

# The Lissamphibian Humerus and Elbow Joint, and the Origins of Modern Amphibians

Trond Sigurdson<sup>1\*</sup> and John R. Bolt<sup>2</sup>

<sup>1</sup>Redpath Museum, McGill University, Montreal, Quebec, Canada H3A 2K6

<sup>2</sup>Field Museum of Natural History, Geology Department, Chicago, Illinois 60605-2496

**ABSTRACT** The origins and evolution of the three major clades of modern amphibians are still a source of controversy, and no general consensus exists as to their relationship to the various known Paleozoic taxa. This may indicate that additional character complexes should be studied to resolve their phylogenetic relationship. The salamander elbow joint has been fundamentally misinterpreted in previous morphological descriptions. In caudates and anurans, both the radius and ulna (fused in anurans) articulate with the characteristically large capitulum (radial condyle), although part of the ulnar articulating surface fits into the smooth trochlear region. The salamander “ulnar condyle” of previous descriptions is in fact the entepicondyle. The condition seen in batrachians (i.e., salamanders and frogs) may be a lissamphibian synapomorphy because the elbow region of the primitive fossil caecilian *Eocaecilia* resembles those of frogs and salamanders. In addition to the large and bulbous capitulum, all lissamphibian humeri lack an entepicondylar foramen, and possess a distally pointing entepicondyle, a low and rounded ectepicondyle, and an elongated shaft. These characters are identified in key fossil forms to assess the support for the different hypotheses proposed for the evolutionary origins of lissamphibians. Temnospondyli is the only group of early tetrapods that shows a progressive evolution of lissamphibian traits in the humerus and elbow joint. Furthermore, among Paleozoic taxa, the dissorophoid temnospondyl *Doleserpeton annectens* is the only taxon that has the full set of humeral features shared by all lissamphibians. These results add support for the theory of a monophyletic origin of lissamphibians from dissorophoid temnospondyls. *J. Morphol.* 270:1443–1453, 2009. © 2009 Wiley-Liss, Inc.

**KEY WORDS:** Lissamphibia; Temnospondyli; *Doleserpeton*; Dissorophoidea; elbow joint; humerus; evolution

## INTRODUCTION

Contemporary phylogenies of modern amphibians vary considerably with respect to their relationship to both living amniotes and fossil forms (reviews in Anderson, 2008; Schoch and Milner, 2004). Lissamphibians have been proposed as a monophyletic group with the fossil amphibamid dissorophoid *Doleserpeton* as closest sister taxon (Bolt, 1969; Ruta and Coates, 2007), or as a monophyletic group allied to the Paleozoic lepospondyls

(Laurin and Reisz, 1997). Furthermore, lissamphibians have been suggested to be a polyphyletic assemblage, with frogs and salamanders closely related to dissorophoids, and caecilians constituting a sister group to the microsaurian lepospondyl genus *Rhynchonkos* (Anderson, 2007; Carroll, 2007). Molecular data tend to confirm the monophyly of lissamphibians relative to amniotes and to show that batrachians (frogs and salamanders) form a monophyletic group, with caecilians as their closest sister taxon (review in Anderson, 2008; Igawa et al., 2008; San Mauro et al., 2004).

A number of traits have been proposed as synapomorphies linking lissamphibians with various Paleozoic groups (e.g., Carroll, 2007; Parsons and Williams, 1962; Schoch and Milner, 2004). However, the structure of the appendicular skeleton is rarely discussed in this context, other than in connection with the evolution of jumping in modern frogs (e.g., Jenkins and Shubin, 1998). The new and intriguing amphibamid *Gerobatrachus* presents some evidence for the evolution of the amphibian postcranial skeleton (Anderson et al., 2008), but many of its features are poorly preserved.

Previous descriptions of the forelimbs of modern amphibians give the impression of completely disparate anatomies, with few, if any, features being shared by frogs, salamanders, and caecilians. When we dissected the elbow joints of modern amphibians, we realized that the anatomy and function of the forelimb of modern salamanders have been misinterpreted by previous workers. Modern interpretations of salamander anatomy

Contract grant sponsor: Natural Sciences and Engineering Research Council of Canada (NSERC).

\*Correspondence to: Trond Sigurdson, McGill University, Redpath Museum, 859 Sherbrooke Street West, Montreal, Canada H3A 2K6. E-mail: trond.sigurdson@mail.mcgill.ca or trondsi@hotmail.com

Received 12 October 2008; Revised 1 May 2009; Accepted 18 May 2009

Published online 23 June 2009 in Wiley InterScience (www.interscience.wiley.com) DOI: 10.1002/jmor.10769

usually are based on the descriptions of Francis (1934). Although his figures are generally accurate, his interpretation of the elbow area is misleading. Francis' description is at odds with available descriptions of anurans (e.g., Gaupp, 1904; Maglia et al., 2007; Ritland, 1955), even though anurans and caudates have many forelimb features in common. This has led to incorrect interpretations making the anatomy of the forelimb of anurans seem more divergent from that of salamanders than it really is (e.g., Duellman and Trueb, 1994; Báez and Basso, 1996). In contrast, the brief descriptions by Miner (1925) and Evans (1946) are fairly accurate but both lack detail and fail to point out the uniqueness of the lissamphibian elbow joint. Here, we describe the lissamphibian humerus and elbow joint, including those of the fossil limbed caecilian *Eocaecilia*. We then compare the relevant fossil forms to modern amphibians, adding much-needed information to the discussion of lissamphibian origins. Although there is no current consensus as to the relationships and origins of extant amphibians, the term "Lissamphibia" is used here to denote modern amphibians, irrespective of the question of monophyly.

## MATERIALS AND METHODS

Modern and fossil tetrapod taxa were sampled as broadly as possible. Within Lissamphibia, basal and derived taxa were examined based on both traditional (Duellman and Trueb, 1994) and recent (Frost et al., 2006) phylogenies. Other tetrapods were sampled with emphasis on stem taxa. The Lower Triassic stem-anuran *Triadobatrachus massinoti* was studied with the kind help of Jean-Claude Rage (Muséum National d'Histoire Naturelle, Paris). Primitive fossil lissamphibians, most notably *Eocaecilia micropodia* and *Prosalirus bitis*, and numerous Paleozoic fossils representing most of the major tetrapod groups were available for study at the Museum of Comparative Zoology, the Field Museum of Natural History, and the Redpath Museum. For a full list of specimens, see the Table A1.

In the following descriptions, as in most descriptions of modern tetrapods, the humeri are assumed to be directed posteriorly and more or less parallel to the axis of the body for purposes of description. Thus, the capitulum (= radial condyle, capitellum, or humeral ball) is situated on the ventral and lateral side of the distal end of the humerus.

Measurements were obtained of the humeri from 19 modern amphibians (representing 15 families), and 30 non-lissamphibian tetrapods (Table A1). Some measurements were taken from published descriptions. The humeral length ( $L$ ), distal width ( $W$ ), and transverse capitulum size ( $C$ ) were measured for all specimens. Most humeri were measured with calipers, but the smallest specimens were measured using outline drawings made with a camera lucida on a microscope, adjusting for the magnification. All measurements were log transformed before the analysis, which was undertaken using PAST (Paleontological Statistics) version 1.90. To test the hypothesis that the capitulum size is larger in lissamphibians than in other tetrapods, we ran an analysis of covariance (one-way ANCOVA). The capitulum size of batrachians and amniotes was analyzed, adjusting for the covariance of the distal humeral width. This is justifiable because the capitulum is located on the distal end of the humerus. We also ran an analysis adjusting for the humeral length. Finally, we analyzed the variables separating the lissamphibian humeri from other taxa, using a discriminant analysis first for batrachians versus amniotes, and then on batrachians versus all "non-batrachians" of this study.

samphibian humeri from other taxa, using a discriminant analysis first for batrachians versus amniotes, and then on batrachians versus all "non-batrachians" of this study.

## Institutional Abbreviations

CAS, California Academy of Sciences, San Francisco, CA; FMNH, Field Museum of Natural History, Chicago, IL; MCZ, Museum of Comparative Zoology, Harvard, MA; MNA, Museum of Northern Arizona, Flagstaff, AZ; RM, Redpath Museum, Montreal, Quebec, Canada.

## RESULTS

### Humerus and Elbow Joint of Salamanders

The salamander humerus is slender (e.g., *Ambystoma*) to moderately robust (e.g., *Andrias*) and no foramina pierce it. As in many other tetrapods, the proximal and distal ends are expanded and twisted about 90° relative to each other. The rounded humeral head is more or less confluent with the deltopectoral crest (=crista ventralis humeri). There is often a dorsal process on the extensor surface of the humeral shaft (absent in Cryptobranchidae and Proteidae). This is the insertion point of the subscapularis muscle. The usually cartilaginous distal end has two prominent protrusions (Figs. 1A,B and 2A). According to Francis (1934), the most medial of these is the ulnar condyle. However, it is better described as the entepicondyle because of its function, as well as its position, which reflect that of the entepicondyle described in other tetrapods (Coates, 1996; Pawley and Warren, 2006; Romer, 1956). The condyle in question is situated medially on the distal end of the bone, and it is directed distally (Figs. 1A and 2A). Although its lateral edge forms part of the trochlear region (described below), the condyle itself does not function as the articulation site of the ulna. Rather, it is the attachment site for tendons of the flexor musculature of the carpus, as are the entepicondyles of other tetrapods. The capitulum (radial condyle) is large and hemispherical (ratio of distal end width to capitulum width about 0.5; Table A1), and it lies immediately lateral to the trochlear region. It extends distally and ventrally from the main body of the humerus and serves as the articulation site of both the radius and the ulna (Fig. 1A,B). The smooth concavity between the capitulum and the entepicondyle is the trochlea (Fig. 2A), which articulates with a rounded facet on the ulna. Unlike the trochlear regions of most amniotes, it is rather indistinct and lacks convexities. Thus, there is no ulnar condyle proper, contrary to the description by Francis (1934). The ectepicondyle (epicondylus lateralis) is the attachment site for the extensor muscles of the lower arm and hand. It is a low, rounded ridge situated lateral and slightly proximal to the capitulum. The ulna has a partially cartilaginous olecranon, which is the attachment site of the anconaeus

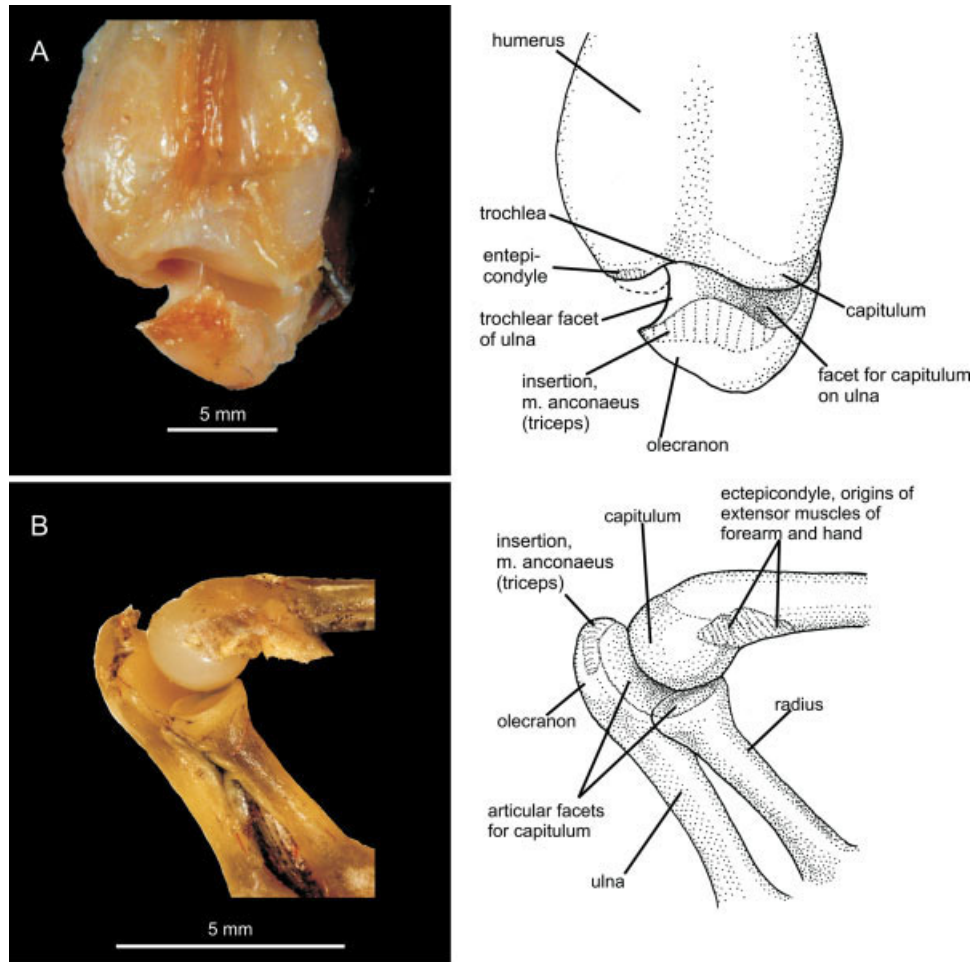


Fig. 1. The elbow joint of salamanders (some features are removed in the drawings for clarity). (A) *Andrias davidianus*, dorsal view. (B) *Ambystoma tigrinum*, lateral view. In both cases, the articular capsule has been opened and the joint surfaces slightly separated. Note that the main articulating surface of the ulna faces the capitulum (radial condyle). [Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).]

musculature (=triceps; Walthall and Ashley-Ross, 2006). The proximal ulnar articulation facet consists of a large concave surface laterally and a smaller rounded facet situated more medially (Fig. 2B). The large concavity articulates entirely with the capitulum, whereas the rounded edge fits into the trochlear region. This structure has been confirmed in all salamander species studied.

### Salientians (Anurans and Proanurans)

The anuran humerus differs from that of salamanders in having a longer deltopectoral crest (Fig. 2C). The shaft is usually slightly sigmoidally curved. The proximal and distal ends are often more highly ossified than in salamanders. The humerus is strikingly similar to that of salamanders in having a large capitulum, a distally directed entepicondyle (epicondylus ulnaris of Gaupp, 1904), and a low, rounded ectepicondyle. In large, highly ossified species, such as *Rana catesbeiana*,

the entepicondyle has a short medial process for the insertion of the flexor carpi musculature (Fig. 2C).

The fused radio-ulna of frogs (Fig. 2D) articulates with the capitulum (the humeral ball of Maglia et al., 2007), which is even larger than that of most salamanders. Part of the ulnar component of the radio-ulna reaches the trochlear region between the capitulum and entepicondyle. This medial ulnar edge is rounded to fit into the trochlear region of the humerus, but the major articulation facet of the ulnar part of the radio-ulna faces the capitulum. Apart from the fusion of the radio-ulna, this is exactly the situation seen in salamanders.

The earliest remains of crown-group anurans are found in the Jurassic. The fossils of such otherwise informative forms as *Vieraella* and *Notobatrachus* have no preserved capitulum (Báez and Nicoli, 2004; Roček, 2000). Furthermore, the humeri of *Prosalirus bitis* are only partly ossified along the outer edge of the capitulum (Shubin and



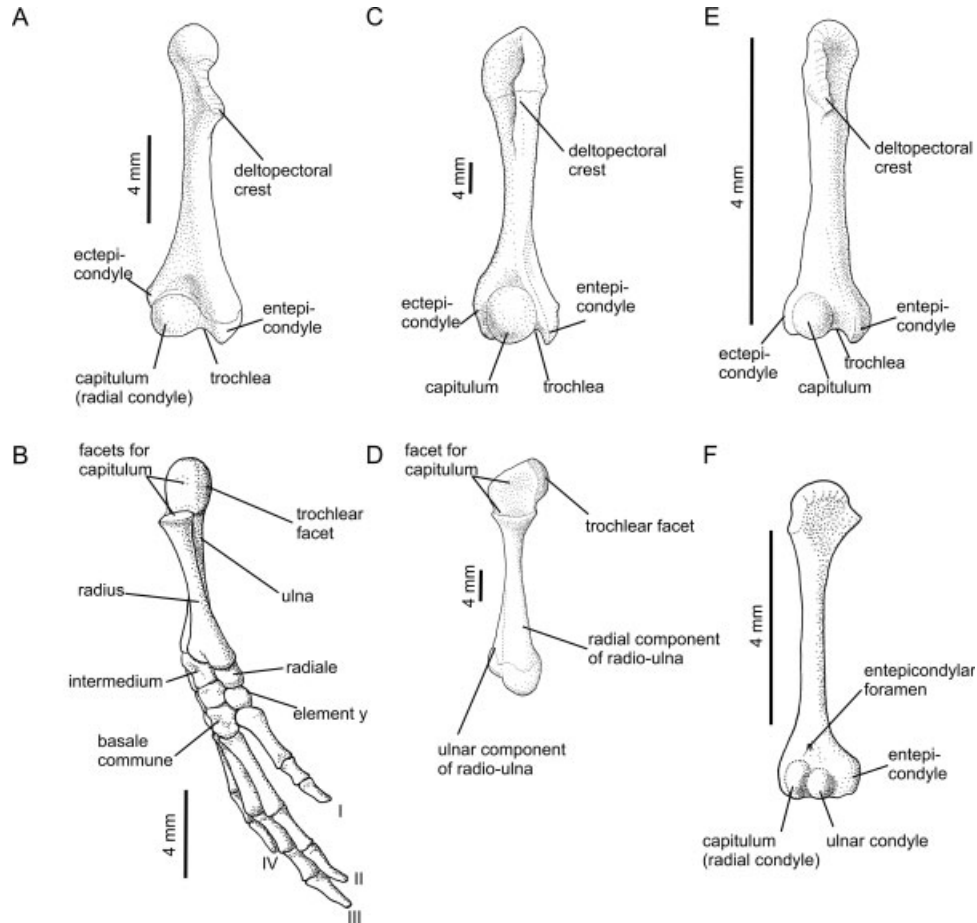


Fig. 2. Tetrapod forelimb elements. All humeri are from the right side and seen in ventral (flexor) view. (A) *Ambystoma tigrinum*, humerus. (B) *Ambystoma tigrinum*, zeugopodium, and autopodium in anterior (radial) view. (C) *Rana catesbeiana*, humerus. (D) *Rana catesbeiana*, radio-ulna in anterior (radial) view. (E) *Eocaecilia micropodia*, humerus (based on MCZ 9163 and 9169). (F) *Lacerta* sp. humerus.

Jenkins, 1995). However, the preserved parts are complete enough to reconstruct the size of this condyle, which was of comparable size with that of modern anurans (Table A1).

The Triassic proanuran *Triadobatrachus massinoti* was redescribed by Roček and Rage (2000). The humeral shaft of this form has a curvature and deltopectoral crest similar to those of most modern anurans. The distal and proximal ends are incomplete due to lack of ossification. However, a large gap distally indicates the presence of a capitulum which may have been similar in size to that of modern anurans. This feature is confirmed in the presumably related Polish form *Czatkobatrachus polonicus* (Evans and Borsuk-Bialynicka, 1998) in which a large capitulum is preserved in an otherwise fragmentary humerus.

### *Eocaecilia*

Although modern caecilians lack limbs, important new evidence is available from the Lower Jurassic form *Eocaecilia micropodia* (Jenkins

et al., 2007). The limb bones of this form are reduced in relative size but well preserved. The humerus is elongated and lacks foramina (Fig. 2E). The entepicondyle is offset slightly medially, but it comes to a sharp point distally as in modern frogs. The trochlear area is smoothly concave as in salamanders, and the capitulum is large and bulbous. The condylar size relative to the width of the bone is somewhat smaller than in frogs but resembles those of some hynobiid and dicamptodontid salamanders examined by the authors (Table A1). The ectepicondyle is a low, rounded ridge similar to those of anurans. The ulna has been described in detail by Jenkins et al. (2007). As in salamanders, the proximal ulnar articulating area has two facets, the larger of which faces the radial side (i.e., facing the capitulum). Overall, the humerus and elbow joint exhibit the structure seen in batrachians, showing all the traits shared by salamanders and frogs. Unlike anurans, the humerus has a dorsal process similar to that of some salamanders (Jenkins et al., 2007). The limb bones of *Eocaecilia* are highly ossified, despite being

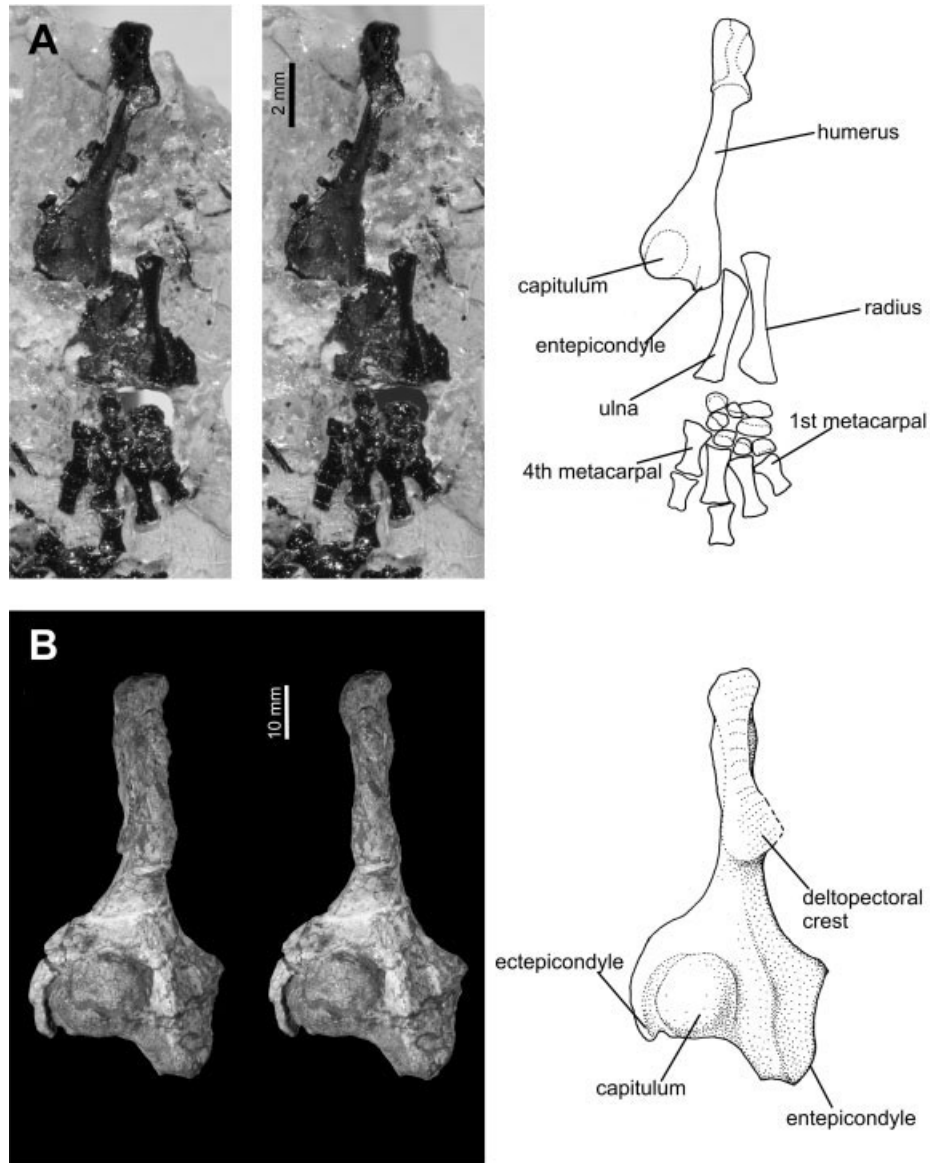


Fig. 3. Humeri and forelimb of dissorophoids. (A) *Doleserpeton annectens* FMNH UR1321. (B) *Dissorophus multicinctus* MCZ 4176. Illustrations are slightly restored based on other specimens. Both show the right element in ventral view.

reduced in size. This may indicate that the limbs were still being used actively in locomotion.

### Other Fossil Forms

Among the known Paleozoic forms, only the dissorophoids have a humeral morphology and an elbow joint resembling those of lissamphibians. A relatively large capitulum seems to be typical of euskelian temnospondyls (Yates and Warren, 2000), although this trait may be present in some primitive temnospondyls as well, judging by the unossified area of the capitulum of *Edops* (unpublished data). A good example of the large temnospondyl capitulum can be seen in the well-studied

form *Eryops* in which the capitulum dominates the distal end of the humerus (Pawley and Warren, 2006). Stronger similarities to modern amphibians can be found in the dissorophoids (Fig. 3A,B). Although the humeri of trematopid dissorophoids such as *Acheloma* are remarkably similar to those of *Eryops* (Olson, 1941), the humeri of *Dissorophus* appears smoother in that it lacks the supinator process (DeMar, 1968). Although the bone of the latter form is relatively short and robust, the distal end is, in fact, remarkably similar to that of modern lissamphibians (Fig. 3A). This includes the distally directed entepicondyle and rounded ectepicondyle and the smooth concavity of the trochlear region. The capitulum of *Dissorophus* is large

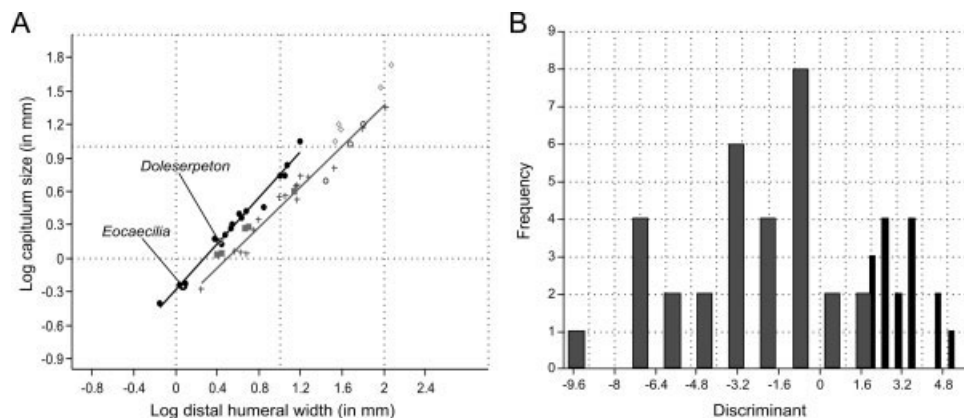


Fig. 4. Analysis of the humeral data. (A) The relationship between the distal humeral width and the size of the capitulum. Major axis regression lines are given for batrachians (black line) and amniotes (gray line). Black circle, batrachian; cross, amniote; gray box, lepospondyl; light gray diamond, temnospondyl; circle, stem tetrapod. (B) Distribution of frequencies along the discriminant axis (defined in the text). Black columns: Batrachians (frogs and salamanders), gray columns: “non-batrachian tetrapods.” The overlap of the columns is due to *Eocaecilia* and *Dolesempeton*.

relative to those of most other early tetrapods, including *Eryops*, although its relative size is not as large as those of most modern amphibians (Table A1). The medial process of the entepicondyle resembles that of modern anurans (Figs. 2C and 3B). The described humeri of *Cacops* (Williston, 1910) resemble more poorly preserved specimens of *Dissorophus* in which the distal end of the bone is incompletely ossified.

In amphibamid dissorophoids, the humeri are generally more slender than in other temnospondyls, perhaps partly due to their small size. This is most pronounced in the Lower Permian form *Dolesempeton annectens*. The humerus of this taxon is a relatively smooth bone lacking an entepicondylar foramen and supinator process. The capitulum is preserved as a mold in the matrix surrounding the distal end of the bone in the type specimen (FMNH UR1308). In a few specimens, such as FMNH UR1321, the large capitulum is preserved (Fig. 3A). It is a large, hemispherical structure situated next to a smoothly concave trochlear region. As in *Dissorophus* and modern amphibians, the entepicondyle is distally directed, and the ectepicondyle is low and rounded. Uniquely, among Paleozoic tetrapods, the humerus of *Dolesempeton* possesses all the characters shared by anurans, salamanders, and *Eocaecilia*. In addition, the radius and ulna of *Dolesempeton* resemble those of modern salamanders. Although the proximal parts are only partly preserved in these bones, the articulating surfaces of the ulna appear to be oriented similarly to those of salamanders.

### Morphometric Comparisons

Batrachians (frogs and salamanders) and amniotes are usually regarded as monophyletic groups (but see review by Anderson, 2008; Carroll,

2007; Ruta and Coates, 2007) and are, therefore, used for comparison to the other taxa in this study. The reduced major axis regression lines of the variables *C* and *W* for amniotes and batrachians are given in Fig. 4A. The ANCOVA gave adjusted means of log *C* as 0.52 for batrachians ( $N = 18$ ) and 0.26 ( $N = 16$ ) for amniotes ( $F = 90.15$ ,  $p < 0.0001$ ), demonstrating the larger relative size of the capitulum in anurans and caudates compared to amniotes. Adjusting for humeral length gave similar results but with somewhat less extreme difference in adjusted means (0.49 and 0.29, respectively,  $p < 0.0001$ ). The regression lines of the other groups did not pass the bootstrap test, but plotting the data points onto the regression lines (Fig. 4A) confirms the observation that *Eocaecilia* and *Dolesempeton* both closely approximate the batrachian condition. After dividing the taxa into two groups consisting of batrachians and “non-batrachians,” respectively, the discriminant analysis (Fig. 4B) applied to the log-transformed measurements identified 95.9% of the taxa as being in the correct group. The discriminant function is defined by:  $v = (21.90 \log C) + (5.93 \log L) - (27.72 \log W)$ . The analysis identified *Eocaecilia* and *Dolesempeton* (included for purposes of the analysis among the “non-batrachians”) as belonging to the same group as batrachians.

## DISCUSSION

### The Lissamphibian Humerus and Elbow Joint

Our results indicate that the specialized elbow region described here may be a shared trait of lissamphibians. The elbow joint consists of a large capitulum articulating with both radius and ulna, although the latter bone also has a rounded facet

articulating with the smooth and relatively featureless trochlear region. A low ectepicondyle and a distally directed entepicondyle are also present. Other traits of the humerus that are shared by these forms include the lack of humeral foramina and the elongation of the humeral shaft.

The elbow joint approximates a ball-and-socket joint rather than a hinge. Such a joint allows for considerable movement, the opposite of the situation seen in some primitive fossil tetrapods, such as pelycosaurs, in which elbow movement was restricted (Jenkins, 1973). Manipulations of freshly dissected specimens indicate that the nature of the lissamphibian elbow joint may allow some fore-and-aft movement of the radius and ulna relative to the humerus, but this movement is restricted by the medial edge of the olecranon fitting into the trochlear region. The joint is clearly flexible enough to allow for the highly divergent morphologies and modes of locomotion seen in anurans, caudates, and primitive gymnophionans.

This forelimb morphology contrasts markedly with the ancestral tetrapod condition in which the humerus is a short bone with an entepicondylar foramen, a small capitulum, and a separate ulnar condyle (Carroll and Holmes, 2007; Holmes, 1980). The entepicondyle of *Acanthostega* is large and medially (posteriorly) directed, although it also has a distally directed edge, making this trait somewhat uncertain in polarity (Coates, 1996). Within the Amniota, a distinct shaft evolved early, but stem amniotes still retain the small capitulum and the entepicondylar foramen (Reisz, 1980, 1981; Sumida, 1997). In modern lizards, there is often a true ulnar condyle between the capitulum and the entepicondyle (Fig. 2F). In some amniotes, the capitulum forms part of the lateral edge of the trochlear region, and a facet of the ulnar articulating surface faces this medial area of the capitulum (Colbert, 1952; Holmes, 1977; Jenkins, 1973). Others, such as many modern mammals, might be said to have a continuous joint surface for the radius and ulna in the form of a wide trochlear-shaped area (Starck, 1979). However, none has an elbow joint in which the major articulating surfaces of both the radius and ulna face a large, bulbous capitulum. The morphology of the lissamphibian humerus and elbow joint thus seems to be unique among modern tetrapods.

### Data Analysis

Because of the extremely fragmentary nature of many of the fossil specimens used in this study, it is hard to assess the effects of body mass on the humeral features discussed. However, several features seem to indicate that body size is not a determining factor for the morphology of the elbow region. For example, the humeral morphology and

elbow region of the smallest caudates resemble those of the giant Chinese salamander (*Andrias davidianus*), which is the largest modern amphibian. Conversely, the approximately similar sized, but unrelated, Paleozoic forms *Eryops* and *Dime-trodon* had strikingly different elbow regions, with the temnospondyl *Eryops* having a larger capitulum perhaps approaching the lissamphibian condition. Warren and Snell (1991) pointed out the lack of size-related variation among temnospondyl humeri, and that humeral morphological differences were likely to reflect phylogenetic relationships. Our observations of various temnospondyl humeri support this view. Also, the lissamphibian-like humerus of the amphibamid temnospondyl *Doleserpeton* is not paralleled by any similar-sized amniote as far as is known. Nor is it apparently paralleled by microsaur or other lepospondyls, although the often incompletely preserved fossils and highly variable morphologies of lepospondyls make this group difficult to interpret at present.

Both the ANCOVA and the discriminant function analysis confirm the distinctiveness of the batrachian humerus relative to that of amniotes and to other tetrapods. Furthermore, the discriminant function analysis classified the humeri of *Eocaecilia* and *Doleserpeton* as belonging to the batrachian group. It should be noted that the latter analysis was not robust when changes were introduced by removing parts of the data. However, *Eocaecilia* and *Doleserpeton* also appear closer to the batrachian regression line than any other tetrapods (Fig. 4A), confirming the close resemblance of the humeri of amphibamids, batrachians, and early caecilians.

### The Evolution of Lissamphibia

Apart from adding to, and correcting, our knowledge on the forelimb morphology of amphibians, our results also provide valuable phylogenetic information. Although it would be unwise to propose a novel phylogeny based on one new character complex, it is informative to compare the distribution of the traits considered here in the light of previously published phylogenies. A wide variety of fossil forms was examined, including lepospondyls, temnospondyls, and early tetrapods. A problematic feature of many of the relevant fossil forms, such as many lepospondyls and amphibamids, is the lack of ossified condyles. However, the position and, with less certainty, the size of the capitulum sometimes can be inferred from the presence of a gap where the cartilaginous condyle was located in life.

In recent phylogenies, temnospondyl dissorophoids, as well as lepospondyl microsaur and lysorophians, have been suggested as possible sister-groups to one, two, or all modern lissamphibians (Anderson et al., 2008; Carroll, 2007; Laurin



and Reisz, 1997; Ruta and Coates, 2007). Some lepospondyls share certain features of the humerus with modern amphibians, such as elongation of the shaft and loss of the entepicondylar foramen, but these are relatively common in other tetrapods as well.

Among the lepospondyls, the microsauro *Cardiocephalus* has been described as having a humerus fitting the lissamphibian descriptions above (Gregory et al., 1956). However, the limb bones assigned to this taxon appear to be identical to elements that are associated with the type specimen of the temnospondyl *Doleserpeton* (Bolt, 1969). Because these taxa occur in the same locality (Fort Sill, Oklahoma), the limb elements assigned to *Cardiocephalus* by Gregory et al. (1956) should be regarded as belonging to *Doleserpeton* until further studies of the former are undertaken. Specimen MCZ 3692, which was attributed to *Cardiocephalus* by Carroll and Gaskill (1978) and Carroll et al. (1998), is a more robust bone with a smaller capitulum than that of *Doleserpeton* and may have been correctly identified as belonging to *Cardiocephalus*. Data for this specimen are given in the Table A1.

In the polyphyletic origins theory (Anderson et al., 2008; Anderson, 2007; Carroll, 2007), salamanders and frogs are proposed to be closely related to branchiosaurids and amphibamids, whereas the microsauro genus *Rhynchonkos* is suggested as a sister taxon to caecilians. This is supported by several traits of the skull and vertebral column (Carroll, 2007) but contradicted by evidence from dentition (Bolt, 1969; Parsons and Williams, 1962) and the inner ear (Clack, 2002; Sigurdson, 2008). The humerus of *Rhynchonkos* shares the lack of an entepicondylar foramen and the elongated shaft with lissamphibians, giving some credence to the hypotheses of a relationship between this form and caecilians. The distal end is poorly ossified, but the capitulum appears to have been medially placed, judging from the figures given by Carroll and Gaskill (1978). The structure of the distal end of the bone might have resembled that of the related microsauro *Trihecaton*, including a medially placed capitulum, and epicondyles that differ from those of lissamphibians (Carroll and Gaskill, 1978). The data presented here fit well with the temnospondyl origins of salamanders and frogs, but they also point to some remarkable similarities among *Eocaecilia*, dissorophoid temnospondyls, and batrachians. Because the humerus of *Eocaecilia* shares the features found in batrachians, and no microsauro has been shown to have the full set of lissamphibian features, the microsauro origin of caecilians is questioned here.

The lysorophians were proposed as immediate sister-group to lissamphibians by Laurin and Reisz (1997). Sadly, the distal ends of the humeri of these forms are poorly preserved. However, the

preserved parts of the lysorophian humeri constitute a short hourglass-shaped bone, with distal and proximal ends situated approximately in the same plane (Wellstead, 1991). These features are strikingly different from the lissamphibian humeri described earlier. Of the well-preserved lepospondyl remains studied or described in the literature, none has the full set of lissamphibian characters. Some nectrideans do have a large capitulum overlapping that of modern amphibians in size (Carroll et al., 1998). However, this character is combined with features that are distinctively different from lissamphibians, such as the retention of an entepicondylar foramen, and a short humeral shaft. These features make the humeri of the nectridean *Scincosaurus* appear more like those of the possible stem amniote *Westlothiania* (Smithson et al., 1994) than those of lissamphibians. From the above evidence, which is admittedly sparse in the case of lepospondyls, it seems unlikely that a lissamphibian type of forelimb occurred within Lepospondyli.

In the phylogeny by Ruta and Coates (2007), the amphibamid *Doleserpeton* is proposed as the closest sister-group to all lissamphibians (including Albanerpetontidae), with *Amphibamus* as the sister taxon to the *Doleserpeton*-Lissamphibia clade. When applying the known morphologies of the humerus and elbow of the relevant taxa to this phylogeny, a gradual evolution of the lissamphibian traits within the temnospondyls appears. Thus, the entepicondylar foramen disappears in primitive temnospondyls. The capitulum of euskelian temnospondyls (such as *Eryops*) is enlarged and the entepicondyle points distally. In *Dissorophus*, the ectepicondyle takes on the shape of a low, rounded ridge, and the supinator process is absent. Finally, in *Doleserpeton*, the capitulum is larger still and the bone is elongated, essentially reaching the lissamphibian condition. Thus, the new data fit well with the phylogeny of Ruta and Coates (2007). However, it should be noted that the frequently poorly ossified distal and proximal ends and the preaxial limb ossification of salamanders may fit the branchiosaurid dissorophoids better than the closely related amphibamids (Fröbisch et al., 2007). Because these traits do not occur in anurans or in amphibamids, Carroll (2007) may be right in allying salamanders to branchiosaurids and frogs to amphibamids. The enigmatic albanerpetontids also share several humeral features with lissamphibians, including the lack of foramina and possession of a large, rounded capitulum (McGowan, 2002). These characters support the presumed lissamphibian affinities of Albanerpetontidae.

A potentially informative pattern is emerging when reviewing the evidence for lissamphibian origins, namely that although some studies find the lepospondyl theory to be more parsimonious



(Laurin and Reisz, 1997; but see Ruta and Coates, 2007), no known uniquely derived features of lissamphibians are shared with any lepospondyl, contrary to the situation for temnospondyls. Although there is always the possibility that convergence has taken place, this seems to be unlikely in the case of lissamphibian limb morphology because of the widely differing modes of locomotion seen in these animals. For instance, although *Eocaecilia* retains its limbs, it shows clear signs of limb reduction and elongation of the body (Jenkins et al., 2007), whereas frogs found at the same location were already highly specialized for saltation (Jenkins and Shubin, 1998). The monophyletic dissorophoid origins hypothesis (e.g., Ruta and Coates, 2007) fits the present data better than the other theories. If this hypothesis is correct, then the structures of the humerus and elbow joint as well as several previously described features such as pedicellate bicuspid teeth (Bolt, 1969; Parsons and Williams, 1963) and the posterior perilymphatic duct (Sigurdson, 2008) all would be uniquely derived traits shared by lissamphibians and their closest relatives among the dissorophoids. We suggest that this is the most likely explanation for the origins and relationships of lissamphibians at present.

## ACKNOWLEDGMENTS

Special thanks goes to Farish A. Jenkins (Harvard University) for making specimens available, adding supporting observations, and suggesting improvements to the manuscript. The authors also thank Robert L. Carroll, David M. Green, and Hans C. E. Larsson (all at McGill University, Montreal), Jean-Claude Rage (Muséum National d'Histoire Naturelle, Paris), Øyvind Hammer (University of Oslo), and Alan Resetar (Field Museum, Chicago) for helping in various ways.

## LITERATURE CITED

- Anderson JS. 2007. Incorporating ontogeny into the matrix: A phylogenetic evaluation of developmental evidence for the origin of modern amphibians. In: Anderson JS, Sues H-D, editors. *Major Transitions in Vertebrate Evolution*. Bloomington, IN: Indiana University Press. pp 182–212.
- Anderson JS. 2008. Focal review: The origin(s) of modern amphibians. *Evol Biol* 35:231–247.
- Anderson JS, Reisz RR, Scott D, Fröbisch NB, Sumida SS. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* 453:515–518.
- Báez AM, Basso NG. 1996. The earliest known frogs of the Jurassic of South America: Review and cladistic appraisal of their relationships. *Münchner Geowiss Abh* 30:131–158.
- Báez AM, Nicoli L. 2004. A new look at an old frog: The Jurassic *Notobatrachus* Reig from Patagonia. *Ameghiniana* 41:257–270.
- Bolt JR. 1969. Lissamphibian origins: Possible protolissamphibian from the Lower Permian of Oklahoma. *Science* 166:888–891.
- Carroll RL. 2007. The Palaeozoic ancestry of salamanders, frogs and caecilians. *Zool J Linn Soc* 150(suppl 1):1–140.
- Carroll RL, Gaskill P. 1978. *The Order Microsauria*, Vol. 126. Philadelphia: Memoirs of the American Philosophical Society. pp1–211.
- Carroll RL, Holmes RB. 2007. Evolution of the appendicular skeleton of amphibians. In: Hall BK, editor. *Fins into Limbs*. Chicago: University of Chicago Press. pp 185–224.
- Carroll RL, Bossy KA, Milner AC, Andrews SM, Wellstead CF. 1998. *Encyclopaedia of Paleoherpology*, part 1, Lepospondyli. München, DE: Verlag Dr. Friedrich Pfeil. 216 pp.
- Clack JA. 2002. *Gaining Ground. The Origin and Evolution of Tetrapods*. Bloomington and Indianapolis, IN: Indiana University Press. 400 pp.
- Coates MI. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: Postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Trans R Soc Edinburgh: Earth Sci* 87:363–421.
- Colbert EH. 1952. A pseudosuchian reptile from Arizona. *Bull Am Mus Nat Hist* 99:561–592.
- DeMar R. 1968. The Permian labyrinthodont amphibian *Dissorophus multictinctus*, and adaptations and phylogeny of the family dissorophidae. *J Paleontol* 42:1210–1242.
- Duellman WE, Trueb L. 1994. *Biology of Amphibians*, 2nd ed. Baltimore, MD: Johns Hopkins University Press. 670 pp.
- Evans FG. 1946. The anatomy and function of the foreleg in salamander locomotion. *Anat Rec* 95:257–281.
- Evans SE, Borsuk-Bialynicka M. 1998. A stem-group frog from the Early Triassic of Poland. *Acta Pal Pol* 43:573–580.
- Francis ETB. 1934. *The Anatomy of the Salamander*. Oxford: The Clarendon Press.
- Fröbisch NB, Carroll RL, Schoch RR. 2007. Limb ossification in the Paleozoic branchiosaurid *Apateon* (Temnospondyli) and the early evolution of preaxial dominance in tetrapod limb development. *Evol and Dev* 9:69–75.
- Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, De Sa RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC. 2006. The amphibian tree of life. *Bull Am Mus Nat Hist* 297:1–370.
- Gaupp E. 1904. *A. Ecker and R. Wiedersheim's Anatomie des Frosches*. Vols. 1-2. Braunschweig: Friedrich Vieweg und Sohn.
- Gregory JT, Peabody FE, Price LI. 1956. Revision of the Gymnarthridae. *American Permian Microsauria*. *Bull Peabody Mus Nat Hist* 10:1–77.
- Holmes R. 1977. The osteology and musculature of the pectoral limb of small captorhinids. *J Morph* 152:101–140.
- Holmes R. 1980. *Proterogyrinus scheelei* and the early evolution of the labyrinthodont pectoral limb. In: Panchen AL, editor. *The Terrestrial Environment and the Origin of Land Vertebrates*. London, EN: Academic Press. pp 351–376.
- Igawa T, Kurabayashi A, Usuki C, Fujii T, Sumida M. 2008. Complete mitochondrial genomes of three neobatrachian anurans: A case study of divergence time estimation using different data and calibration settings. *Gene* 407:116–129.
- Jenkins FA. 1973. The functional anatomy and evolution of the mammalian humero-ulnar articulation. *Am J Anat* 137:281–298.
- Jenkins FA, Shubin NH. 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. *J Vert Pal* 18:495–510.
- Jenkins FA, Walsh DM, Carroll RL. 2007. Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic. *Bull Mus Comp Zool* 158:285–365.
- Laurin M, Reisz RR. 1997. A new perspective on tetrapod phylogeny. In: Sumida SS, Martin KLM, editors. *Amniote Origins: Completing the Transition to Land*. New York, NY: Academic Press. pp 9–59.
- Maglia AM, Pugener LA, Mueller JM. 2007. Skeletal morphology and postmetamorphic ontogeny of *Acris crepitans* (Anura: Hylidae): a case of miniaturization in frogs. *J Morphol* 268:194–223.

- McGowan GJ. 2002. Albanerpetontid amphibians from the Lower Cretaceous of Spain and Italy: a description and reconsideration of their systematics. *Zool J Linn Soc* 135:1–32.
- Miner RW. 1925. The pectoral limb of Eryops and other primitive tetrapods. *Bull Am Mus Nat Hist* 51:145–312.
- Olson EC. 1941. The family Trematopsidae. *J Geol* 49:149–176.
- Parsons TS, Williams EE. 1962. The teeth of Amphibia and their relation to amphibian phylogeny. *J Morphol* 110:375–389.
- Pawley K, Warren A. 2006. The appendicular skeleton of Eryops megacephalus Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. *J Paleont* 80:561–580.
- Reisz RR. 1980. A protorothyridid captorinomorph reptile from the lower Permian of Oklahoma. *Life Sci Contrib R Ont Mus* 121:1–16.
- Reisz RR. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Spec Publ Mus Nat Hist Univ Kansas* 7:1–74.
- Ritland RM. 1955. Studies on the post-cranial morphology of *Ascaphus truei*. *J Morph* 97:215–282.
- Roček Z. 2000. Mesozoic anurans. In: Heatwole H, Carroll RL, editors. *Amphibian Biology, Volume 4: Palaeontology*. Chipping Norton: Surrey Beatty & Sons PTY Limited. pp 1295–1331.
- Roček Z, Rage J-C. 2000. Proanuran stages (*Triadobatrachus*, *Czatkobatrachus*). In: Heatwole H, Carroll RL, editors. *Amphibian Biology, Volume 4: Palaeontology*. Chipping Norton: Surrey Beatty & Sons PTY Limited. pp 1282–1294.
- Romer AS. 1956. *Osteology of the Reptiles*. Chicago, IL: University of Chicago Press. 772 pp.
- Ruta M, Coates MI. 2007. Dates, nodes and character conflict: Addressing the lissamphibian origin problem. *J Syst Paleontol* 5:69–122.
- San Mauro D, Gower DJ, Oommen OV, Wilkinson M, Zardoya R. 2004. Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1. *Mol Phylogenet Evol* 33:413–427.
- Schoch RR, Milner AR. 2004. Structure and implications of theories on the origin of lissamphibians. In: Arratia G, Wilson MVH, Cloutier R, editors. *Recent Advances in the Origin and Early Radiation of Vertebrates*. München: Verlag Dr. Friedrich Pfeil. pp 345–377.
- Shubin NH, Jenkins FA. 1995. An Early Jurassic jumping frog. *Nature* 377:49–52.
- Sigurdson T. 2008. The otic region of *Doleserpeton* (Temnospondyli) and its implications for the evolutionary origin of frogs. *Zool J Linn Soc* 154:738–751.
- Smithson TR, Carroll RL, Panchen AL, Andrews SM. 1993. *Westlothiana lizziae* from the Viséan of East Kirkton, West Lothian, Scotland, and the amniote stem. *Trans R Soc Edinburgh: Earth Sci* 84:383–412.
- Starck D. 1979. *Vergleichende Anatomie der Wirbeltiere auf evolutionsbiologischer Grundlage, Band 2: Das Skelettsystem*. New York, NY: Springer-Verlag. 776 pp.
- Sumida SS. 1997. Locomotor features of taxa spanning the origin of amniotes. In: Sumida SS, Martin KLM, editors. *Amniote origins, completing the transition to land*. New York, NY: Academic Press. pp 353–398.
- Walthall JC, Ashley-Ross MA. 2006. Postcranial myology of the California Newt, *Taricha torosa*. *Anat Rec* 288A:46–57.
- Warren AA, Snell N. 1991. The postcranial skeleton of Mesozoic temnospondyl amphibians: A review. *Alcheringa* 15:43–64.
- Wellstead CF. 1991. Taxonomic revision of the Lysorophia. Permo-Carboniferous Lepospondyl amphibians. *Bull Am Mus Nat Hist* 209:1–90.
- Williston SW. 1910. *Cacops*. *Desmospondylus*; new genera of Permian vertebrates. *Geol Soc Am, Bull* 21:249–284.
- Yates AM, Warren AA. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zool J Linn Soc* 128:77–121.

## APPENDIX

TABLE A1. Humeral measurements used in the analysis. Distal humeral width and capitulum width were measured perpendicularly to the length axis of the bone

Species	Specimen number/ reference	Humeral length (mm) = L	Distal humeral width (mm) = W	Capitulum width (mm) = C
<i>Ascaphus truei</i>	RM 4430	11.61	2.70	1.40
<i>Leiopelma hochstetteri</i>	RM 2215	9.29	2.58	1.40
<i>Prosalirus bitis</i>	MNA V 8725	11.30	3.00	1.60
<i>Xenopus laevis</i>	RM 2230	16.00	3.41	1.85
<i>Scaphiopus holbrookii</i>	RM 2425	17.80	4.00	2.50
<i>Bufo americanus</i>	RM 4999	37.50	9.90	5.50
<i>Acris crepitans</i>	Maglia et al. (2007)	10.52	2.33	1.47
<i>Dendropsophus koehlini</i>	RM 1226	5.37	1.09	0.57
<i>Conraua goliath</i>	FMNH 248829	57.00	15.50	11.00
<i>Rana catesbeiana</i>	RM 2785	41.50	11.70	6.80
<i>Rana pipiens</i>	RM2812	16.00	3.50	2.00
<i>Hynobius nigrescens</i>	MCZ 22513	10.10	2.77	1.31
<i>Andrias davidianus</i>	FMNH 166872	39.00	11.00	5.50
<i>Salamandra salamandra</i>	Francis, 1934	16.20	4.76	2.62
<i>Necturus maculosus</i>	RM 5002	25.70	6.89	2.85
<i>Ambystoma tigrinum</i>	RM 2161	13.50	4.30	2.30
<i>Desmognathus sp.</i>	RM 1601	3.10	0.70	0.39
<i>Dicamptodon tenebrosus</i>	CAS 210347	5.56	1.24	0.58
<i>Eocaecilia micropodia</i>	MCZ 9163	4.25	1.18	0.55
<i>Edops sp.</i>	MCZ 1781	187.50	115.40	54.20
<i>Eryops megacephalus</i>	MCZ 1220	138.70	93.70	33.80
<i>Acheloma sp.</i>	MCZ 2524	74.70	38.40	14.30
<i>Cacops aspideophorus</i>	Williston (1910)	59.70	33.50	11.10
<i>Dissorophus multicinctus</i>	MCZ 4176	77.20	36.50	15.80
<i>Doleserpeton annectens</i>	FMNH UR 1321	8.50	2.70	1.40
<i>Pantylus sp.</i>	MCZ 3692	26.90	13.90	4.00
<i>Trihecaton howardinus</i>	Carroll and Gaskill (1978)	13.70	5.00	1.90
<i>Cardiocephalus peabodyi</i>	MCZ 3692	8.25	2.75	1.10
<i>?Euryodus sp.</i>	FMNH PR 983	11.86	4.67	1.87
<i>Scincosaurus sp.</i>	Carroll et al. (1998)	5.80	2.50	1.09
<i>Westlothiania lizziae</i> <sup>a</sup>	Smithson et al. (1994)	9.31	3.60	1.16
<i>Captorhinus aguti</i>	Holmes (1977)	30.50	14.40	3.30
Captorhinidae inc. sed. <sup>b</sup>	S12-7e	89.45	61.60	14.65
Protorothyridae inc. sed.	Reisz (1980)	22.50	6.12	2.25
<i>Chrysemys picta</i>	RM 5004	44.00	11.10	3.60
<i>Petrolacosaurus sp.</i>	Reisz (1981)	53.33	15.46	5.40
<i>Sphenodon punctatus</i>	FMNH 11113	36.90	14.30	4.50
<i>Varanus albigularis</i>	RM 5003	83.50	32.60	6.50
<i>Crotaphytus sp.</i>	RM 5000	18.60	4.70	1.10
<i>Lacerta sp.</i>	RM 3556	6.59	1.74	0.52
<i>Shinisaurus crocodilurus</i>	Conrad (2006)	18.93	5.50	1.80
<i>Hesperosuchus agilis</i>	Colbert (1952)	94.00	13.87	4.37
<i>Alligator mississippiensis</i> (juv.)	RM 5005	41.70	9.70	3.50
<i>Dimetrodon limbatus</i>	MCZ 1347	168.00	102.00	22.50
<i>Eozostrodon sp.</i>	Jenkins and Parrington (1976)	13.88	4.13	1.13
<i>Didelphis virginiana</i>	RM 5020	62.80	18.50	5.30
<i>Proterogyrinus scheelei</i>	Holmes (1984)	76.66	47.52	10.47
<i>Ichthyostega sp.</i>	Jarvik (1996)	123.88	62.50	15.63
<i>Acanthostega gunnarii</i>	Coates (1996)	35.52	27.43	4.83

<sup>a</sup>*Westlothiania* was regarded as a stem amniote for the purposes of this study (Carroll and Holmes, 2007).<sup>b</sup>Uncataloged captorhinid specimen from Niger, field number is given, currently located in the Redpath Museum, Montreal.