Parallelism and convergence in anuran fangs

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Abstract

The anuran lower jaw is composed of three pairs of bones: dentaries, angulosplenials and mentomeckelians. Although the lower jaw is toothless, except in *Gastrotheca guentheri*, enlarged fangs or odontoids have evolved at least four times independently in some myobatrachids, hylids, ranids and leptodactylids through both parallel and convergent evolutionary events. Fangs seem to represent the single best design solution to enable an anuran to inflict a bite-like wound, but the biological role of biting varies among species. Fangs are projections of the dentaries in ranids, but in the hylid frog *Hemiphractus* and in ceratophryine leptodactylids, they form a sinosteotic unit with the dentaries and mentomeckelians. Comparisons of morphology, behaviour and diet among frog taxa with enlarged fangs reveal that the fangs may be the result of either sexual or natural selection. Those fangs that evolved in response to sexual selection seem to be relatively larger than those that resulted of natural selection.

Key words: Anura, odontoid, convergence, parallelism, evolution

INTRODUCTION

Interesting, but little-studied, morphological features of some anuran amphibians are fang-like outgrowths of the lower jaw, usually referred to as odontoids (Fig. 1). Traditionally, the term odontoid has been applied to rigid structures superficially similar but not equivalent to true teeth (Trueb, 1973). Although rare, odontoids have evolved independently in species belonging to four families of frogs: ranids, myobatrachids, leptodactylids and hylids (Noble, 1931; Duellman & Trueb, 1986; Ford & Cannatella, 1993) (Fig. 2). Furthermore, they seem to have arisen more than once within the subfamily Raninae (Bossuyt & Milinkovitch, 2000) and within the family Hylidae (Sheil *et al.*, 2001). Although the biological role of fangs (*sensu* Bock & Von Wahlert, 1965) has not been examined in most species, their functional significance is clear. The structures inflict a bite-like wound when the frog closes its jaws on an object.

Frog odontoids provide an excellent opportunity to learn more about the repeated, independent evolution of similar structures, an evolutionary phenomenon that is often cited as evidence of the strong influence of selection in the evolution of effective functional design (Dawkins, 1987). Frog odontoids have evolved in a sufficient number of different taxa to allow phylogenetic comparison of both the ontogenetic pathways and evolutionary processes producing the fangs. Herein, we (1) describe the interspecific similarities and differences in the developmental pathways and adult phenotypic structure of frog odontoids; (2) determine the biological role(s) of fangs in species that possess them; (3) discuss our findings in the context of other recent work on parallelism and convergence (e.g. Hodin, 2000).

MATERIALS AND METHODS

The odontoids of species belonging to the Ranidae, Hylidae and Leptodactylidae were examined. *Dimorphognathus* (subfamily Petropedetinae, family Ranidae) was the only genus known to have species with odontoids that was not part of the study. Species included were *Aubria subsigillata*, *Ceratobatrachus guentheri*, *Conraua alleni*, *Conraua crassipes*, *Conraua goliath*, *Hoplobatrachus occipitalis*, *Nyctibatrachus major*, *Occidozyga laevis*, *Platymantis guyypi*, *Platymantis vitiensis*, *Ptychadena anchietae*, *Ptychadena mascareniensis*, *Ptychadena mossambicus*, *Pyxicephalus adspersus*, *Rana cancrivora*, *Rana corrugata*, *Rana cyanophlyctis*, *Rana hexadactyla*, *Rana limnocharis*, *Rana rugulosa*, *Rana tigrina*, *Sphaerotheca pluvialis* and *Sphaerotheca cryptotis* (Ranidae); *Hemiphractus fasciatus*, *Hemiphractus proboscideus* and *Phyllodytes auratus* (Hylidae); *Ceratophrys cranwelli*, *Chacophrys pierotti*, *Lepidobatrachus asper*, *Lepidobatrachus laevis*, *Lepidobatrachus*

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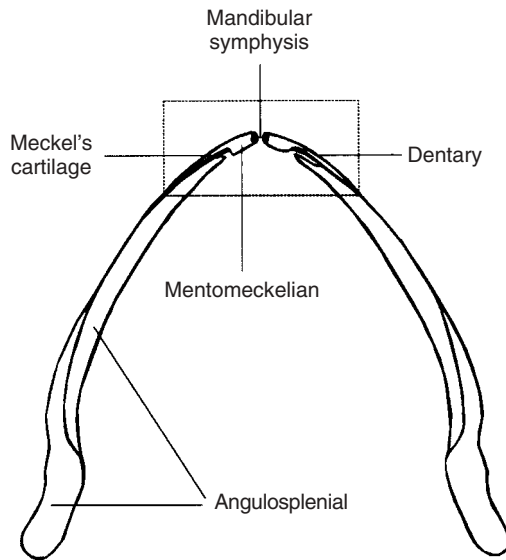E-mail: museo@unsa.edu.ar

Fig. 1. Elements of a typical anuran mandible. Rectangle delimits the portion in which the odontoids usually are present.
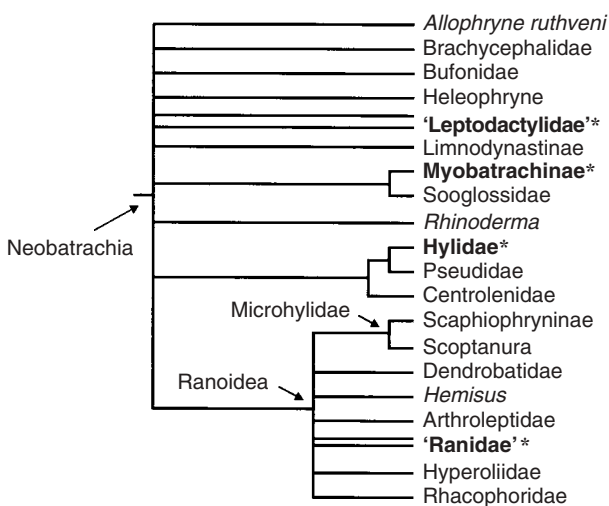

Fig. 2. Phylogenetic hypothesis of relationships among neobatrachian taxa (Ford & Cannatella, 1993) in which families containing species with odontoids are marked with an asterisk.

llanensis, *Leptodactylus chaquensis*, *Leptodactylus labyrinthicus* and *Leptodactylus laticeps* (Leptodactylidae). Information on *Adelotus brevis* was taken from the literature. Examined specimens are catalogued in the

herpetological collections of Instituto de Herpetología, Fundación Miguel Lillo (FML), in Tucumán (Argentina), Museo de Ciencias Naturales (MCN and RFL), Universidad Nacional de Salta, in Salta (Argentina); The Field Museum of Natural History (FMNH) in Chicago; The American Museum of Natural History (AMNH) New York City, and The Museum of Comparative Zoology (MCZ) in Cambridge (see Appendix).

The morphology of the odontoids was studied in both dry skeletons and alcohol-preserved specimens. For some species, whole mounts of larvae and adults were cleared and differentially stained for cartilage and bone using alcian blue and alizarin red (Wassersug, 1976; Hanken & Wassersug, 1981). The normal table of Gosner (1960) was used for staging larvae. Illustrations were prepared with the aid of a stereo microscope with camera lucida and/or photographed.

Intra- and interspecific quantitative differences in odontoids were studied by measuring snout–vent lengths (SVL) and fang lengths in preserved specimens. Fang length is defined as the perpendicular distance between the ventral border of the mandible and the tip of the odontoid process (after Emerson, 1994). It was necessary to include jaw depth, as well as odontoid length because preliminary studies indicated that measurements of fang length alone lacked repeatability. All measurements were converted to log base$_{10}$ and then graphed as a series of bivariate plots to examine whether or not there is sexual dimorphism in the sizes of the odontoids. Regression equations describing the quantitative relationship between log fang length and log SVL were calculated using JMP 3.1. ANCOVA was used to test for significant effects of size and sex on fang length. For interspecific comparisons, mean fang length and mean SVL for males are used to represent each species.

A phylogeny for the fanged frogs and relatives in the subfamily Raninae was constructed from molecular data of the 12S and 16S portions of the mitochondrial genome (sequences from GenBank) using PAUP 4.0b8*. Taxa included in the analysis were *Aubria subsigillata*, *Ceratobatrachus guentheri*, *Hoplobatrachus occipitalis*, *Limnonectes kuhlii*, *Limnonectes leporina*, *Nyctibatrachus major*, *Occidozyga laevis*, *Platymantis vitiensis*, *Pyxicephalus adspersus*, *Rana cancrivora*, *Rana corrugata*, *Rana limnocharis*, *Rana temporaria* and *Sphaerotheca pluvialis*. For *Aubria subsigillata*, *Ceratobatrachus guentheri*, *Platymantis vitiensis* and *Pyxicephalus adspersus* only 16S data were available. In these taxa the 12S portion of the genome was scored as

Fig. 3. Internal views of the anterior portion of frog lower jaws: (a) right mandible of *Aubria subsigillata* (RFL 212) with an odontoid projection from the dentary; (b) right mandible of *Hoplobatrachus occipitalis* (RFL 348) with a laminar odontoid from the dentary; (c) right mandible of *Conraua crassipes* (RFL 246); (d) pseudo-odontoid of *Leptodactylus laticeps* (FML 3982), a mound of connective tissue at the mandibular symphysis protrudes between the two mentomeckelian bones; (e) paired odontoids of *Chacophrys pierotti* (FML 1019), immediately lateral to the mandibular symphysis; (f) right mandible of *Ceratophrys cranwelli* (FML 5471); (g) paired odontoids of juvenile *Lepidobatrachus asper* (FML 5479), vestiges of Meckel's cartilages are still present; (h) right mandible of adult *Lepidobatrachus asper* (FML 549); (i) right mandible of *Lepidobatrachus laevis* (FML 620); (j) right mandible of *Lepidobatrachus llanensis* (FML 420). ang, angulosplenial; den, dentary; Mc, Meckel's cartilage; mmk, mentomeckelian; o, odontoid; po, pseudo-odontoid. Scale bars = 1mm.
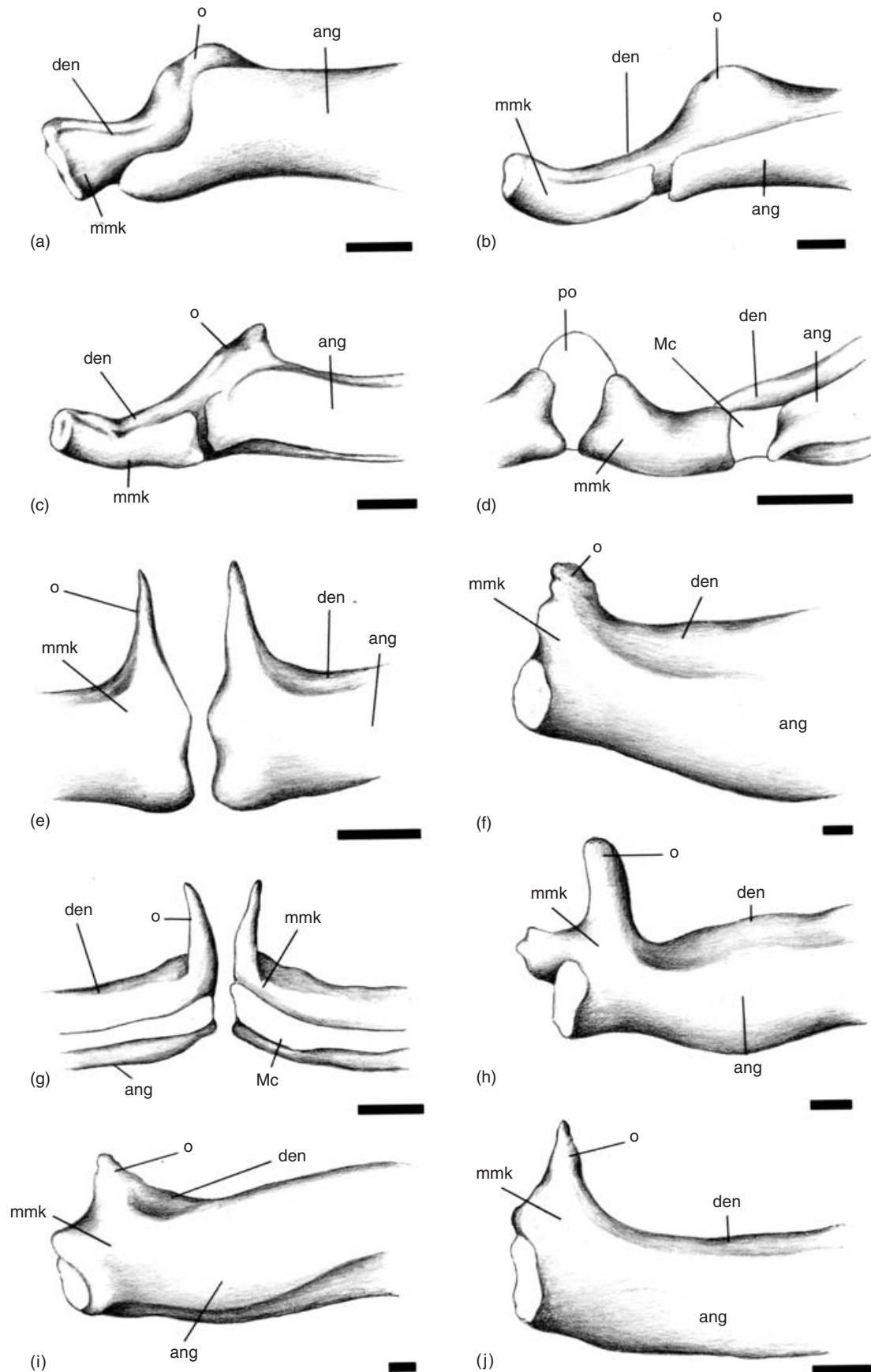
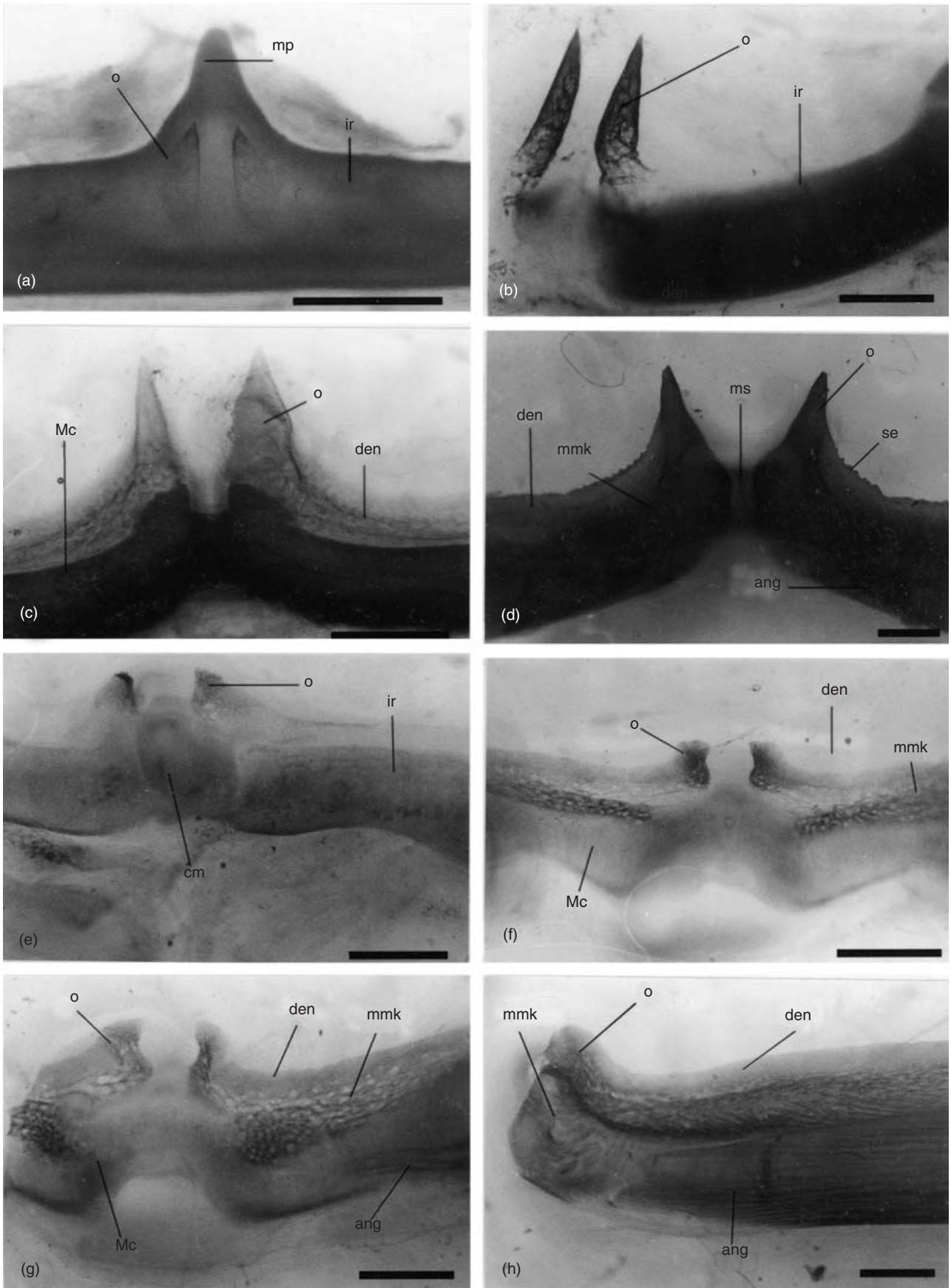**Fig. 3.** For caption see facing page.

Fig. 4. For caption see facing page.

missing. *Nesomantis thomasseti* (Sooglossidae) was used as the outgroup in the analysis (Ford & Cannatella, 1993). Transitions and transversions were weighted equally. Sequences were analysed using the heuristic search option and 10 replicate searches with random addition of taxa were performed. Non-parametric bootstrap analyses with 100 replicates were run to evaluate the strength of the groupings. Fang characters were mapped on this phylogenetic hypothesis using MacClade (Maddison & Maddison, 1992).

RESULTS

Qualitative variation in odontoid morphology

The anuran lower jaw consists of four elements on each side: a symphyseal bone (= mentomeckelian), and the dermal dentary and angulosplenial that invest Meckel's cartilage (Fig. 1) (Trueb, 1973). The fang-like outgrowths of the lower jaw found among frog species vary considerably in their ontogenies, adult shapes and relative sizes (Figs 3–5).

Some species of ranines (Brown, 1952; Bossuyt & Milinkovitch, 2000; Emerson, Inger & Iskandar, 2000 and references therein) have a pair of odontoids in the lower jaw (Fig. 3). The sizes of odontoids vary interspecifically (described below), but in all ranines examined each odontoid develops as a laminar projection from the dentary, somewhat lateral to the mandibular symphysis. In *A. subsigillata* (Fig. 3a), *C. guentheri*, *C. crassipes* (Fig. 3c), *H. occipitalis* (Fig. 3b), *Limnonectes* spp. (*sensu* Emerson *et al.*, 2000), *P. adspersus* and *R. corrugata*, only the upper or dorsal edge of the dentary contributes to the formation of the odontoids. Ontogenetically, the odontoid processes differentiate post-metamorphically. When the mouth is closed, each odontoid abuts the lingual surface of the upper mandible at the level of the premaxillary– maxillary articulation. In species of *Limnonectes*, *A. subsigillata*, *H. occipitalis* and *P. adspersus*, the extreme anterior portion of the pars palatina of the maxilla is concave and delimits a space where the lateral odontoids fit when the jaws are closed (Clarke, 1981).

In addition to the presence of lateral odontoids, some fanged ranines also posses a well-developed mound of connective tissue between the mentomeckelian bones
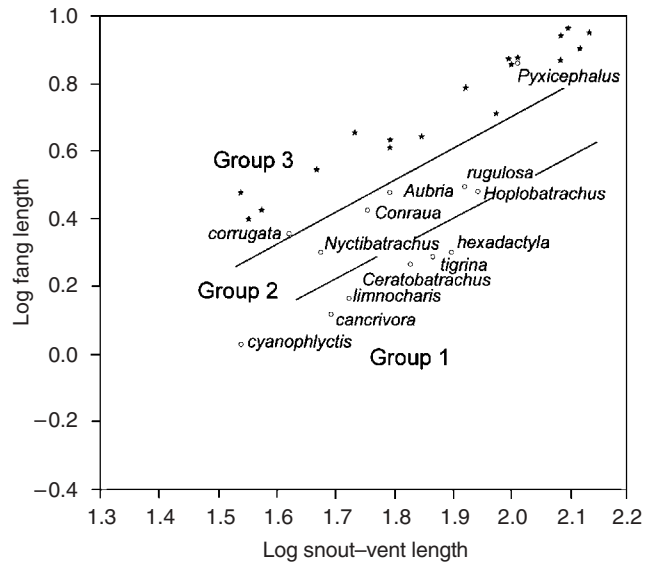

Fig. 5. Relationships between log fang length and log snout–vent length in species of male ranine frogs. Stars without labels are species of *Limnonectes*. Non-capitalized names are species of the genus *Rana*. Three groups delineating three sizes of relative fang length are shown by black lines.

that sometimes stains with alcian blue. Some authors have referred to this structure as an additional fang (e.g. Stewart, 1967; Passmore & Carruthers, 1979; Poynton & Broadlley, 1985). Structurally, this pseudo-odontoid represents hypertrophied connective tissue of the mandibular symphysis and does not include any mandibular bone. A similar pseudo-odontoid also occurs in species of *Leptodactylus* (Leptodactylidae) (Fig. 3d) and some bufonids (M. Fabrezi, pers. obs.).

Ceratophryine leptodactylids have a pair of pointed, robust and fully ossified odontoids, with the fangs flanking each side of the mandibular symphysis (Fig. 3e–h). Because the mandibular bones of these taxa are strongly fused, it is difficult to determine the limits of each element. It seems, however, that each odontoid is synostotically united to dentary and mentomeckelian. When the mouth is closed, the odontoid abuts the superficial lingual part of the alar process of the premaxilla; the palatal shelf of the premaxilla is absent in Ceratophryinae (Lynch, 1971).

Fig. 4. Internal views of odontoid development in ceratophryine leptodactylids: (a) *Lepidobatrachus llanensis* larval stage 42 (MCN 567): odontoid germs have differentiated on both sides of the medial process of the infrarostral cartilage; (b) *Lepidobatrachus llanensis* larval stage 43 (FML 4678): odontoid germs are larger and the medial process of infrarostral is beginning to reabsorb; (c) *Lepidobatrachus llanensis* larval stage 45 (MCN 667): odontoid is fused with the dentary and the mentomeckelian ossification is progressing; (d) *Lepidobatrachus llanensis* sub-adult (MCN 668): odontoid, dentary, and mentomeckelian form a single complex but individual elements still can be recognized; (e) *Ceratophrys cranwelli* larval stage 43 (MCN 669): odontoid germs are amorphous, appearing as the medial process of the infrarostral begins to reabsorb; (f) *Ceratophrys cranwelli* larval stage 44 (MCN 669): dentary and mentomeckelian ossifications have differentiated and the odontoid is fused with the dentary; (g) *Ceratophrys cranwelli* larval stage 45 (MCN 669): amorphous odontoid is fused with the mentomeckelian; (h) *Ceratophrys cranwelli*, recently metamorphosed specimen (MCN 005): ossification of lower jaw is strong, limits of the odontoid, dentary, and mentomeckelian are not clear. ir, infrarostral; mp, medial process of infrarostral; se, dentary serration; others as Fig. 3. Scale bars = 1 mm.

Table 1. Intraspecific patterns of relationships between fang length and snout–vent length (SVL)

	Regression equation	95% CI
Ceratobatrachus guentheri	Log fang = −1.57 + 1.04 log SVL	0.71–1.38
Pyxicephalus adspersus	Log fang = −1.50 + 1.14 log SVL	0.64–1.63
Aubria subsigillata	Log fang = −1.55 + 1.05 log SVL	0.87–1.22
Conraua crassipes		
Male	Log fang = −1.79 + 1.25 log SVL	0.10–2.4
Female	Log fang = −1.49 + 1.02 log SVL	0.57–1.47
Hemiphractus fasciatus	Log fang = −0.63 + 0.59 log SVL	0.33–0.86
Ceratophrys cranwelli	Log fang = −1.11 + 0.92 log SVL	0.54–1.29
Lepidobatrachus llanensis	Log fang = −0.22 + 0.51 log SVL	0.34–0.68
Lepidobatrachus laevis	Log fang = −0.32 + 0.58 log SVL	0.21–0.92

Morphological and molecular data indicate that *Ceratophrys*, *Chacophrys* and *Lepidobatrachus* are a monophyletic group (Lynch, 1971; Maxon & Ruibal, 1988). Ontogenetically, the development of their odontoids is similar, although there is some variation in the timing of emergence, the shape and size of the initial odontoid condensations, and the relationship between odontoid size and body size at the end of metamorphosis. In *L. llanensis*, they flank each side of the medial projection of the infrarostral cartilage by larval Stage 41 (Fig. 4a). These condensations stain positive with alizarin red. Each odontoid lengthens and becomes sharper during development (Fig. 4b). Differentiating dentary tissue fuses with the odontoid condensation as it ossifies (Fig. 4c). By the end of metamorphosis, the dentary and the mentomeckelian ossifications are fused completely. In contrast, the odontoid is not fully incorporated into the angulosplenial until later in ontogeny in the juvenile stages (Fig. 4d).

In *Ceratophrys cranwelli*, the odontoid condensations are present and stain positive for bone in larval Stage 43 (Fig. 4e). They remain as amorphous ossifications that grow slowly while dentary ossification proceeds (Fig. 4f–g). By the end of metamorphosis, the odontoid and dentary are fused. After metamorphosis, the odontoid fuses with the mentomeckelian, but a suture is visible (Fig. 4h).

In *A. brevis* (family Myobatrachidae) the odontoid is derived from both the mentomeckelian and the dentary (L. Trueb, pers. comm.). There is a diastema in the maxillary tooth row; presumably this accommodates the odontoid when the jaws are closed (Lynch, 1971).

In species of *Hemiphractus* (family Hylidae), the odontoid is derived from the dentary and is located adjacent to the mandibular symphysis (Trueb, 1974; Shaw, 1989) in a position similar to that of the odontoids of ceratophryine leptodactylids. In contrast to the latter, however, only the odontoids and the dentary of *Hemiphractus* are synostotically united (Shaw, 1989) as *Hemiphractus* lacks mentomeckelians (Trueb, 1974). There is a medial diastema in the premaxillary teeth where the odontoids fit when the jaws are closed. In *Phyllodytes* (family Hylidae), the fang is located immediately lateral to the mandibular symphysis (Miranda-Ribeiro, 1926) as well, but apparently it is derived entirely from the mentomeckelian (L. Trueb, pers. comm.).

Quantitative variation in the morphology of the odontoids

Intraspecific plots of fang length against SVL for the various species reveal interesting and different patterns. In two species of ceratophryine leptodactylids, *Lepidobatrachus laevis* and *Leptobatrachus llanensis*, and in the hylid *Hemiphractus fasciatus*, fang length scales with a significant negative allometry with respect to SVL (Table 1). Females are larger than males in these species, but both sexes are described by a single regression equation. As a result of the negative allometry in the fang length to SVL relationship in these species, recently metamorphosed and juvenile frogs have relatively larger fangs than older, larger adults. In *C. cranwelli*, fang length scales isometrically with SVL. The males and females are described by a single regression equation and there is no difference in relative fang length between juveniles and adults (Table 1).

In the myobatrachid *A. brevis*, fang size scales with a strong positive allometry with SVL in males (Katsikaros & Shine, 1997). In contrast, the females have almost no fangs (Katsikaros & Shine, 1997). Males are larger than females and therefore have relatively and absolutely larger fangs than females.

Among the ranine species, there are different intraspecific patterns of relationship between fang length and SVL. In *A. subsigillata*, *C. guentheri*, *P. adspersus* and *H. occipitalis*, there are isometric relationships between fang size and snout–vent size (Table 1; Emerson, 1994). Females are larger than males in *Aubria*, *Hoplobatrachus* and *Ceratobatrachus*, but there is no significant difference between sexes in relative fang length at the same SVL. Males and females are described by a single regression equation (Table 1; Emerson, 1994). In *P. adspersus*, males are larger than females, but, again, the sexes do not differ significantly in relative fang length at the same SVL (Table 1) and males and females are described by a single regression equation. Only six individuals of *R. corrugata* were available for measurement; for these males and females of the same SVL, males had significantly larger fangs than females ($P < 0.02$). In *C. crassipes*, ANCOVA indicates a significant effect of both size and sex on fang length (SVL, F-ratio = 3.57, $P < 0.0001$; sex, F-ratio = 23.01,
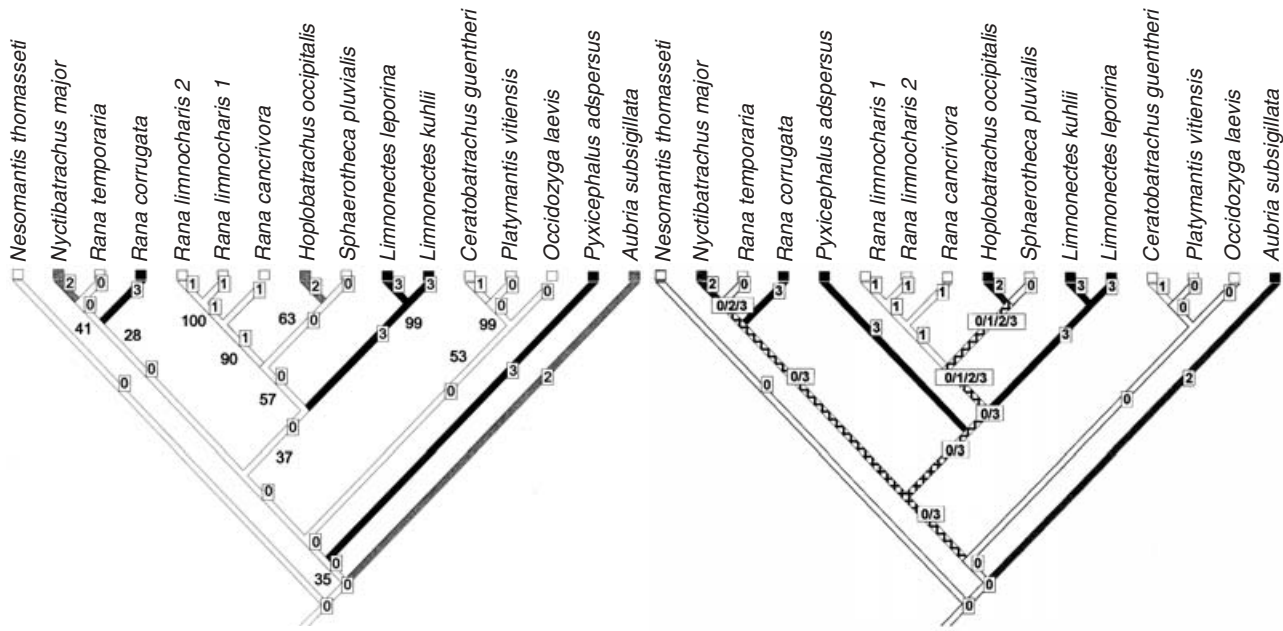
Fig. 6. Two equally parsimonious hypotheses of phylogenetic relationships among selected species of ranine frogs. Numbers without boxes are bootstrap values. Boxed numbers and grey shades represent fang character states: 0 (white), no fangs; 1 (light grey), small fangs; 2 (medium grey), intermediate fang size; 3 (black), large fangs. Character state is ambiguous where hatching or multiple numbers appear in a box. Relative fang size is defined in Fig. 5.

$P < 0.0004$). In fanged species of *Limnonectes*, both males and females have well-developed odontoids, but there are marked differences between males and females in relative fang size (Emerson, 1994). The males of most species show a strong positive allometry to the relationship between fang size and SVL (Emerson, 1994), whereas the relationship between fang size and SVL tends to be isometric in females (Emerson, 1994).

Interspecifically, the fang length of males in ranine species varies across a wide range of body sizes. In Fig. 5, at least three groups can be identified on the basis of a species morphocline in relative fang length. The male fanged frogs of *P. adspersus*, *R. corrugata* and the genus *Limnonectes* have the largest relative fang lengths (Group 3, Fig. 5). *Aubria subsigillata*, *H. occipitalis*, *R. rugulosa*, *N. major* and *C. crassipes* have intermediate relative fang lengths (Group 2, Fig. 5). *Ceratobatrachus guentheri*, *R. hexadactyla*, *R. tigrina*, *R. limnocharis*, *R. cancrivora* and *R. cyanophlyctis* have the smallest relative fang lengths (Group 1, Fig. 5). In these latter taxa, the bumps on the dentary often are so small that they can be seen only in skeletal preparations of the mandible. *Occidozyga laevis*, *O. lima*, *P. anchietae*, *P. vitiensis*, *P. guppyi* and *S. pluvialis* lack fangs.

To understand the pattern of fang evolution in ranines, the three categories of relative odontoid size (taken from the log plot of fang size and SVL) were mapped on the two equally parsimonious phylogenetic hypotheses of ranine relationships generated from the molecular data set (Fig. 6). Even with 332 parsimony-informative characters, the phylogenetic relationships are not well resolved (Fig. 6). As a consequence, these hypotheses must be considered very preliminary. None the less, from the mapping exercise, it seems that fangs evolved at least three and possibly as many as five times in ranine frogs (Fig. 6). Furthermore, it does not seem that the (relatively) large-fanged species necessarily evolved from species that had smaller fangs or bumps on the dentary.

DISCUSSION

Often parallelism and convergence are distinguished by whether the same (parallelism) or different (convergence) developmental pathways are involved in the independent formation of the similar phenotypes (Wake, 1991; Hodin, 2000). Based on these definitions, independent evolution of similar structures in more closely related species may be more likely to be the result of parallelism than convergence. More closely related species share a more recent common ancestor and (presumably) would also be more likely to have common developmental pathways (Hodin, 2000 and references therein). In contrast, similarity of structure in distantly related species would be expected to be the result of convergence as presumably the structures in these species would be more likely to have arisen by different developmental pathways (Hodin, 2000 and references therein). Comparison of the ontogenetic development of fangs in anurans supports this distinction. The multiple, independent evolution of fangs within the ranines always involves the same ontogenetic pathway. In all ranines, the fangs develop through allometric growth of a portion of the dentary after metamorphosis (Fig. 3). This pattern is a classic example of parallelism. In contrast,

Table 2. Comparisons of morphological and behavioural features, and diet across fanged frogs. Data were taken from Balinsky & Balinsky, 1954; Brown, 1952; Channing *et al.*, 1994; Duellman, 1978; Fabrezi, 2001; Hanken, 1993; Hughes, 1979; Katsikaros & Shine, 1997; Knoepffler, 1965; Lynch, 1971; Noble, 1924; Orlov, 1997; Perret, 1994; Reig & Limeses, 1963; Shaw, 1989; Sheil *et al.*, 200l; Wild, 1999

Taxon	Body size	Relative fang size	Hyper-ossification skull	Aggressive biting behaviour	Male–male combat	Diet	Teeth
Chacophrys	Female > male	?	Yes	?	?	Relatively large vertebrate prey	Monocuspid/ non-pedicellate
Ceratophrys	Female > male	Female = male	Yes	Yes	No	Relatively large vertebrate prey	Monocuspid/ non-pedicellate
Lepidobatrachus	Female > male	Female = male	Yes	Yes	No	Relatively large vertebrate prey	Monocuspid/ non-pedicellate
Hemiphractus	Female > male	Female = male	Yes	Yes	?	Relatively large vertebrate prey	Monocuspid/ pedicellate
Phyllodytes	Female > male	Male > female	No	No	Yes	?	?
Adelotus	Male > female	Male > female	No	No	Yes	Occasional vertebrates	Bicuspid/ pedicellate
Limnonectes	Male > female	Male > female	No	No	Yes	Occasional vertebrates	Bicuspid/ pedicellate
Conraua	Female > male	Male > female	No	No	?	Occasional vertebrates	Bicuspid/ pedicellate
Hoplobatrachus	Female > male	Female = male	No	No	?	Arthropods, frogs	Bicuspid/ pedicellate
Aubria	Female > male	Female = male	Yes	Yes	No	Relatively large vertebrate prey	Monocuspid/ pedicellate
Pyxicephalus	Male > female	Female = male	Yes	Yes	Yes	Relatively large vertebrate prey	Monocuspid/ non-pedicellate
Rana corrugata	Female > male	Male > female	No	?	?	?	?
Ceratobatrachus	Female > male	Female = male	Yes	?	?	?	?

the evolution of fangs in species in different families involves different ontogenetic pathways. In ceratophryine leptodactylids, fangs develop from independent odontoid tissue condensations that form and fuse to portions of the mandibular bones near metamorphosis (Fig. 4). This process differs from that observed in either ranine frogs or the fanged hylid species of the genus *Hemiphractus* (Shaw, 1989). Thus, the occurrence of fangs in different anuran families is an example of convergent evolution.

One of the most interesting aspects of the repeated, independent evolution of frog fangs is that they seem to be the result of more than one type of selection pressure. Comparisons of morphology, behaviour and diet across frog taxa with odontoids (Table 2) reveal broad patterns which suggest that both sexual and natural selection may have been involved in the evolution of fangs.

In some species, the presence of fangs seems to be correlated with dietary specialization and to be the result of natural selection. These species of fanged frogs eat relatively large prey compared to their fangless relatives. In *H. occipitalis* and *A. subsigillata*, frogs are a common part of the diet (Noble, 1924; Hughes, 1979; Perret, 1994; Table 2). The ceratophryine leptodactylids, species of *Hemiphractus*, and *P. adspersus* also specialize in eating relatively large vertebrate prey including frogs, small mammals, lizards and birds (Loveridge, 1950; Duellman, 1978; Cei, 1981; Hanken, 1993; Duellman & Lizana, 1994). These species are characterized by aggressive biting behaviour, hyperossification of the cranium and monocuspid teeth (Table 2). Additionally, *P. adspersus*

and the ceratophryine leptodactylids have non-pedicellate teeth, a rare condition among anurans (Smirnov & Vasil'eva, 1995; Fabrezi, 2001). (In these species, the absence of pedicellate teeth is associated with a rapid, intense calcification of the tooth germ that suppresses the typical zone of weakness found in pedicellate teeth; Smirnov & Vasil'eva, 1995; Fabrezi, 2001.)

In contrast, there is no significant effect of fang size on relative prey size in the fanged species of *Limnonectes* and *A. brevis* (Emerson & Voris, 1991; Emerson, 1994; Katsikaros & Shine, 1997). These species do not seem to specialize in eating large vertebrates, although they do occur occasionally in their diet. Aggressive biting behaviour and non-pedicellate teeth have not been reported for any of these species.

Fanged frog species lacking a diet of relatively large prey are generally sexually dimorphic in relative fang sizes, suggesting that in these taxa, sexual selection may have been important in odontoid evolution. In *P. adspersus*, *P. luteolus*, *A. brevis* and species of *Limnonectes*, males are larger than females and all taxa except *P. adspersus* have marked sexual dimorphism in relative fang sizes. Furthermore, in *P. adspersus*, *P. luteolus*, *A. brevis* and species of *Limnonectes*, enlarged fangs are used in male–male combat (Balinsky & Balinsky, 1954; Weygoldt, 1981; Orlov, 1997; Katsikaros & Shine, 1997; Tsuji & Kuang, 2000). In contrast, male combat has not been reported for the fanged species of *Chacophrys*, *Ceratophrys* or *Lepidobatrachus* that specialize in relatively large prey. Furthermore, none of

these species exhibits a sexual dimorphism in relative fang sizes and males are smaller than females.

Pyxicephalus adspersus is unique among the taxa with fangs in that it has both male–male combat and a specialized diet of relatively large vertebrate prey (Channing, Perez & Passmore, 1994). Furthermore, *Pyxicephalus* exhibits aggressive biting behaviour and has hyperossified cranial bones. There is no significant difference in relative fang sizes between males and females at the same SVL but, commonly, males are larger than females. Uniquely, the males of this species show adaptive male parental care, which includes attacking predators of their larvae including birds and other frogs (Cook, Ferguson & Telford, 2001).

Pertinent details of breeding behaviour and/or diet are not known for *R. corrugata*, *N. major*, *C. crassipes* and *C. guentheri*, but some morphological data are available (described in Results). Females are larger than males and there is no sexual dimorphism in relative fang size in species of *Hemiphractus*, *N. major* and *C. guentheri*; this suggests that the presence of fangs in these species may be related to diet specialization. In contrast, in *C. crassipes* and *R. corrugata*, there is sexual dimorphism in fang size with males having relatively larger fangs. These findings suggest that fangs in these species may be related to intrasexual competition.

Fangs in frogs seem to solve a common problem. They are a means of handling relatively large, resistant prey or foe. At the same time, fangs have not evolved under a single selection regime. An interesting question is whether natural and sexual selection left different 'signatures' on frog fang morphology. This might occur because sexually dimorphic features are thought to be under especially strong selection (West-Eberhard, 1983). If this were true, one might predict that the fangs would be relatively larger in species with male–male combat and sexual selection than in species in which the fangs evolved through natural selection to take relatively larger prey. In fact, this seems to be the situation, whether the fangs are the result of parallel or convergent evolution. Within the ranine frogs, species of *Limnonectes* have the relatively largest fang lengths (Fig. 4). This is a group characterized by a history of sexual selection (Emerson, 1994; 2001). Among families, the fangs of *A. brevis*, *P. auratus* and the species of *Limnonectes* are relatively larger than those of ceratophryine leptodactylids, species of *Hemiphractus*, and *C. guentheri* (Emerson, 1994; Katsikaros & Shine, 1997; pers. obs). This first group of species are those whose fangs seem to have evolved through sexual selection. The presence of fangs, sexual dimorphism in fang size and fang use in male–male competition are all derived characters for the various taxa (Weygoldt, 1981; Emerson, 1994; Katsikaros & Shine, 1997).

In conclusion, enlarged fangs have evolved independently through both parallelism and convergence in anuran amphibians. Depending on the species, these enlarged odontoids can be the result of either sexual or natural selection. Those fangs that evolved under sexual selection seem to be relatively larger than those resulting from natural selection.

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APPENDIX. SPECIMENS EXAMINED

Museum codes

ACZ: The Museum of Comparative Zoology, Cambridge.
AMNH: The American Museum of Natural History, New York City.
FML: Fundación Miguel Lillo, Tucumán, Argentina.
FMNH: The Field Museum of Natural History, Chicago.
MCN: Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina.
RFL: Raymond Ferdinand Laurent, personal collection.

Ranidae

Aubria subsigillata: MCZ 21790–91, 557, 26944, 2963; AMNH 75121, 11905, 12922–26; FMNH 190815, 168848; FML 3154 (five specimens); RFL 212, 209 (two specimens).

Ceratobatrachus guentheri: FMNH 13717, 13743, 13745–46, 13855, 25897, 44528, 44786–87, 44789, 44791, 44794, 44799, 44912.

Conraua alleni: AMNH 140823, 140825–29, 83301–03.

Conraua crassipes: MCZ 5580–81, 3458, 13213–14, 23266, 23247–48; AMNH 11908–10, 23101, 23105, 63549–51; FML 3068 (five specimens); RFL 246 (two specimens).

Conraua goliath: FMNH 15980; MCZ 15738, 85228.

Hoplobatrachus occipitalis: FMNH 20830 (46 specimens), 22184, 160886, 160888–90, 160894, 160899; FML 1192 (10 specimens); RFL 348 (two specimens).

Nyctibatrachus major: FMNH 218202, 218204, 218206, 218209, 21815, 21819, 218223–24, 218226, 218228, 218231–32, 218234, 218237, 218766.

Occidozyga laevis: FMNH 24113, 234899–904, 234907–08, 234910, 234914–16, 234918–20.

Platymantis guppyi: FMNH 44584.

Platymantis vitiensis: FMNH 23000.

Ptychadena anchietae: MCZ 36241–44, 36246, 36248, 36250, 36252–53, 36257.

Ptychadena mascariensis: FMNH 175773.

Ptychadena mossambicus: MCZ 28622.

Pyxicephalus adspersus: FMNH 17153, 232743, 215535, 17148, 20745; MCZ 7265, 10368, 10788, 10826, 16483–84, 21359, 21362, 25374–75; FML 2050.

Rana cancrivora: FMNH 131485, 143433, 143436, 143439, 143451–52, 143457–59, 143462, 143468–69, 143497, 143500–03, 143506, 143510, 143515–16, 143527, 143534, 200965, 200972–74, 200977, 200981.

Rana corrugata: FMNH 81229; AMNH 74244–45, 77474–78.

Rana cyanophylyctis: FMNH 166716, 167178–79, 16790, 167207–09, 167213–14, 167219–20, 167236, 167240, 167244, 167248, 167265, 167353, 167356–57, 167359, 167362, 167364, 167371–72, 167323–24, 167333.

Rana hexadactyla: MCZ 31517–21.

Rana limnocharis: FMNH 196141, 1716, 50161, 50167–68, 50172, 50174–77, 50179, 50181, 50187, 50193, 50198, 50204–06, 50208, 51124, 51132, 51134, 51137, 51141, 51146–47, 51150, 51152, 51157, 51166–67, 51173, 51182.

Rana rugulosa: MCZ 13241–42; FMNH 196212, 8636, 7762, 24506, 21926, 13099, 176321.

Rana tigrina: MCZ 31548–49, 132420–21.

Sphaerotheca pluvialis: MCZ 412, 1275; FMNH 211889.

Sphaerotheca cryptotis: MCZ 24014–15, 107074.

Hylidae

Hemiphractus fasciatus: AMNH 124113–20, 92668, 98078, 98363, 107955–56, 108288.

Hemiphractus proboscideus: MCZ 90345, 90347, 91463, 92274, 97772, 17937.

Phyllodytes auratus: FMNH 218984, MCZ 15611–13, 80487–88.

Leptodactylidae

Ceratophrys cranwelli: FMNH 69164–66, 69075; FML 4573–4, 4534 (seven tadpoles between larval stages 40 and 46), 4777, 5471–2, 8961–70; MCN 005 (two specimens), 188, 260 (six specimens), 669 (12 specimens between larval stages 40 and 46).

Chacophrys pierotti: FML 9046–49, 1094 (six specimens), 428 (two specimens), 1019 (four specimens), 9013.

Lepidobatrachus asper: FML 1386 (three specimens), 5669, 5470, 5479.

Lepidobatrachus laevis: FML 8102 4914 (three specimens), 1090, 620; MCN 109, 666, 695, 696 (three specimens), 663 (eight tadpoles between larval stages 39 and 42).

Lepidobatrachus llanensis: FML 4856 (six specimens), 1016, 5220–21, 4678 (three tadpoles at larval stages 41, 42, 43); MCN 667 (three specimens), 667, 081, 567 (12 tadpoles between larval stages 38 and 42), 665 (six tadpoles at larval stages 41–43).

Leptodactylus chaquensis: FML 4406; MCN 039 (two specimens), 082, 124, 142 (four specimens), 261 (two specimens), 449, 477.

Leptodactylus labyrinthicus: FML 0829 (four specimens).

Leptodactylus laticeps: FML 0269, 02181 (four specimens), 03645 (two specimens); MCN 104.