

## Focal Review: The Origin(s) of Modern Amphibians

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**Abstract** The recent description of the stem batrachian *Gerobatrachus* has changed the terms of the ongoing debate on the origin of extant amphibians (Lissamphibia: frogs, salamanders, and the limbless caecilians). This important fossil, through a shared mosaic of unique derived salientian and urodele characters, links frogs and salamanders with an archaic group of fossil amphibians known as amphibamid temnospondyls. The present paper reviews the impact of this fossil on morphological and molecular phylogenies, and divergence timing estimates based on molecular models and the fossil record. In morphology, most recent efforts have focused on better characterizing the anatomy and relationships of amphibamid temnospondyls. Progress has also been made with the complete description of the earliest caecilian *Eocaecilia*; however, the question of caecilian origins remains unresolved at present. The large scale phylogenetic analyses all agree on the overall tetrapod tree phylogenetic structure, and the largest analyses agree that the origin of at least frogs and salamanders among fossils from family Amphibamidae. Conversely, all molecular based analyses find a monophyletic Lissamphibia, and a Batrachia terminal dichotomy, which raises questions over either the validity of morphological analyses that support lissamphibian polyphyly or about the possibility of long branch attraction given the short internal divergences and long subsequent branches. Paradoxically, the estimated date of the lissamphibian divergence best matches the fossil record if timed to the split between lepospondyls and temnospondyls. Future research should focus on development and fine details of cranial

anatomy of fossil and extant amphibians to produce new evidence and clarity into the question of lissamphibian, and especially caecilian, origins.

**Keywords** Lissamphibia · Temnospondyli · Lepospondyli · Molecular clock · Divergence estimate · Origins hypothesis · *Gerobatrachus* · Phylogenetic analysis · Development

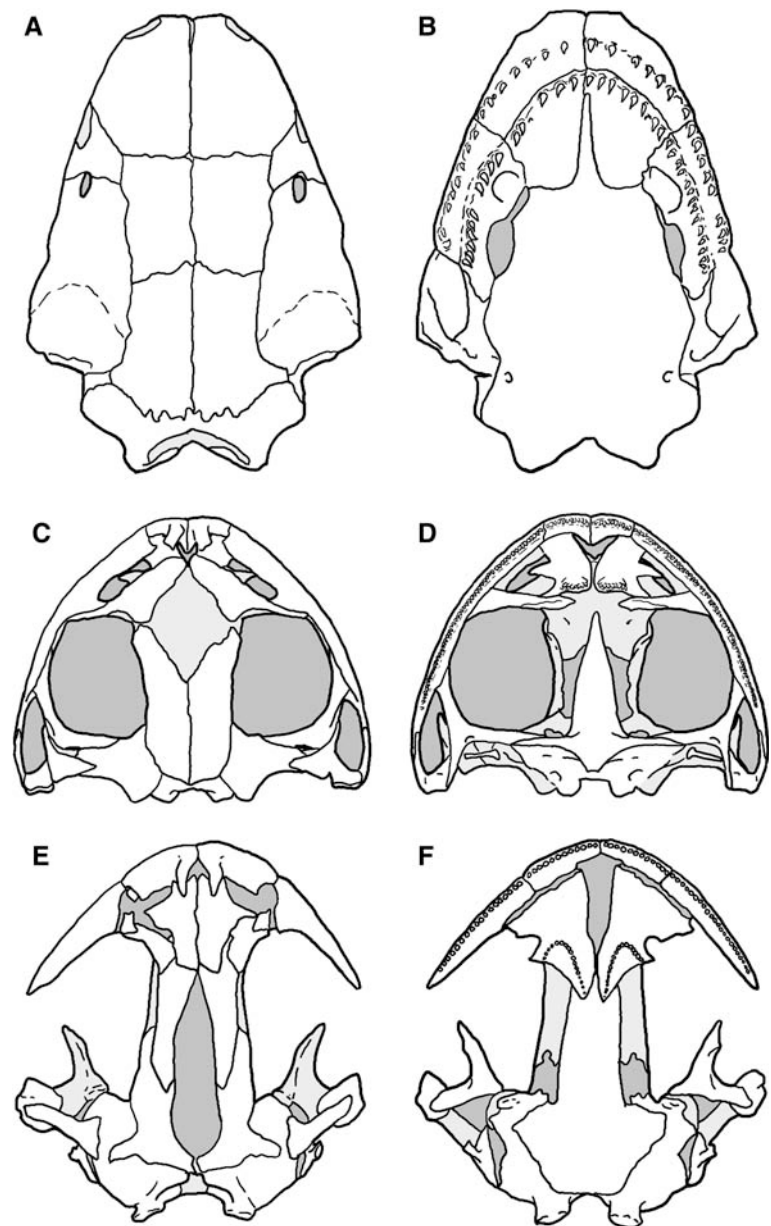
### Introduction

The origin of modern amphibians (Lissamphibia: frogs, salamanders, and the limbless caecilians; Fig. 1) has been one of the more contentious questions in vertebrate evolution in recent years. Recently, colleagues and I described an important new fossil (Anderson et al. 2008b), which phylogenetic analysis placed near the Batrachian (frog–salamander) divergence. If correct, this fossil has wide ranging implications to the ongoing discussions of modern amphibian origins, which are reviewed here. Considering the amount of controversy that has surrounded this question, the present review is presented as a focal review, with commentary by many of the principals in the debate to follow in order to present as broad a consensus as possible given the current evidence at hand and the vastly differing opinions involved. Because the debate over lissamphibian origins is fundamentally about which fossil group is sister group to each of the lissamphibian orders, the primary focus of the review is on the paleontological literature, but molecular phylogenetics and development are more and more frequently being marshaled into this debate, so it is hoped this review and subsequent discussion will be interesting to both the interested paleontologist and the herpetologist alike.

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**Fig. 1** Lissamphibians. The caecilian *Dermophis mexicanus* in **a** dorsal, and **b** palatal views. Redrawn from Wake & Hanken (1982). The anuran *Gastrotheca walkeri* in **c** dorsal and **d** palatal views. The caudatan *Salamandrella keyserlingii* in **e** dorsal and **f** palatal views. Both redrawn from Duellman and Trueb (1994)



First, there should be a brief word on the use of taxon names throughout the paper. Whereas Linnean classification is the predominant paradigm in the biological sciences, its orderly system of families, orders, etc., does not easily fit into current techniques of phylogenetic reconstruction and the modern concept of monophyly (de Queiroz and Gauthier 1990, 1992; de Queiroz 1992). Subsequently, many of the taxon names used throughout this paper have been defined following Phylogenetic Nomenclature as set out by de Queiroz and Gauthier (1990, 1992) in order to preserve both the traditional taxonomic content of the groups but more in keeping with current thinking on monophyly. This leads to some awkward statements throughout the paper where higher taxa (say, Batrachia or Lissamphibia) are said to be nested within lower taxa, like

families (say, Amphibamidae). The reader should keep in mind that this refers to the pattern of relationships of the relevant groups on a phylogenetic tree in instances where the family is paraphyletic with respect to the origin of one of the higher taxonomic groups. This awkwardness stems from a clash between phylogenetic methods and a class-based, typological classification system. The overall classification could be revised in light of new findings of relationship, of course, but because the phylogeny of these groups is still uncertain, the names of groups rendered paraphyletic in this fashion are retained for convenience of communication.

A brief summary of the problem of lissamphibian origins as it currently stands follows in order to provide necessary background for the subsequent discussion, but

the interested reader is encouraged to see the more detailed historical reviews in Schoch and Milner (2004) and the recently published translation of the work by Lebedkina (2004) for a fuller context. For the purposes of this discussion, tetrapod monophyly is assumed, and previous ideas of an independent salamander origin among different sarcopterygian “fish” than all other tetrapods are disregarded. Since the focus of this review is on the question of lissamphibian origins, attention will be focused primarily on the first exemplars of crown lissamphibians and their putative sister taxa, and will not address the perhaps equally controversial questions of the relationships and divergence timing estimates within the crown groups.

Three hypotheses have been at the center of the debate: a monophyletic origin within Temnospondyli (Temnospondyl Hypothesis, TH), a monophyletic origin within Lepospondyli (Lepospondyl Hypothesis, LH), or a polyphyletic origin within both Temnospondyli and Lepospondyli (Polyphyly Hypothesis, PH; Fig. 2). Historically, as exemplified by the classification of Romer (1945), modern amphibians were not considered to have a single evolutionary origin. Romer placed Salientia (crown group frogs, or Anura, and their fossil stem group) as a superorder within subclass Aspidospondyli, with most Paleozoic fossil amphibians (the paraphyletic “Labyrinthodontia”, including temnospondyls, embolomeres, semouriamorphs, baphetids, and ichthyostegids). Caudata (crown group salamanders, or Urodela, and their fossil stem group) and Gymnophiona (crown group caecilians, or Apoda, and their fossil stem group) were recognized as two of several orders of Lepospondyli, along with Aïstopoda, Nectridea, and Microsauria. From this perspective, the PH should be viewed as the historical opinion on lissamphibian origins.

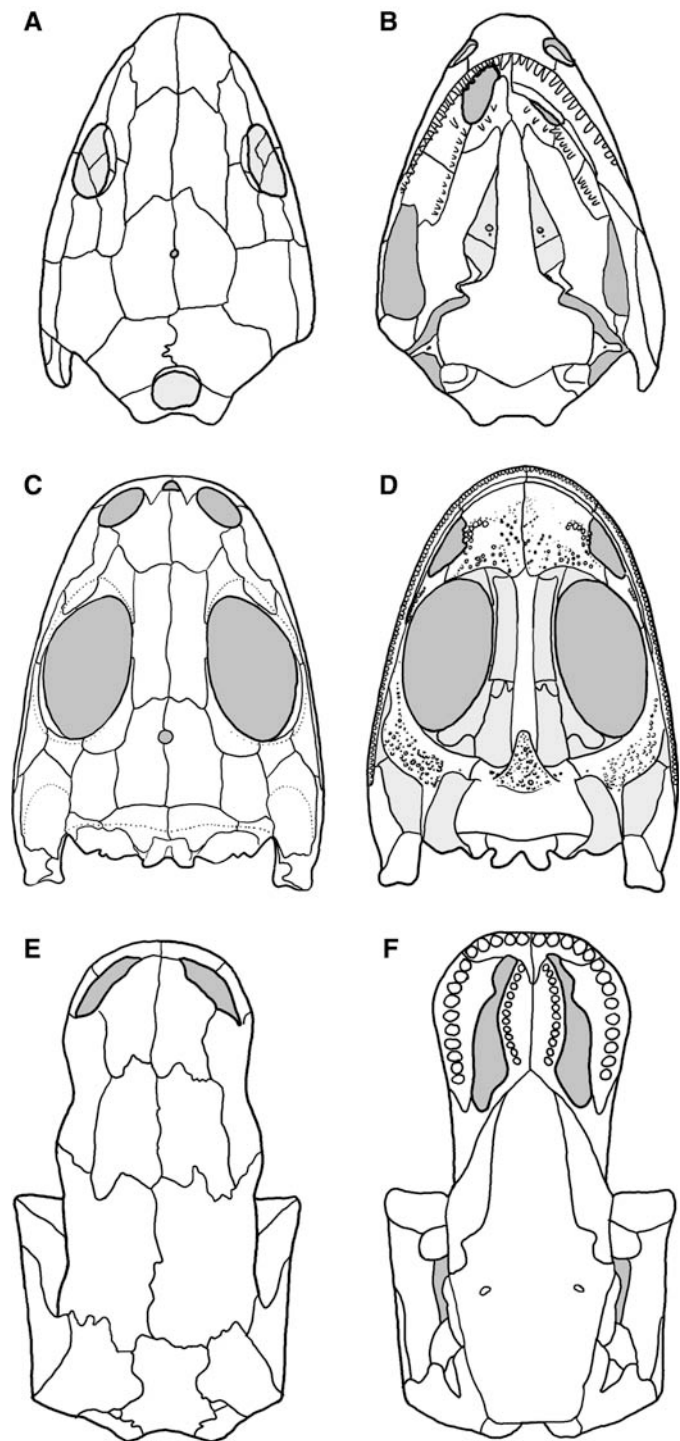
This view changed after the publication of a seminal paper by Parsons and Williams (1963). In it Parsons and Williams reviewed commonalities in anatomy between frogs, salamanders, and caecilians, and concluded that the number of shared, unique features they found supported a monophyletic origin for lissamphibians (Table 1). The majority of these features are based in soft tissue anatomy, and thus not observable in the fossil record. However, two features, pedicellate teeth (where the cusp and base of the tooth are separated by a “dividing zone” of poorly ossified matrix; see (Davit-Beal et al. 2007) for a recent review of this feature) and the operculum–opercularis complex of the middle ear (the operculum is a bone that sits in the fenestra vestibuli in articulation with the footplate of the stapes in the middle ear) are based on hard tissues and are unique to at least some lissamphibians (extant caecilians, lacking a pectoral girdle, do not have an operculum, but see below). A third feature, the presence of an unique patch of sensory tissue in the inner ear known as the amphibian papilla, may also have an osseous correlate (Sigurdson 2008). With the

description of the important “protolissamphibian”, the amphibamid temnospondyl *Doleserpeton* (Bolt 1969), which demonstrated for the first time the presence of pedicellate teeth in a fossil amphibian, the majority view became that a monophyletic Lissamphibia is derived within Temnospondyli (Fig. 3). The TH remains by far the majority view on the question of lissamphibian origins.

However, this view was not universally adopted. In particular, Carroll and colleagues argued for retaining Romer’s view in a series of papers, citing cranial anatomical similarities (Carroll and Currie 1975) and inferred passage of cranial nerves around jaw adductor musculature (Carroll and Holmes 1980) as evidence for considering caecilians and salamanders, respectively, as descended from lepospondyls. More recent, detailed studies of the development of branchiosaurs in comparison with salamanders (Schoch 1992, 2002) have changed Carroll’s views on salamander origins. Carroll argues that a secession of ossification at an early stage of the ontogeny of branchiosaurs would produce a salamander, and he also cites as evidence the similarity in the pattern of gill rakers seen in branchiosaurs and hynobid salamanders (Schoch and Carroll 2003; Carroll 2004, 2007). This is the current formulation of the PH, where frogs and salamanders have their origins within temnospondyls (with either a monophyletic Batrachia nested within a paraphyletic assemblage of amphibiamids, or a branchiosaur–salamander and amphibamid–frog sister group relationship), and caecilians within lepospondyl “microsaurs” (Fig. 4). Until recently, (Anderson 2007; Anderson et al. 2008b) this view has not been supported by a large scale phylogenetic analysis, but recent analyses by myself and colleagues, based on an expanded version of an earlier phylogenetic analysis of lepospondyls (Anderson 2001), are now finding some support for this idea.

The LH is the other minority view, championed by Laurin and colleagues (Laurin and Reisz 1997, 1999; Laurin 1998; Vallin and Laurin 2004). According to this hypothesis, lissamphibians have a monophyletic origin within lepospondyls, specifically as sister taxa to the elongate, aquatically adapted lysorophians (Wellstead 1991, 1998) within a paraphyletic Microsauria (Fig. 5). Lissamphibians in this hypothesis are arranged with frogs as the first group to branch off, and salamanders and caecilians formed the terminal dichotomy, an arrangement named Procera. This hypothesis has engendered some pointed discussions in the literature (Coates and Ruta 2000; Laurin et al. 2000a, b; Anderson 2001, 2002b; Laurin 2002; Ruta et al. 2003; Laurin and Anderson 2004) stemming primarily from the redefinition of some well-known names with long histories based on this analysis rather than the tree shape per se. In their review, however, Schoch and Milner (2004) commented on the adequacy of the matrix underlying this

**Fig. 2** Possible fossil outgroups to lissamphibians. The recumbirostran (“microsaur”) lepospondyl *Rhynchonkos* in **a** dorsal and **b** palatal views. Redrawn from Carroll (2007). The amphibamid temnospondyl *Dolesempetron* in **c** dorsal and **d** palatal views. Redrawn from Bolt (1969). The lysorophian lepospondyl *Brachydectes* in **e** dorsal and **f** palatal views. Redrawn from Wellstead (1991)



hypothesis, criticizing the limited number of taxa analyzed (see also Ruta et al. 2003). They were particularly critical of the preponderance of “loss characters” supporting the LH tree shape, given the relative ease these losses can arise via paedomorphosis, which appears to evolve repeatedly.

This brief historical background brings us to the review of Schoch and Milner (2004), whose main conclusion, after a thorough review of the literature, was that the TH

involved fewer “unparsimonious assumptions”. They also concluded that the internal relationships of Lissamphibia supported a Procerata-Salientia arrangement rather than a Batrachia- (frogs and salamanders as sister taxa) Gymniophiona topology. In the remaining paper I will discuss how these ideas have been supported or refuted in more recent years, with an emphasis on the challenges presented by recent fossil discoveries.



**Table 1** Characters cited by Parsons and Williams (1963) as evidence for the monophyletic status of Lissamphibia

<b>Pedicellate teeth</b>
<b>Operculum–pectrum complex</b>
<b>Papilla amphibiorum</b>
Green rods
Structure of m. levator bulbi
Fat bodies associated with gonads
Structure of skin glands
Cutaneous respiration
Chromosomes and DNA content

Characters that are potentially observable in fossils are indicated by bold text. From Anderson (2007)

**New Fossils**

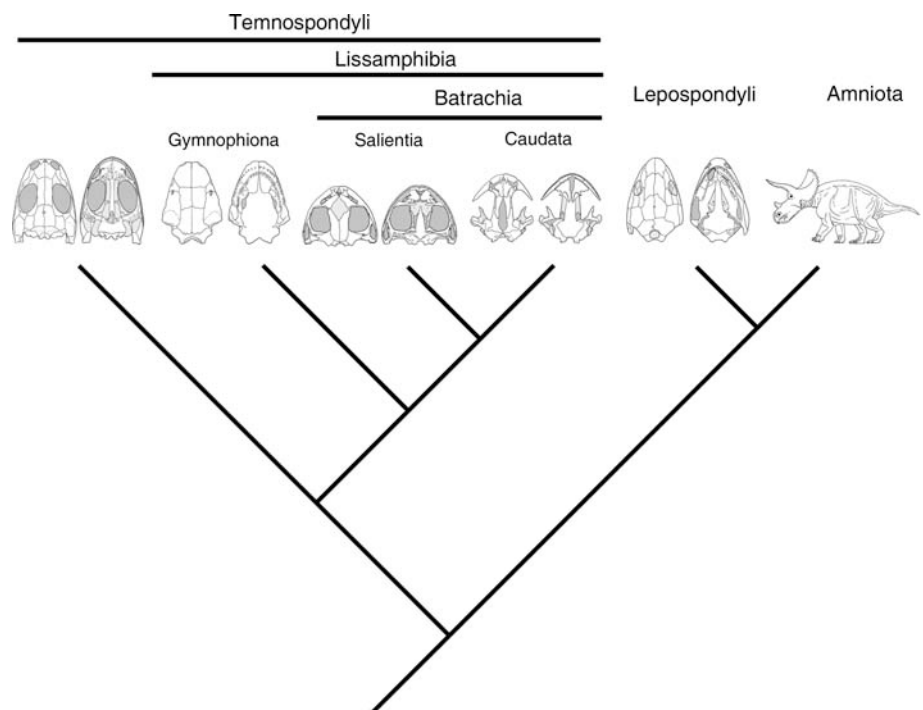
The on going debate over lissamphibian origins has motivated intensive new research into the putative fossil sister taxa at the heart of the various hypotheses. New taxa have been described, and previously studied taxa have been revised in an effort to discover new, or unrecognized, characters that would provide additional insight into this question.

The most significant new fossil to be described since the review of Schoch and Milner (2004) is the stem batrachian *Gerobatrachus* (Anderson et al. 2008b). This fossil is nearly perfectly intermediary between derived amphibamid temnospondyls such as *Doleserpeon* (Bolt 1969) and the

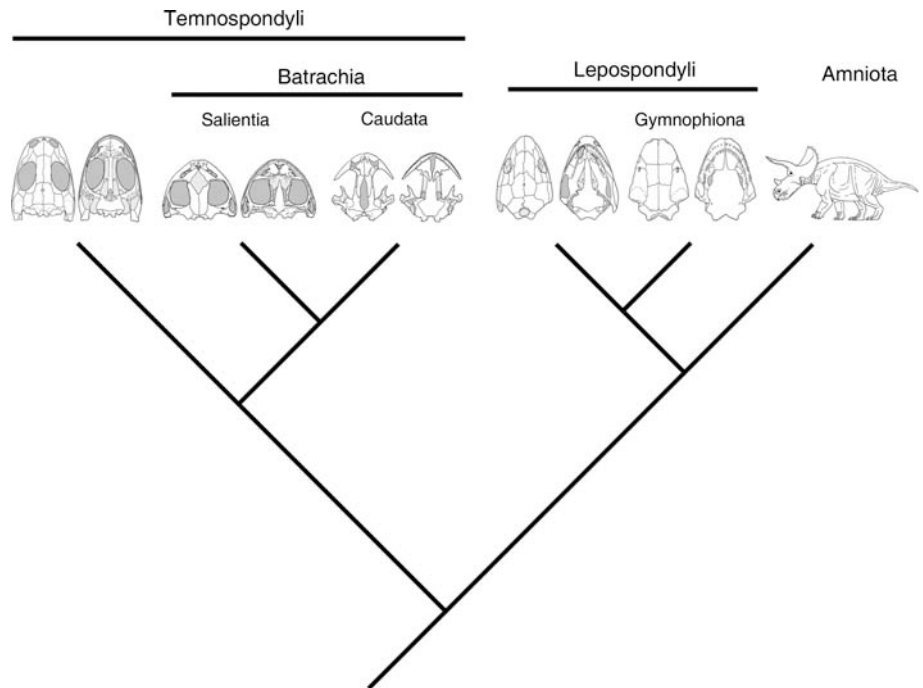
earliest frogs and salamanders (Fig. 6), but shows these features in a mosaic pattern compared with the presumably more canalized morphology of the extant batrachians. Like frogs, it has a lightly built, strut-like, broad and open skull with large otic notches, an anteroposteriorly narrowed vomer with rows of evenly sized teeth on raised patches instead of fang and pit pairs, and a laterally directed, rod-like anterior ramus of the palatine. The pterygoids are reduced in their anterior extent, barely reaching the marginal tooth row. *Gerobatrachus* shares with salamanders the unique feature of a basale commune, or an integrated distal tarsal one and two, in the pes, which also is suggestive of the presence of a digital arch that passes in a preaxial direction. This pattern of digital development is uniquely known in salamanders (Shubin and Wake 2003), and was recently described in branchiosaurid temnospondyls, which might be sister group to, or nested within, Amphibamidae (Fröbisch et al. 2007). The vertebral column of *Gerobatrachus* has 17 presacral vertebrae, which is intermediate in number between derived amphibamids like *Amphibamus* (21) and the stem frog *Triadobatrachus* (14) and stem salamanders *Chunerpeton* and *Kaururus* (14–15). In filling the morphological gap between frogs and salamanders on the one hand and amphibamids on the other, *Gerobatrachus* solidifies the TH or PH, and in my mind the question of lissamphibian origins now becomes the question of caecilian origins.

On this point, the past year has seen the publication of the detailed description of the first caecilian, the limbed

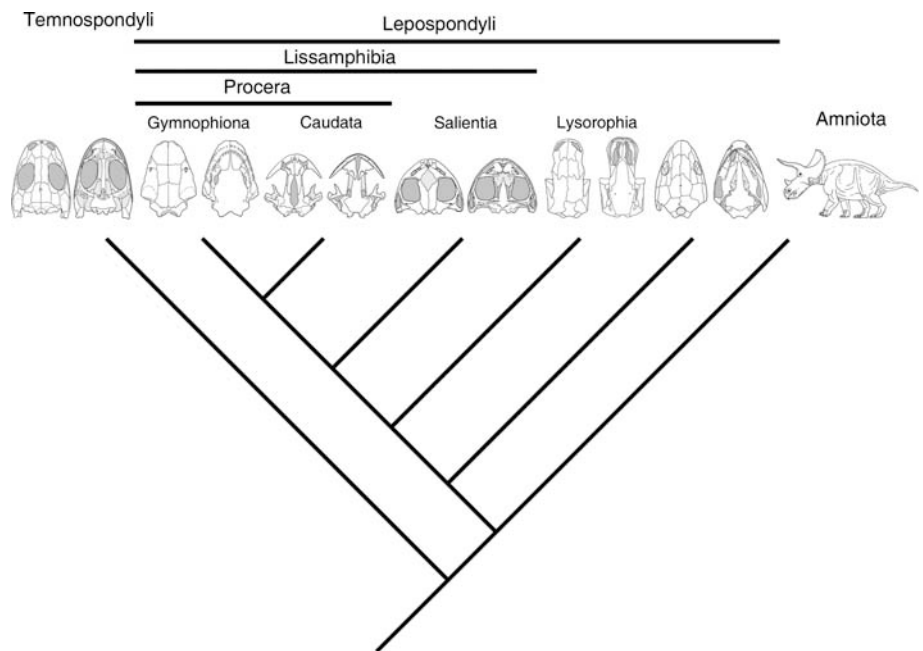
**Fig. 3** The tetrapod tree under the Temnospondyl Hypothesis. Numerous intervening taxa removed for clarity



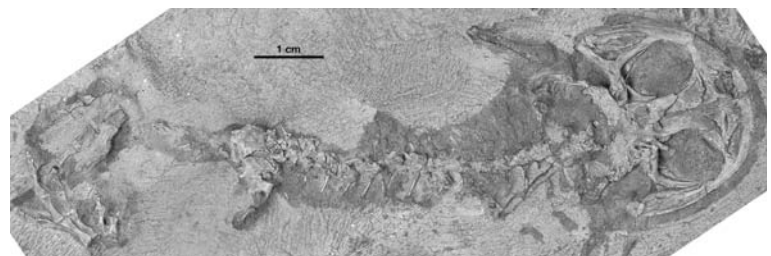
**Fig. 4** The tetrapod tree under the Polyphyly Hypothesis



**Fig. 5** The tetrapod tree under the Lepospondyl Hypothesis



**Fig. 6** The stem batrachian *Gerobatrachus* Anderson et al. (2008b)



*Eocaecilia* from the Jurassic (Jenkins et al. 2007). *Eocaecilia* is significant in polarizing a number of uncertain caecilian features, for instance it has a stegokrotaphic skull, and retains limbs, a shorter presacral skeleton, and longer caudal skeleton. Unique caecilian features are seen to be in early stages of evolutionary transformation, such as the degree of coossification throughout the skull, and the jaw adductor system. The tentacle may be evidenced in an early stage of elaboration as a groove in the anteroventral portion of the orbit. Significant for the lissamphibian origins question, *Eocaecilia* has been described as having an operculum, which would make it the only caecilian to retain this structure, held to be a lissamphibian synapomorphy. However, the placement of this structure, medial to the described fused quadrate and stapes and fully infilling the fenestra vestibularis, is unique among lissamphibians, which raises questions about the identified homologies in this region of the skull.

*Eocaecilia* indicates that stegokrotaphy in the caecilian skull is a primitive, not derived, state, although it is always possible that the skull was open like frogs and salamanders deeper in the caecilian stem lineage, considering the young (Jurassic) age of the fossil. Wake (2003) recently reviewed the history and evidence of this issue, and concluded that stegokrotaphy was derived. As evidence, she cited the developmental data of Wake and Hanken (1982), who studied the caecilian *Dermophis* and found that early in ontogeny caecilians have both an open and mobile skull, which closed and became more rigid in adulthood. This they took to mean that stegokrotaphy was incomplete throughout most of the life of a caecilian, and the roofing of the skull a convergence with microsaur due to the shared burrowing mode of life. Wake also cited the work of Nussbaum (1983), who offered four lines of evidence for secondary stegokrotaphy: the absence of temporal bones between the parietal and squamosal, a unique postorbital region suggesting remodeling, the weak stegokrotaphy of ichthyophids and zygokrotaphic skulls of rhinatrematids, and the poorly developed dual jaw closing mechanism of rhinatrematids. However, the trend towards the reduction of the temporal seems to have already commenced in microsaur, when gymnarhrids, *Rhynchonkos*, and brachystelechids are considered in a transitional series (Carroll 2000; Anderson 2001, 2007; Jenkins et al. 2007; Anderson et al. 2008b). Furthermore, the dual jaw closing mechanism appears to have been present in *Eocaecilia* (Jenkins et al. 2007), which suggests that it is secondarily reduced in rhinatrematids.

In filling in the morphological gap between crown caecilians and the more archaic putative sister groups, *Eocaecilia* is critical for exploring the difficult question of caecilian origins. I remain struck by how divergent *Eocaecilia* is from the batrachians and amphibamid

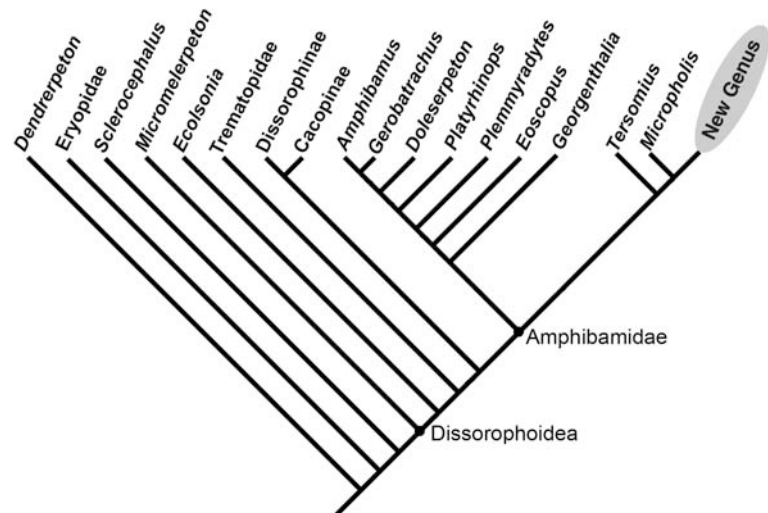
temnospondyls, but acknowledge there also remains a gap (now much narrowed) between *Eocaecilia* and the recumbirostran (pantylid, gymnarhrid, ostodolepid, brachystelechid, and goniiorhynchid “microsaurs”) lepospondyls. For example, *Eocaecilia* has not fully coossified all elements into the highly consolidated skull seen in extant caecilians (Wake 2003) and appears in this respect transitional between the somewhat consolidated skull of *Rhynchonkos* and the extant forms (Carroll 2007). On the other hand, *Eocaecilia* has a much wider interpterygoid vacuity, as seen in temnospondyls, not lepospondyls (Anderson 2001). A major challenge to paleontology is to fill in the significant gaps in the caecilian fossil record, both between *Eocaecilia* and the first crown caecilian fossils, and between *Eocaecilia* and the putative lepospondyl and temnospondyl sister taxa.

Among the putative fossil sister groups, relatively little has been done to provide new knowledge of lepospondyl “microsaur” anatomy since the review of Schoch and Milner (2004). Anderson and Reisz (2003) described a new gymnarhrid “microsaur” from the fissure fill deposits near Richard’s Spur (Ft. Sill), Oklahoma. This new taxon, *Bolterpeton*, seems to demonstrate weakly bicuspid teeth, a possible first stage in the development of the fully bicuspid teeth seen in lissamphibians (Bolt 1980). Vallin and Laurin described for the first time the anterior portion of the palate of *Microbrachis*, a “microsaurian” lepospondyl. Whereas there were few lepospondyl descriptions published recently, lepospondyls currently are receiving intensive study from a number of research groups around the world, and the next couple of years will see the publication of a number of studies that will be relevant to evaluating the question of lissamphibian origins.

The most progress has been made in our understanding of the anatomy and relationships among amphibamid temnospondyls, at the heart of the TH and PH. Bolt established the importance of the group from his description of *Doleserpeton*, and subsequent descriptions of tooth pedicely and bicuspidality in *Amphibamus* and “*Tersomius*” (Bolt 1969, 1977, 1979, 1980, 1991). Because of this, many of the first phylogenetic studies assumed the TH and instead of testing lissamphibian monophyly examined the in group relationships of lissamphibians within dissorophoid temnospondyls (e.g., Bolt 1991; Trueb and Cloutier 1991). This recent work on amphibamids (Schoch and Rubidge 2005; Huttenlocker et al. 2007; Anderson et al. 2008a; Fröbisch and Reisz 2008) has established a detailed new view of amphibamid relationships (Fig. 7) by naming several new taxa, identifying a number of key amphibamid characters, and extending earlier phylogenetic studies (Bolt 1991; Trueb and Cloutier 1991; Clack and Milner 1993).

These new studies have achieved a significant improvement in our understanding of the interrelationships of the

**Fig. 7** Tree of amphibamid temnospondyl relationships, from Fröbisch and Reisz (2008)



small, generalized temnospondyls that are probably the sister group of some, or all, lissamphibians. Most significant is the emerging view of two clades of amphibamids, one of longer-headed, more plesiomorphic forms, and a clade of smaller forms leading to crown batrachians or lissamphibians. In the latter clade, significant morphological trends towards the batrachian condition are emerging, perhaps driven by pedomorphosis. The skull takes on a broadly rounded shape in dorsal view. The orbits and otic notches, large at younger sizes, continue to dominate the skull with positive allometric growth so that the orbits are placed very closely together on the dorsal skull roof and are a significant proportion of the total skull length, and the otic notches project anterior to nearly articulate with the postorbital bar. The dermal cranial architecture has had to adjust to accommodate the larger sensory capsules, evidenced by the posteriorly constricted frontals (leading to an anterolateral flaring) and a distinctive falciform (sickle-shaped) post-frontal. The interpterygoid vacuities are widely rounded laterally, and because of this, the anterior portion of the palatine changes to a rod-like, more mediolaterally directed strut rather than a broad and more anteriorly oriented tooth bearing surface. The vomers become anteroposteriorly constricted and lose the plate-like morphology seen in more basal forms, whereas in the intervomerine depression a foramen opens, which in crown batrachians becomes quite extensive. Palatal fangs are lost, and are replaced by patches of small teeth arranged in rows on raised surfaces like in batrachians. The marginal teeth become small and numerous, and, in the most derived amphibamids, pedicellate and bicuspid. These changes reach their epitome in the stem batrachian *Gerobatrachus*, which further reinforces the changes seen in cranial architecture with the previously mentioned postcranial modifications characteristic of the batrachian condition.

Additionally, Schoch and Fröbisch (2006) described the postmetamorphic portion of the ontogeny of the paedomorphic branchiosaur *Apateon* for the first time. Branchiosaurs are closely related to amphibamids, if not included in the latter group (e.g., Anderson 2007), and have been suggested to be closely related to salamanders because of shared similarities in the sequence of cranial ossification (Schoch 1992; Carroll 2004; Schoch and Fröbisch 2006; Carroll 2007). Schoch and Fröbisch described a fully metamorphosed branchiosaur, which turned out to be very amphibamid-like in its superficial dermatocranial anatomy (the palate remains distinct in a number of features). This study is significant because it solidifies branchiosaurs as a distinct group of Paleozoic amphibians rather than an early developmental stage of another taxon, as had been the case of a number of earlier members of Branchiosauridae (Boy and Sues 2000).

Phylogenetic hypotheses are tested by the discovery of new taxa and new characters. To find the latter, there is a new emphasis on the study of extremely small, internal structures previously overlooked, or unobservable, by morphologists. Sigurdson (2008) has examined the otic region, one of the two osseous features previously cited as uniting lissamphibians (Table 1), of the amphibamid *Dolesempetron* in great detail using microscopy, and has found some similarities to the condition seen in modern frogs. Frogs uniquely among lissamphibians have a mating system based on auditory calls, and have retained the large otic notches seen in derived amphibamids. He identified the presence of possible attachment sites for the tympanic annulus on the otic capsule, the possible locations for some of the auditory papillae, and evidence supporting the presence of a frog-like perilymphatic duct. He also identified a jugular foramen closely associated with a perilymphatic foramen, based in part on a recent



description of a basal temnospondyl braincase revealed by CT (Robinson et al. 2005).

However, these observations need to be made in a wider number of taxa before concluding that *Dolesempetron* and frogs share uniquely derived otic features, rather than retaining states from a much deeper ancestor. Further work to understand detailed braincase anatomy and ontogeny in temnospondyls closer to Amphibamidae than *Dendrerpeton*, in this case a trematopid, is already underway in my lab (Maddin et al. 2007) and others, and will help establish how widespread the features described by Sigurdson might be. We are also studying lepospondyl braincase anatomy to search for the same features in the other putative lissamphibian out group (Maddin and Anderson 2008), and to explore how far down in to the fossil record the diversity seen in the modern amphibians extends. This work will provide further resolution to the lissamphibian problem and hopefully will explain how the highly divergent caecilian skull came to be.

### Fossils and Molecules: Topologies and Timing

The discovery of *Gerobatrachus* has challenged more than just the morphological phylogenies of a few paleontologists; its position of this fossil in the stratigraphic column has implications for discussions about divergence timing

estimates and phylogenies constructed from molecular data. Most large scale morphological analyses (Laurin and Reisz 1997; Laurin 1998; Anderson 2001, 2007; Ruta et al. 2003; Vallin and Laurin 2004; Ruta and Coates 2007; Anderson et al. 2008b) have found lepospondyls to be sister taxa to amniotes and their stem, which means the expectation for molecular phylogenies is that lissamphibians should be paraphyletic with respect to Amniota under the PH. However, all molecular analyses published since early 2003 (the latest literature considered in the review of Schoch and Milner 2004) have found support for a monophyletic Lissamphibia, and all but one (and the exception was weakly supported) supported the terminal dichotomy of Batrachia (frogs and salamanders; Table 2). Additionally, all molecular estimates of divergence time find dates more ancient than the fossil record suggests from a literal reading. These results present several challenges, which I will address as areas where future research could be best focused.

This contradiction between the molecular and some morphology-based phylogenies has led some authors to call for the rejection of the PH (Laurin 2002; Marjanović and Laurin 2007). However, the authors of one of the larger molecular studies take a very different stance, stating, “Testing lissamphibian monophyly and the relationships among the three crown groups of amphibians was and continues to be daunting because morphologically the

**Table 2** A summary of molecular based studies published since early 2003

Study	Gene(s)	Monophyly?	Terminal dichotomy	Basal divergence estimate (MA)	Terminal divergence estimate
Zardoya et al. (2003)	Protein coding mitochondrial genome (amino acids) (3.7 kb)	Yes	Batrachia	Clock-like tree rejected	Clock-like tree rejected
Zhang et al. (2003)	Protein coding, rRNA, tRNA mitochondrial genome (9.4 kb)	Yes	Procera	N/A	N/A
San Mauro et al. (2004)	Complete mitochondrial genome, nuclear RAG1 (3.9 kb)	Yes	Batrachia	N/A	N/A
San Mauro et al. (2005)	Nuclear RAG1 (1.4 kb)	Yes	Batrachia	367 (417–328)	357 (405–317)
Zhang et al. (2005)	2 rRNA and 12 protein coding mitochondrial genes (7.7 kb)	Yes	Batrachia	337 (321–353)	308 (289–328)
Frost et al. (2006)	Mitochondrial transcription unit H1; nuclear genes histone H3, rhodopsin, tyrosinase, seven in absentia, and the large ribosomal subunit 28S (2.3 kb)	Yes	Batrachia	N/A	N/A
Roelants et al. (2007)	Mitochondrial 16 s, Nuclear CXCR4, NCX1, RAG1, and SLC8A3 (3.75 kb)	Yes	Batrachia	369 (344–396)	358 (333–385)
Hugall et al. (2007)	RAG1 (3 kb)	Yes	Batrachia	323 (304–332) 292 (264–320) AA	274 (253–295) 267 (238–296) AA
Vieites et al. (2007)	RAG1, BDNF, POMC (2.7 kb)	N/A	Batrachia*	N/A	322 (308–336)
Igawa et al. (2008)	Whole mitochondrial genomes; ([1] 3197 AA, [2] 11 kb)	Yes	Batrachia	355 (370–340)	335 (352–317)

\* Caecilians were not included in the analysis; Batrachia assumed

groups are mutually very divergent and temporally distant from each other and from nonamphibian relatives. Furthermore, testing lissamphibian monophyly may be outside the ability of this study to address inasmuch as the major controversy has to do with the phylogenetic structure of various fossil groups.” (Frost et al. 2006, p. 23)

Those that call for the rejection of the PH overlook two other possible sources for error, so further investigation should address all three alternatives. The first possibility, implied by Marjanović and Laurin (2007), is that the studies supporting the PH (Anderson 2007; Carroll 2007; Anderson et al. 2008b) are incorrectly displacing caecilians away from batrachians. When dealing with large taxonomic samples spanning a large degree of morphological divergence, specific positive synapomorphies can be overwhelmed by a large number of “loss features” of questionable homology (Ruta et al. 2003; Schoch and Milner 2004; Ruta and Coates 2007) and homoplasies driven by animals in the same adaptive zones, if the characters are not studied and coded with care. Additional characters should be sought by, for example, exploring fine details of cranial anatomy in lepospondyls, temnospondyls, and lissamphibians such as the braincase, inner ear, and middle ear, which will test the caecilian–microsaur relationship. New taxa are the best source of new phylogenetic data, and they in turn suggest new areas for additional investigation for new character data as well, as exemplified by the detailed information we now have on *Eocaecilia* (Jenkins et al. 2007).

The second possibility is that the molecular trees are systematically biased to find the incorrect topology. The lissamphibian problem is particularly difficult not only for morphology but for molecules because of its ancientness. The lissamphibian topology found by the molecular studies is typified by rapid divergences (i.e., short internodes) followed by long branches, and thus potentially falls into the Felsenstein Zone (Felsenstein 1978; Huelsenbeck and Hillis 1993) where parsimony, and all other methods of phylogenetic inference (as reviewed in Bergsten 2005), can be positively misleading. In this “zone”, simply adding additional characters (which are readily available in molecular phylogenetics) can make the problem worse as it will reinforce the strength of association of the long branches, as measured by various support metrics (Felsenstein 1978). Similarly, adding taxa to break down the long branches can reinforce incorrect topologies if the added taxa are from towards the tip (Kim 1996; Poe and Swofford 1999), and it is with this final point that the lissamphibian problem is most intractable for molecular analyses.

Assuming the divergence dates of San Mauro et al. (2005), for example (which also provides one of the oldest divergence estimates, but the precise dates are not critical

to this argument), are accurate relatively, the problem becomes quickly clear. The lissamphibian origin was dated at 367 Ma, and the Batrachian divergence at 357 Ma. However, the divergences within crown caecilians, frogs and salamanders date to only 214, 262, and 273 Ma, respectively. In other words, the first 90–150 million years of lissamphibian evolution—the stems of all crown groups—is unavailable to molecular sampling; only the tips can be added, and the long branches cannot be broken down. These numbers are also probably overestimates too; when one examines the divergence dates of the modern families the dates quickly get much younger (i.e., Ranoidea at 99 Ma, Hyloidea at 66 Ma). Perhaps magnifying the affect of the short internal branches of interest is the fact that the actinopterygian and sarcopterigian outgroups commonly used are themselves very distantly removed from the internal branches of interest; one study estimated the “rhipidistian/dipnoan—tetrapod” split as occurring 50 Ma before the basal lissamphibian divergence from amniotes (Zhang et al. 2005). One possible approach to resolving possible long-branch attraction comes from adding morphology to the molecular datasets (Bergsten 2005), but here we run into the same problem outlined in the introduction, that morphology in lissamphibians is highly divergent from the archaic amphibians at the heart of the lissamphibian origins debate, which cannot be sampled molecularly. In morphology and molecules we have two distinct datasets, which only narrowly overlap at present.

There are a few other points to consider with the molecular data used for phylogenetic inference to date, including: the relatively small number of genes used (are we seeing gene trees or actual phylogenies?); the differing sets of genes used, which evolve at different rates from one another; whether the nuclear genes evolve fast enough to capture this rapid divergence; what effects out groups like lungfish and coelacanths have on extremely distantly related taxa with rapid internal divergences; and issues of saturation in the mitochondrial genomic data. However, the larger point is that the molecular phylogenetic trees should not be accepted without critical examination. It is especially important to test these results because the definition of statistical inconsistency is that the bias present will strongly support the incorrect answer (Felsenstein 1978).

The third possibility, perhaps least likely because of the consensus that current larger scale morphological phylogenies of tetrapods seem to have achieved but conceivable given how little we really know about the early divergence of tetrapods, is that the deeper pattern of tetrapod relationships is incorrect. The typical tree topology of tetrapods has a basal divergence of the Devonian tetrapods *Ichthyostega* and *Acanthostega*, then a number of archaic groups such as baphetids, and whatcheeriids, both of which are

still incompletely described, then temnospondyls. It is probable that new discoveries from the late Devonian and early Carboniferous will be placed into this stem area, which will have unpredictable impact on the rest of the tetrapod tree topology. Subsequent to this stem, the classic “anthracosaurs” can be found as a series of groups basal to the amniote crown. However, departing from traditional views, lepospondyls are placed between seymouriamorphs and diadectomorphs on the amniote stem.

While this result appears to be robust in that it has been found by several different research groups, there is also the real possibility that the vast morphological disparity between the Paleozoic tetrapods, necessarily included in ever growing numbers, may lead to an over inflation of superficial pseudosynapomorphies. Already mentioned above is the preponderance of “loss features”, which are easy to code but difficult to establish homology, in some matrices studying large scale Paleozoic tetrapod phylogeny. These characters clearly evolve independently in many lineages, but are treated as putatively homologous in many analyses. It is critical to redouble efforts at good character analysis, and better establish the putative homologies through preanalysis tests of homology. Given the large amount of homoplasy present in these large matrices, the discovery of new, positive, synapomorphies, better description of known morphology in light of detailed studies of the extant groups, and discovery of new taxa have a high likelihood of drastically changing relationships throughout the tetrapod tree. Should the basal tetrapod tree shift in fairly minor ways back to the batrachomorph–tetrapodomorph topology accepted before the current swath of large scale analyses (i.e., Panchen and Smithson 1988), displacing lepospondyls from the amniote stem, then the conflict between morphology and molecules under the PH would be resolved.

Divergence estimation is influenced by choice of calibration points, and most current authors are sensitive to these problems, opting for multiple calibrations, both shallow and deep (San Mauro et al. 2005; Hugall et al. 2007; Roelants et al. 2007; Vieites et al. 2007; Igawa et al. 2008). The dates produced by these studies vary, with studies clustering results into two groups having dates in either the Upper Devonian or Lower Carboniferous for Lissamphibia, and Upper Devonian or Lower Permian for Batrachia (Table 2), the latter of which being the age of *Gerobatrachus*. In the studies surveyed here, both mitochondrial and nuclear genes produced estimates falling into both the ancient and really ancient clusters, so the different age estimates are not due to the differing types of molecular data. As well, the dates estimated are relatively consistent among the different nuclear genes. All this could mean that the molecular estimates are converging on a “correct” date, and targeted hunting will reveal the

currently unknown fossils implied by those dates. On the other hand, all studies use the same relatively few constraining calibration points from the fossil record, and so all of these studies are systematically led to the same errors of estimation. New, deeper, calibration points such as might be offered by fossils such as *Gerobatrachus* might help improve the precision of the estimates.

Some recent studies based on the fossil record alone have attempted to date the divergence of Lissamphibia (Benton and Donoghue 2007; Marjanović and Laurin 2007). Not surprisingly, the dates derived depended upon the preferred phylogeny of tetrapods assumed by the authors. Benton and Donoghue (2007) assume the TH, and the date they estimate for the amphibian–amniote divergence is the appearance of the first reptilomorph (lepospondyls + amniotes) in the fossil record, the aistopod *Lethiscus*, from the Viséan ( $332.4 \pm 2$  mya). This is the same date that is estimated for Lissamphibia from the fossil record under the PH (Lee and Anderson 2006), and is consistent with the dates derived from the molecular studies (Table 2). Marjanović and Laurin (2007), on the other hand, assume a short stem, and consequently derive a younger age (260 mya), which diverges strongly from the molecular estimates.

Marjanović and Laurin (2007) employed controversial methods, such as hard maxima from the fossil record, rather than the soft maxima argued for by other paleontologists (i.e., Benton and Donoghue 2007) because fossils always underestimate the time for first divergence (i.e., Benton 1994; Benton and Ayala 2003; Benton and Donoghue 2007). This action was justified by the authors through a test of the consistency of the clade structure of their supertree with the inferred sequence of first appearance in the fossil record, using a program called Ghost (Wills 1999). This program computes the Gap Excess Ratio (GER; Wills 1999), the Stratigraphic Consistency Index (SCI; Huelsenbeck 1994), and the Relative Completeness Index (RCI; Benton 1994), and performs a permutation test to see whether the calculated measure of clade-to-stratigraphy consistency is significantly better than random. The authors stated that this could test the completeness of the fossil record if their phylogenetic tree (the topology of which was assumed) were sufficiently reliable, “because if the fossil record were very poor, we would expect a congruence between the order of cladogenesis and order of appearance in the fossil record no better than random” (Marjanović and Laurin 2007, p. 373). When the test revealed an “excellent and highly significant stratigraphic fit,” they concluded the fossil record of the Lissamphibia was “probably not too incomplete” for the purposes of their study (p. 385).

The question to me is whether this test has sufficient power to support these conclusions. Most phylogenies that have been tested have been shown to be significantly

consistent with the fossil record (Benton 1994; Huelsenbeck 1994; Benton 2003), yet it is not asserted that there are no gaps in the fossil record, or gaps in our understanding of the evolution of the study group, as a result. Huelsenbeck (1994) demonstrated that a relatively low number of consistent nodes (four in his example) are necessary to find significant consistency of the tree with the fossil record, and this significant consistency remains present in all trees several steps from most parsimonious. Wills (1999) specifically states that his GER does not reflect inferred completeness of the fossil record, but congruence alone. Moreover, the fossil record of lissamphibians is known to be very incomplete. As one example, the data presented by Marjanović and Laurin contains a gap of approximately 45 million years between *Eocaecilia* and the next caecilian in the fossil record, *Rubricacaecilia*, and another gap of around 45 million between *Rubricacaecilia* and the scrappy fossils that represent the first crown caecilians. How can one be certain that *Eocaecilia* is placed in the fossil record close to the real time of divergence with no ghost lineage, when above it in the stratigraphic column there are two known ghost lineages totaling approximately 90 million years? These known gaps speak to a porous fossil record, and it does not seem justified to treat dates derived from fossils as precise temporal records of first occurrence.

### New Directions

Throughout this paper I have made specific suggestions for areas where further research on specific subjects would be beneficial. For example, I suggested it would be useful to perform a combined morphology–molecular analysis, to guard against possible long-branch effects in the latter data. I have also called for the description of detailed, fine scale anatomy, and revision of particular fossil taxa. In this section I would like to emphasize the use of developmental data to reveal new clues into the origins of lissamphibians. I have recently (Anderson 2007) discussed a number of the data from development that have been used in attempts to work out lissamphibian origins and the difficulties associated with incorporating these data into phylogenetic analysis, and will not reiterate that work at present. Instead, I will highlight two larger approaches to the use of developmental data as case studies for future work.

### Development in Fossils

The study of development in fossils has already proven critical to the lissamphibian problem. Schoch and colleagues, for instance (Schoch 1992, 2002, 2003, 2004; Schoch and Fröbisch 2006), have done extensive work on

the pattern of cranial ossification in the branchiosaurid *Apateon*, which has compared very closely with the sequence of cranial ossification seen in salamanders (Schoch and Carroll 2003; Carroll 2004, 2007). This work has broken new ground, and set the bar very high for quality and elegance of the study. Unfortunately, this sort of detail, derived from a combination of exquisite preservation and a slow rate of ossification of the skull, is very rarely seen in fossil taxa (Anderson 2007); we only know the sequence of ossification in one other group of Paleozoic tetrapod, the aistopod *Phlegethontia* (Anderson 2002a, 2007; Anderson et al. 2003). Therefore, anytime we can generate even limited knowledge on the pattern of development of a fossil taxon, it could have wide ranging implications.

One recent example of how true this is comes, again, from the branchiosaurid *Apateon*. Fröbisch et al. (2007) recently described the pattern of limb ossification in this taxon. They discovered something quite interesting, that the sequence in the chondrification and ossification of the podials and digits passes from a pre- to post-axial direction, so the second digit is the first to appear, followed by the third and first, then fourth, then fifth. All tetrapods, with the sole exception of salamanders, have the opposite, post- to preaxial developmental axis, where the fourth digit appears first, followed by the third and fifth (if it is present), then second, then first (Shubin and Wake 2003). Because branchiosaurids are dissorophoid temnospondyls closely associated with, if not included within, amphibamids, it raises a question about what is going on in the rest of these taxa, since it is clearly present in salamanders and branchiosaurids. In other words, is the pattern that Fröbisch et al. call “preaxial dominance” independently derived in those two taxa, or is it also present in all intervening taxa, so that it is the primitive state for Batrachians (caecilians, not having limbs except for *Eocaecilia*, do not weigh into this discussion directly)? This can be tested should the pattern of development be established in an amphibamid (several would be better).

An intriguing clue to the possible answer is present in the stem batrachian *Gerobatrachus* (Anderson et al. 2008b). *Gerobatrachus* is known from a single specimen, so no developmental data are available directly. However, *Gerobatrachus* preserves some distal tarsal elements, a large, fairly well ossified combined distal tarsal 1 and 2 known as a basale commune, a structure uniquely known in salamanders, and a less well ossified, determined by the superficial bone texture and different color, distal tarsal three. No other tarsals are present. In salamanders, the preaxial digital arch is established through the basale commune, which is a precociously forming element, followed by distal tarsal three, and later on the proximal tarsals form (Shubin and Wake 2003). In all other



tetrapods, the proximal tarsals are the first to appear. So, it appears that the basale commune is associated with the presence of a preaxial pattern of digital development, and if so *Gerobatrachus* would also have had a preaxial pattern. Unfortunately, branchiosaurids do not ossify the carpals and tarsals, being paedomorphic, aquatic amphibians, so the inferred correlation between the basale commune and “preaxial dominance” must remain speculative. But it is intriguing that this unique pattern might actually be a hold over of a much more ancient and widespread pattern that has been reversed in frogs, perhaps due to the more dramatic metamorphosis they undergo in comparison with what is seen in salamanders, caecilians, and branchiosaurids.

### Development in Extant Amphibians

At several points throughout this paper I have mentioned that, in my opinion, the problem of lissamphibian origins has become the problem of caecilian origins. Of all of the modern groups of amphibians caecilians are the most derived, with a heavily ossified, closed, skull (Duellman and Trueb 1994). The roofing bones have incorporated several centers of ossification, and as a result the skull is comprised of composite bones with names reflecting these common origins (i.e., maxillopalatine, pseudangular, os basale) (Wake 2003). This trend towards composite bones began as far back in evolutionary time as *Eocaecilia*, from the Jurassic (Jenkins et al. 2007), and even earlier if one accepts the “microsaurian” origin hypothesis (i.e., fused supratemporal and tabular; Carroll and Gaskill 1978). Were these ossifications to remain separate, it would perhaps be easier to make comparisons with the archaic fossil amphibians, but they would still remain divergent from frogs and salamanders, which have a very different pattern of cranial architecture.

We understand very little still about the development that leads to the caecilian skull (but see Wake and Hanken 1982), and perhaps closer work on this modern amphibian would help in drawing comparisons with fossils. Such work is now underway. Müller and colleagues (Müller et al. 2005; Müller 2006) have been publishing a number of careful descriptions of the pattern of ossification of caecilian skulls that have been very insightful. Because of the highly coossified skulls of caecilians, a lot of previous work (i.e., Marcus et al. 1935) focused on finding early centers of ossification, and then making homology statements for those centers, and thus potential comparisons with archaic amphibians with multiple cranial bones. However, Müller and colleagues have shown that in several instances these statements prove unfounded. For example, earlier statements that the caecilian stapes is a composite bone, the footplate being derived from the otic

capsule wall and thus homologized with the operculum of frogs and salamanders, are unfounded in their developmental series, which shows the stapes to form from a single ossification only, and begins with a suspensorial support role as in some salamanders (Müller et al. 2005). On the other hand, they found support for the presence of a lacrimal bone, based in part on corresponding articulations with the highly modified nasolacrimal duct portion of the tentacular organ.

Such careful descriptive developmental work has enabled further study of patterns of evolutionary change in cranial ossification sequence data. Schoch (2006) compared the ossification sequence data for all tetrapods for which these data are available, including that for the caecilian *Gaganeophis* of Müller et al. (2005) and the branchiosaur *Apateon* (Schoch 1992, 2004), using event-pair cracking. He found that assertions of a close relationship between branchiosaurs and salamanders (Schoch and Carroll 2003) were primarily based on shared primitive patterns. In fact, using his event-pair changes he found little phylogenetic structure in these data. Instead, he found that the sequence of ossification is highly conserved throughout vertebrates, a conclusion I came to separately (Anderson 2007). He furthermore identified several developmental modules, and discussed some of the functional and developmental constraints preventing a large degree of variation within the ossification sequence. The sequence data could not even distinguish the three modern lissamphibians from one another, although he tentatively suggested that the postdisplacement of the premaxilla seen in some salamanders and frogs to be a possible shared, derived sequence heterochrony supporting Batrachia.

There is also a lot of ongoing work to establish patterns in the sequence in ossification in the lissamphibian postcranial skeleton. Shearman (2008) has recently documented the sequence in ossification of the pectoral girdle in two basal salamanders and two basal frogs, which are potentially critical baseline data for making broader comparisons both with more derived frogs and with possible fossil sister groups. These efforts with the extant taxa mirror similar efforts using growth series of fossil frogs (Roček and Van Dijk 2006) and the extant archaebatrachian *Discoglossis*, which have so far provided new information on the development of the pelvic (Roczková and Roček 2005) and pectoral girdles (Havelková and Roček 2006). Comparisons in the latter two papers have focused primarily on temnospondyls and *Triadobatrachus* in order to build evolutionary scenarios for those structures, so similar studies on more distantly related forms will be necessary to discover new synapomorphies to be used in phylogenetic analysis. It will be interesting to test some of these ideas using the new intermediary form *Gerobatrachus* in the near future.

## Conclusions

An incredible amount of work has been completed in the few years since the publication of the review of lissamphibian origins by Schoch and Milner (2004), and in a number of areas we appear to be approaching resolution to this subject. New transitional fossils like the stem batrachian *Gerobatrachus* have filled in the morphological gap between amphibamid temnospondyls and the earliest frogs and salamanders, and this portion of the lissamphibian origins question appears very well supported. The stem caecilian *Eocaecilia* has been more completely described, which should improve our understanding of early caecilian origins, while at the same time complicating the issue somewhat with the description of the possibly fused stapes and quadrate in this species. Are there problems of sampling in morphological analyses finding a diphyletic Lissamphibia, or is this idea based on new characters not considered in the other studies? The molecular analyses have nearly unanimously supported a monophyletic Lissamphibia, and a terminal Batrachia, but might there be long-branch artifacts affecting the short lissamphibian internodes?

I have repeatedly stated that the problem of lissamphibian origins appears to now be the problem of caecilian origins. Future research should continue to document the pattern of developmental sequences in order to increase the comparative database. The study of the morphogenesis of the caecilian skull I hope will provide clues into how the very different cranial architecture of frogs and salamanders can be altered to produce the derived caecilian skull (Haas and Kleinteich 2007), or clues into alternate patterns of phylogenetic relationship. As finer levels of anatomy are opened through technology like Micro-CT, additional data will be generated that will have a bearing on, and help resolve, this long standing problem of vertebrate evolution.

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