 female specimen. Whole mount stained for bone and cartilage.
- Kassina senegalensis*, RFL s/n, Bukowa: 2 juvenile specimens. Whole mounts stained for bone and cartilage.
- Lepidobatrachus laevis*, MCN 491: 6 tadpoles. Whole mounts stained for bone and cartilage.
- Leptodactylus bufonius*, MCN 110:1 specimen; MCN 200: 15 tadpoles. Whole mounts stained for bone and cartilage.
- Leptodactylus chaquensis*, MCN 082: 2 specimens (male and female); MCN 048: 20 tadpoles; MCN 070: 22 tadpoles; MCN 240: 10 tadpoles. Whole mounts stained for bone and cartilage.
- Leptodactylus latinasus*, MCN 059: 4 specimens. Whole mounts stained for bone and cartilage.
- Leptopelis christyi*, RFL 135: 4 specimens. Whole mounts stained for bone and cartilage.
- Limnonectes limnocharis*, MNHN 1987-2367: 1 specimen. Whole mount stained for bone and cartilage.
- Lysapsus limellus*, FML 716: 1 specimen. Whole mount stained for bone and cartilage.
- Mantella betsileo*, MNHN 1978-2980: 1 specimen. Whole mount stained for bone.
- Mantella cowani*, MNHN 1953-A136: 1 specimen. Whole mount stained for bone.
- Mantidactylus betsileanus*, MNHN 1978-2969: 1 specimen. Whole mount stained for bone.
- Mantydactylus biporus*, MNHN 1978-2959: 1 specimen. Whole mount stained for bone.
- Mantydactylus boulengeri*, MNHN 1978-2971: 1 specimen. Whole mount stained for bone.
- Mantydactylus curtus*, MNHN 1978-2964: 1 specimen. Whole mount stained for bone.
- Mantydactylus elegans*, MNHN 1978-2975: 1 specimen. Whole mount stained for bone.
- Mantydactylus femoralis*, MNHN 1978-2962: 1 specimen. Whole mount stained for bone.
- Mantydactylus madecassus*, MNHN 1978-3078: 1 specimen. Whole mount stained for bone.
- Mantydactylus pulcher*, MNHN 1978-1976: 1 specimen. Whole mount stained for bone.
- Melanophryniscus rubriventris*, MCN 071: 1 specimens; FML 2502: 1 specimen. Whole mounts stained for bone and cartilage.
- Micrixalus fuscus*, BMNH 74.4.291508: X-ray film, deposited in Laboratoire des Reptiles et Amphibiens, MNHN.
- Neobatrachus pictus*, FML 3772: 1 specimen. Whole mount stained for bone and cartilage.
- Odontophrynus americanus*, MCN 091: 6 specimens. Whole mounts stained for bone and cartilage.
- Odontophrynus lavillai*, MCN 230: 30 tadpoles. Whole mounts stained for bone and cartilage.
- Opisthothylax immaculatus*, RFL s/n.: 1 specimen. Whole mount stained for bone and cartilage.
- Paa fasciculispina*, MNHN 6110: 1 specimen. Dry skeleton.
- Paa feae*, MNHN 29301: 1 specimen. Dry skeleton.
- Pelodytes punctatus*, FML 045: 1 specimen. Whole mount stained for bone and cartilage.
- Phlyctimantis verrucosus*, RFL 81b: 4 specimens (2 males and 1 female). Whole mounts stained for bone and cartilage.
- Phrynobatrachus acutirostris*, RFL C1: 2 male specimens. Whole mounts stained for bone and cartilage.
- Phrynobatrachus asper*, RFL C18: 1 female specimen, RFL C5: 2 juvenile specimens. Whole mounts stained for bone and cartilage.
- Phrynobatrachus dendrobates*, RFL C10: 2 specimens. Whole mounts stained for bone and cartilage.
- Phrynobatrachus natalensis*, RFL 438: 2 specimens (male and female). Whole mounts stained for bone and cartilage.
- Phrynobatrachus petropedetoides*, RFL C6: 2 specimens (male and female). Whole mounts stained for bone and cartilage.
- Phrynobatrachus sulfureogularis*, RFL 346: 2 female specimens. Whole mounts stained for bone and cartilage.
- Phrynobatrachus versicolor*, RFL 430 2 specimens (male and female). Whole mounts stained for bone and cartilage.
- Phrynoglossus laevis*, MNHN 1987-8698: 1 specimen. Whole mount stained for bone and cartilage.
- Phrynohyas venulosa*, FML 1303: 1 specimen, MCN 238: 15 tadpoles. Whole mounts stained for bone and cartilage.
- Phyllomedusa sawagii*, MCN 258: 1 specimen; MCN 061: 27 tadpoles. Whole mounts stained for bone and cartilage.
- Phynomantis bifasciatus*, RFL 368: 4 specimens (2 males and 2 females). Whole mounts stained for bone and cartilage.
- Physalaemus biligonigerus*, MCN 157: 4 specimens; MCN 076: 21 tadpoles. Whole mounts stained for bone and cartilage.
- Physalaemus cuqui*, MCN 158: 4 specimens. Whole mounts stained for bone and cartilage.
- Pleurodema borellii*, MCN 065: 3 specimens. Whole mounts stained for bone and cartilage.
- Pleurodema cinerea*, MCN 100: 2 specimens. Whole mounts stained for bone and cartilage.
- Pseudis paradoxa*, FML 1055: 1 specimen. Whole mount stained for bone and cartilage.
- Ptychadena aequiplicata*, RFL 59: 1 specimen. Whole mount stained for bone and cartilage.
- Ptychadena christyi*, RFL 76: 1 specimen. Whole mount stained for bone and cartilage.
- Ptychadena chrysogaster*, RFL 141-143: 2 specimens. Whole mounts stained for bone and cartilage.

- Ptychadena guibei*, RFL 163: 1 specimen. Whole mount stained for bone and cartilage.
- Ptychadena mascareniensis*, RFL 120–123–124: 4 specimens. Whole mounts stained for bone and cartilage.
- Ptychadena perreti*, RFL 72–99: 2 specimens. Whole mounts stained for bone and cartilage.
- Ptychadena porosissima*, RFL Cr1: 2 specimens. Whole mounts stained for bone and cartilage.
- Ptychadena uzungwensis*, RFL 157: 1 specimen. Whole mount stained for bone and cartilage.
- Rana cubitalis*, FMNH 125945, X-ray film, deposited in Laboratoire des Reptiles et Amphibiens, MNHN.
- Rana humeralis*, BMNH 1947.2.3.64, X-ray film, deposited in Laboratoire des Reptiles et Amphibiens, MNHN.
- Rana lateralis*, MNHN 174131: 1 specimen. Dry skeleton.
- Rana sierramadrensis*, FMNH 124485, X-ray film, deposited in Laboratoire des Reptiles et Amphibiens, MNHN.
- Rana temporaria*, MNHN 1991–1287: 1 specimen. Dry skeleton.
- Rana warszewitschii*, FMNH 101576, X-ray film, deposited in Laboratoire des Reptiles et Amphibiens, MNHN.
- Rhinoderma darwinii*, FML 3694: 1 male specimen. Whole mount stained for bone and cartilage.
- Scaphiophryne calacarata*, MNHN 1978–2959: 1 specimen. Whole mount stained for bone.
- Scaphiophryne marmorata*, MNHN 1978–2985: 1 specimen. Whole mount stained for bone.
- Scinax fuscovarius*, MCN 382: 1 specimen; MCN 106: 2 specimens; MCN 239: 17 tadpoles. Whole mounts stained for bone and cartilage.
- Xenopus fraseri*, RFL 186: 3 specimens. Whole mounts stained for bone and cartilage.
- Xenopus laevis*, MCN 490: 15 tadpoles. Whole mounts stained for bone and cartilage.
- Xenopus wittei*, RFL 337–343: 6 specimens (4 adults and 2 juveniles). Whole mounts stained for bone and cartilage.