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The phylogeny of amphibian metamorphosis

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Summary

Frogs have one of the most extreme metamorphoses among vertebrates. How did this metamorphosis evolve? By combining the methods previously proposed by Mabee and Humphries (1993) and Velhagen (1997), I develop a phylogenetic method suited for rigorous analysis of this question. In a preliminary analysis using 12 transformation sequence characters and 36 associated event sequence characters, all drawn from the osteology of the skull, the evolution of metamorphosis is traced on an assumed phylogeny. This phylogeny has lissamphibians (frogs, salamanders, and caecilians) monophyletic, with frogs the sister group of salamanders. Successive outgroups used are temnospondyls and discosauriscids, both of which are fossil groups for which ontogenetic data are available. In the reconstruction of character evolution, an unambiguous change (synapomorphy) along the branch leading to lissamphibians is a delay in the lengthening of the maxilla until metamorphosis, in accordance with my previous suggestion (Reiss, 1996). However, widening of the interpterygoid vacuity does not appear as a synapomophy of lissamphibians, due to variation in the character states in the outgroups. From a more theoretical perspective, the reconstructed evolution of amphibian metamorphosis involves examples of heterochrony, through the shift of ancestral premetamorphic events to the metamorphic period, caenogenesis, through the origin of new larval features, and terminal addition, through the origin of new adult features. Other changes don't readily fit these categories. This preliminary study provides evidence that metamorphic changes in frogs arose as further modifications of changes unique to lissamphibians, as well as a new method by which such questions can be examined.

Key words: Lissamphibia, larvae, metamorphosis, evolution, ontogeny

Introduction

The metamorphosis from tadpole to froglet is one of the most dramatic postembryonic transformations among vertebrates. From the standpoint of developmental biology, metamorphosis is a fascinating model for the hormonal control of postembryonic development (Gilbert et al., 1996; Shi, 2000). As a phenomenon, it is also an amazing example of physiological and morphological restructuring (Fox, 1984; Duellman and Trueb, 1986; Rose and Reiss, 1993).

Most of the morphological changes of metamorphosis can be regarded as adapting the larva for three major functional changes: (1) a change in environment, from water to land (air), (2) a change in locomotion, from swimming to hopping, and (3) a change in feeding, from suspension feeding to predation. Related to the change in environment, the skin thickens and glands develop, the eyelids develop, the gills are lost and gill slits close, the shape of the lens changes, the lateral line is lost, the nose remodels, and the middle ear forms. Related to the change in locomotion, the limbs develop and the tail is lost. Related to the change in feeding, most of the skull bones form, the jaws lengthen, the tongue forms, the eyes develop binocular vision, the gut shortens, and the stomach forms.

I wish to consider how this dramatic metamorphosis evolved: what changes along the evolutionary lineage leading to frogs resulted in the amazing phenomenon we see today? I wish to consider this purely at the mor-

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phological level, without considering the hormonal control mechanisms or the physiological changes. This issue has received surprisingly little attention (Hanken, 1999), and only a few previous studies have addressed the morphological changes involved in the evolutionary origins of the tadpole larva and metamorphosis (e.g., Orton, 1953; Szarski, 1957; Sokol, 1975; Wassersug and Hoff, 1982; Fritzsch, 1990). Instead, much more attention has been focused on the structure and diversification of the tadpole larva within frogs, as exemplified in a recent comprehensive review of tadpole biology (McDiarmid and Altig, 1999). This is most likely due to the great morphological gap that separates tadpoles from other amphibian larvae.

Phylogenetic context

To understand the evolutionary origin of metamorphosis, one must look at the phylogenetic context. Frogs (Anura or Salientia) are one of three living 'amphibian' groups (orders), salamanders (Caudata or Urodela) and caecilians (Gymnophiona or Apoda) being the other two. All of the living amphibians are generally considered to represent a monophyletic group, the Lissamphibia (Duellman and Trueb, 1986; Milner, 1988; Bolt, 1991; Trueb and Cloutier, 1991; Milner, 1993; Hay et al., 1995; Feller and Hedges, 1998). Although a wide variety of life history patterns is found within each of the living amphibian groups (Duellman and Trueb, 1986), metamorphosis from an aquatic larvae to a more or less terrestrial adult is primitive for each (Fig. 1; see Hanken, 1999). Metamorphosis can be defined as a concentrated period of postembryonic development (Alberch, 1989; Rose and Reiss, 1993). It is usually, though not always, associated with a marked change in habitat. If we plot metamorphosis as a simple character on a cladogram showing lissamphibian relationships among living taxa (Fig. 2), we find that parsimony requires that metamorphosis itself be a lissamphibian synapomorphy; neither the amniotes (the sister group of amphibians) nor the lungfishes and coelacanths (successive outgroups) have any real metamorphosis (Rose and Reiss, 1993).

The hypothesis that metamorphosis is a lissamphibian synapomorphy has some support in the morphological changes of metamorphosis, in that a few obvious metamorphic changes are shared among the groups. For example, in all three groups the tail fin is lost, the gill slits close, and skin glands form. Thyroid hormone also appears to be involved in metamorphosis in all three groups. These are not especially impressive similarities, however, because (except for the thyroid involvement) they are all rather obviously functionally related to the change in environment.

Moreover, considering what we know in general about tetrapod evolution, it is clear that metamorphosis as such cannot be a lissamphibian synapomorphy, though components of the metamorphic pattern might be.

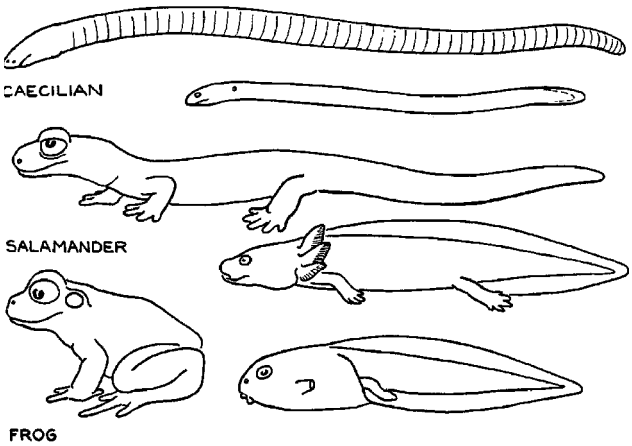

Fig. 1. External morphology of adults and larvae of the three living amphibian groups (modified from Orton, 1953). The differences among the larvae are more obvious than the similarities. Such similarities include the presence of external gill slits, tail fin, and a relatively small gape. Note that external gills are present only in salamander larvae; they are lost around the time of hatching in caecilians, and are found only in very young frog larvae.

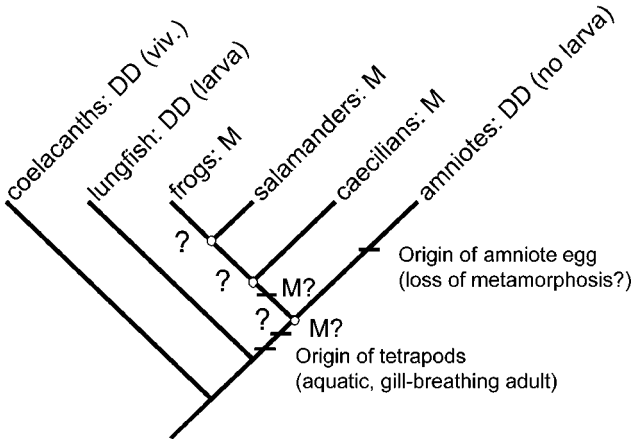

Fig. 2. Distribution of life histories among extant sarcopterygians. Frogs, salamanders, and caecilians (lissamphibians) are unique in having a distinct metamorphosis (**M**); other taxa have various forms of direct development (**DD**). Two alternative positions for the origin of metamorphosis are indicated (**M?**). The question marks (**?**) indicate the three nodes representing common ancestors for which metamorphic patterns might be reconstructed based on data from the terminal taxa.

When tetrapods originated (i.e., at the level of *Acanthostega*) the adult was still aquatic (Coates and Clack, 1991; Coates and Clack, 1995). Somewhere along the branch leading to the living tetrapods (lissamphibians + amniotes) the adult became at least somewhat terrestrial, and this change must have been associated with the evolution of a morphological and physiological metamorphosis of some sort. On the branch leading to amniotes, metamorphosis was lost by elimination of the larval stage, while on the branch leading to lissamphibians it was maintained and/or elaborated. In an explicit phylogenetic context (Fig. 2), the fundamental question we might hope to answer is what sort of metamorphic pattern was found in the common ancestor of 1) lissamphibians and amniotes, 2) all lissamphibians, and 3) frogs and salamanders? If we can answer this question, we will have a good outline of the morphological path by which anuran metamorphosis evolved.

Our knowledge of metamorphosis in these common ancestors can be derived from two sources of information: living animals and extinct animals. Clearly, information on ontogenies of extinct taxa will greatly help in the resolution of this problem, especially for common ancestors 1 and 2 in the above list, because amniotes show no metamorphosis and thus make a poor outgroup. Ontogenetic information is available for a number of fossil "amphibian" taxa (reviewed by Boy and Sues, 2000; Schoch, 2001). These fossils fall into two groups, the temnospondyls and the discosauriscids. In temnospondyls, early larval through metamorphic stages are known only for branchiosaurs, but late larval and metamorphic stages are known for a variety of taxa, and paedomorphic adults are also known (e.g., *Dvinosaurus*, *Gerrothorax*). In discosauriscids early larval through metamorphic stages are known, similar to the situation in branchiosaurs.

Several morphological changes can be used as indices of metamorphosis in fossil taxa (Boy and Sues, 2000; Schoch, 2001). The main evidence for metamorphosis is the loss of bony gill denticles ("branchial ossicles") and/or external gills past a certain size. This loss is presumed to be correlated with reduction of the cartilaginous ceratobranchials and closure of the gill slits. Other events occurring around the same size include increased sculpturing of the dermal skull roof, enclosure of the nasolacrimal duct in a lacrimal canal, and the ossification of the basibranchial. The temporal relations of these events appear to be quite variable among taxa (Schoch, 2001), although complete growth series are lacking for most.

The phylogenetic relations of these fossil forms to living taxa are controversial. There are two major current views. In what I'll call the "traditional" view (Fig. 3A), lissamphibians are a monophyletic lineage within temnospondyls, whereas the seymouriamorphs (including discosauriscids) are the sister group to diadectomorphs and amniotes (Milner, 1988; Bolt, 1991; Trueb and Cloutier, 1991; Milner, 1993; Coates and Ruta, 2000).

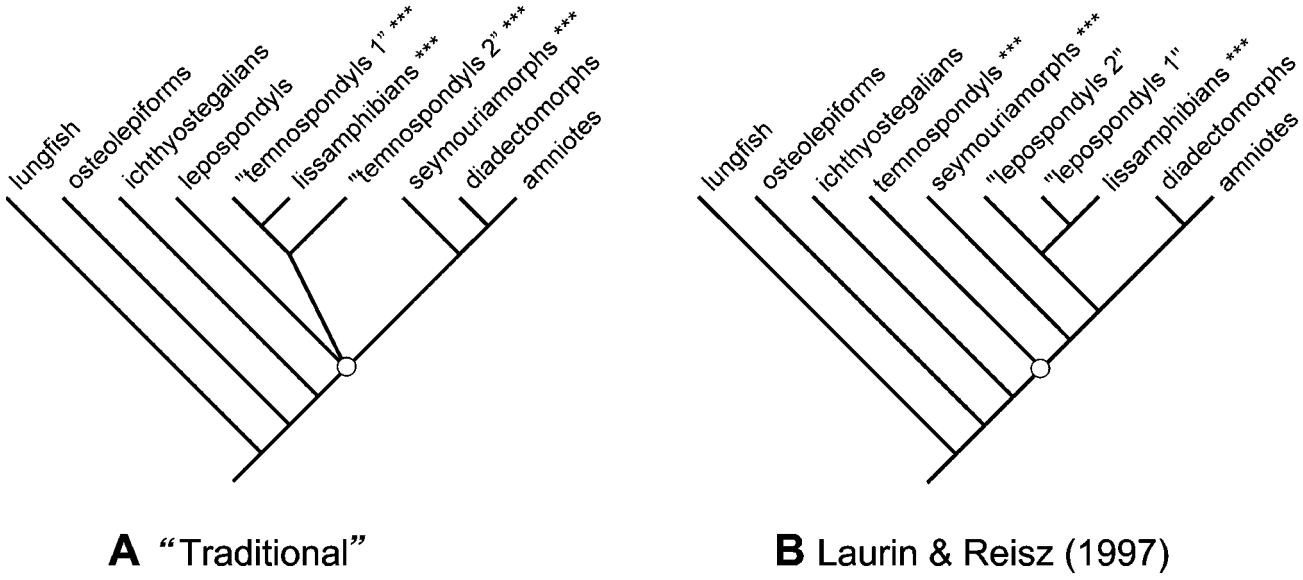

Fig. 3. Contrast between the "traditional" phylogeny **(A)** and the new phylogeny **(B)** proposed by Laurin and Reisz (1997). Taxa for which ontogenetic information is available are indicated by *******. The marked node indicates the common ancestor of all these taxa. In **(A)** this ancestor is the common ancestor of lissamphibians and amniotes, whereas in **(B)** it is more basal than this common ancestor.

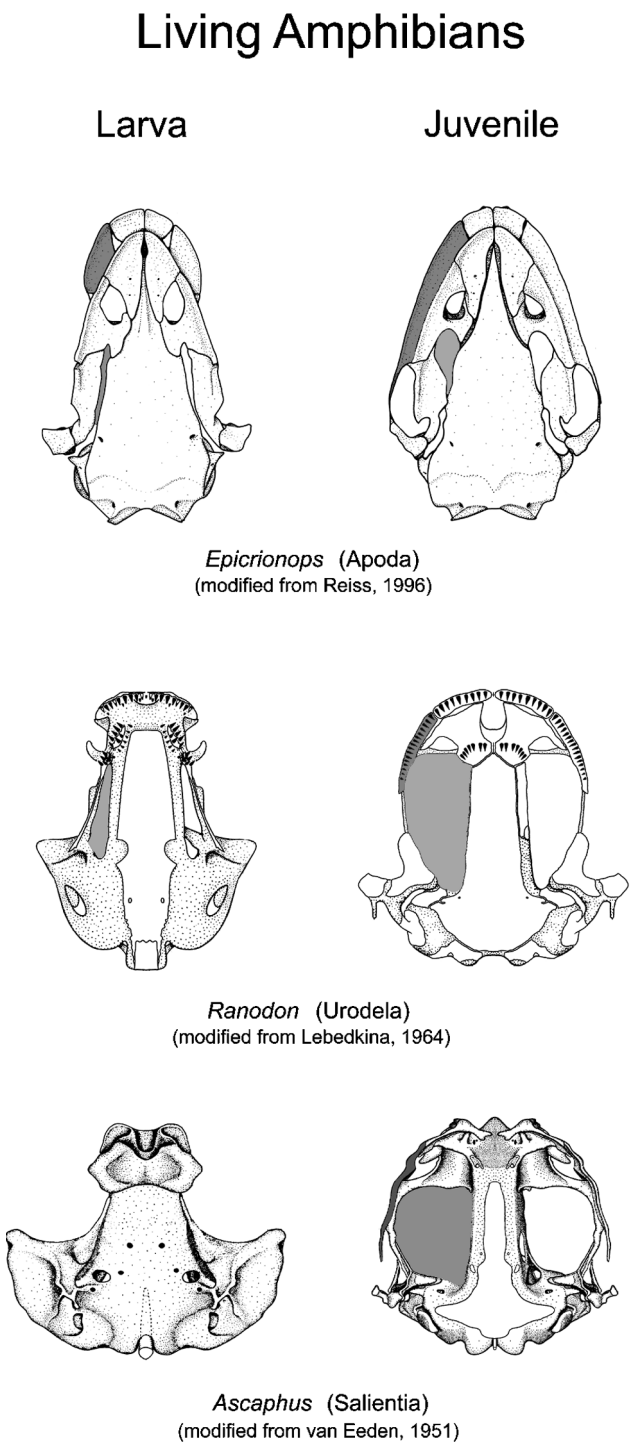

Fig. 4. Palatal metamorphosis in living amphibians (modified from van Eeden, 1951; Lebedkina, 1964; Reiss, 1996). On the left side of the figures the maxilla is darkly shaded and the interpterygoid vacuity is lightly shaded. Note the increase in length of the maxilla and the widening of the interpterygoid vacuity between larval and juvenile forms in all three groups.

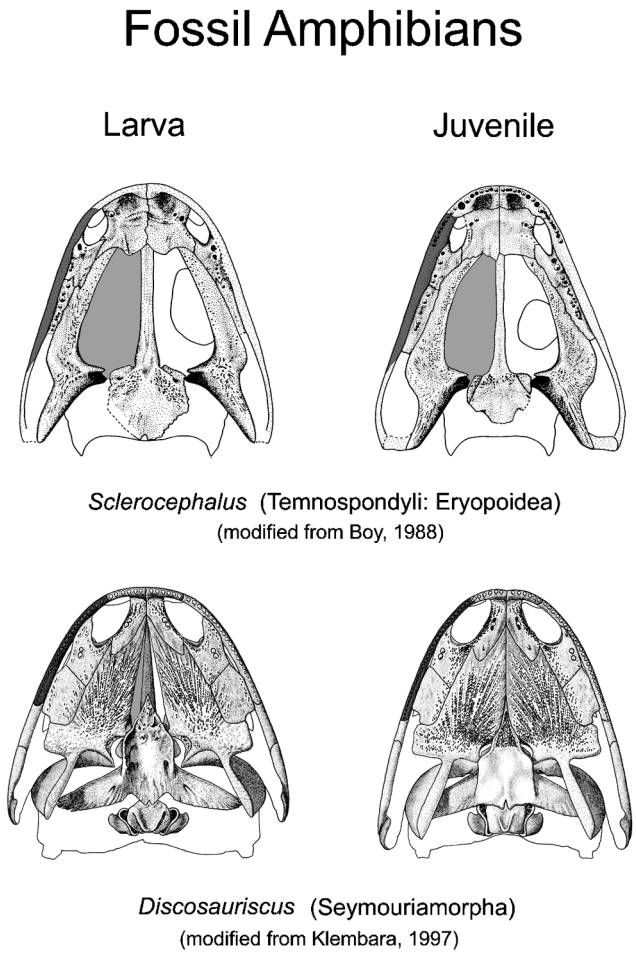

Fig. 5. Palatal metamorphosis in fossil amphibians (modified from Boy, 1988; Klembara, 1997). On the left side of the figures the maxilla is darkly shaded and the interpterygoid vacuity is lightly shaded. Note the general lack of change between larval and juvenile forms.

In contrast, in a recently proposed phylogeny (Fig. 3B; Laurin and Reisz, 1997; Laurin, 1998; Laurin et al., 2000), seymouriamorphs and temnospondyls are successive outgroups to a clade including lissamphibians, 'lepospondyls,' and amniotes, and lissamphibians are a monophyletic lineage within the lepospondyls. The major differences between these phylogenies are not, however, critical for present purposes; under either phylogenetic hypothesis the fossil taxa can serve as outgroups to help reconstruct a common ancestral metamorphic pattern (the labelled nodes in Fig. 3) from which lissamphibian metamorphosis evolved.

To use the fossil taxa as lissamphibian outgroups, one must focus on metamorphic changes in osteology, because these are generally the only features that can be observed in fossils. My interest in the phylogeny of

metamorphosis came initially from the observation that frogs, salamanders and caecilians all show extensive remodelling of the bony (or cartilaginous) palate during metamorphosis (Fig. 4; Rose and Reiss, 1993; Reiss, 1996). Two specific changes in the palate during metamorphosis are shared by all the living amphibians: 1) the interpterygoid vacuity widens, and 2) the maxilla lengthens. These shared changes suggest that all three groups evolved their metamorphic pattern from a common ancestral pattern. Moreover, the temnospondyls and discosauriscids used as outgroups in general show no evidence of such a pattern (Fig. 5; Boy and Sues, 2000). Metamorphic remodelling of the palate thus appears to be a derived feature of lissamphibians in general, which is merely taken to an extreme in frogs (Wassersug and Hoff, 1982; Reiss, 1996). In the present paper I attempt to examine this conclusion more rigorously, by conducting a phylogenetic analysis of metamorphic changes in cranial osteology.

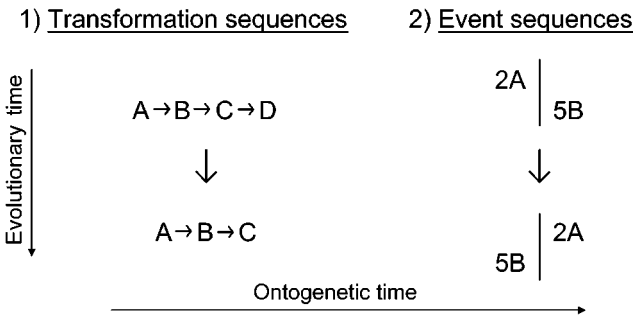

Fig. 6. The two types of ontogenetic sequences that can be observed (Velhagen, 1997). Transformation sequences consist of the ontogenetic change within a single character. Evolutionary change results in a modification of the observed sequence (here from ABCD → ABC). Event sequences consist of the sequence in which two independent events occur. For example, for character 2 (with transformation sequence ABC) and character 5 (with transformation sequence ABC) event 2A can occur either before or after event 5B. Evolutionary change results in modification of the order of the two events, here from 2A, 5B to 5B, 2A.

Materials and methods

To analyze the evolution of metamorphosis, one must realize that there are two distinct aspects of ontogeny to analyze (Fig. 6; Velhagen, 1997): 1) transformation sequences, which are successive states within a character, and 2) event sequences, which are temporal relations between characters. Mabee and Humphries (1993) proposed a method to look at the evolution of transformation sequences in which the entire sequence of static morphological states is treated as the character state, and the distance between states is the difference in shared states (e.g., ABCD differs by one step from ABC). These distances are encoded in a step matrix containing distances between all possible pairs of states, and the evolution of the character is then analyzed using standard parsimony assumptions. On the other hand, Velhagen (1997; see also Mabee and Trendler, 1996; Smith, 1996, 2001) proposed a method for analyzing event sequence evolution in which pairs of events are the characters (e.g., 2A-5B in Fig. 6). The character states are coded as 1 if the first event (2A in the example) occurs first, 2 if the second event (5B) occurs first, and either 1.5 or equivocal if it is impossible to tell which is first. Character evolution again can be analyzed with standard parsimony methods.

To trace the evolution of metamorphosis, a method that combines these two methods is necessary, because it is important to know not only how the ontogenies of individual features evolved, but how the timing of these ontogenies relative to metamorphosis evolved. Two major problems must be avoided: 1) reconstructing event sequences for events reconstructed as absent (e.g., event 3D does not occur but sequence 3D, 7C does), and 2)

Transformation sequence character: Interpterygoid vacuity

Static states:	Transformation sequences:	
A = narrow	Frogs	ABCD
B = moderately narrow	Salamanders	ABCD
C = moderately wide	Caecilians	ABC
D = wide	(not observed)	AB
E = absent	(not observed)	A
	(not observed)	BCD
	Temnospondyls	BC
	Discosauriscids	AE

Event sequence characters: Interpterygoid vacuity

Coding for metamorphosis:	Data matrix:	
		ABCDE
b = before metamorphosis	Frogs	b d d d i
d = during metamorphosis	Salamanders	b b d d i
a = after metamorphosis	Caecilians	b d d i i
i = inapplicable	Temnospondyls	i b d i i
	Discosauriscids	b i i i a

Fig. 7. Example of the character coding used, shown here for the interpterygoid vacuity. Two distinct codings were used. For transformation sequence characters, a series of static character states were defined. Each taxon was then assigned the transformation sequence character state consisting of the appropriate sequence of static states (e.g., **ABCD** for frogs). For event sequence characters, each of the static character states defined above was treated as a separate character, and coded for its temporal relation to metamorphosis (or inapplicable, if it never occurred). Each taxon could then be assigned the appropriate states for each of the static characters (e.g., for characters A to E, frogs have states **b**, **d**, **d**, **d**, and **i**, respectively).

conflicts between reconstructed transformation and event sequences (e.g., for transformation sequence 3B → 3C, event 3B occurs after 7C, but 3C occurs before 7C).

For the present analysis I developed a simple method that combines previous approaches, and appears to avoid these problems. Transformation sequences were coded as step matrices, and events were coded as occurring either before (*b*), during (*d*), or after (*a*) metamorphosis, or as inapplicable (*i*). Although metamorphosis is clearly not a strictly defined period, but rather a pattern of ontogeny (Rose and Reiss, 1993), for the purposes of this paper it was considered to occur from the beginning to the end of gill slit closure (inferred for fossil taxa). The event sequences were treated as partially ordered characters, with a distance of one step between states *b* and *d*, and *d* and *a*, but a distance of two steps between states *b* and *a*. State *i* was considered to be three steps away from any of the other states, so that it would not be reconstructed as an intermediate between any of the other states.

To give an example of how this works, let us look at the coding for the interpterygoid vacuity (Fig. 7). As a transformation sequence character, a number of distinct states can be defined; frogs (with state ABCD) and discosauriscids (with state AE) are the most divergent. It is also possible to include states that were not observed, but are plausible intermediates between observed states; this allows such intermediates to be reconstructed as ancestors. For the same feature there are also event sequence characters, five for this example. Note that the event sequence coding *includes* transfor-

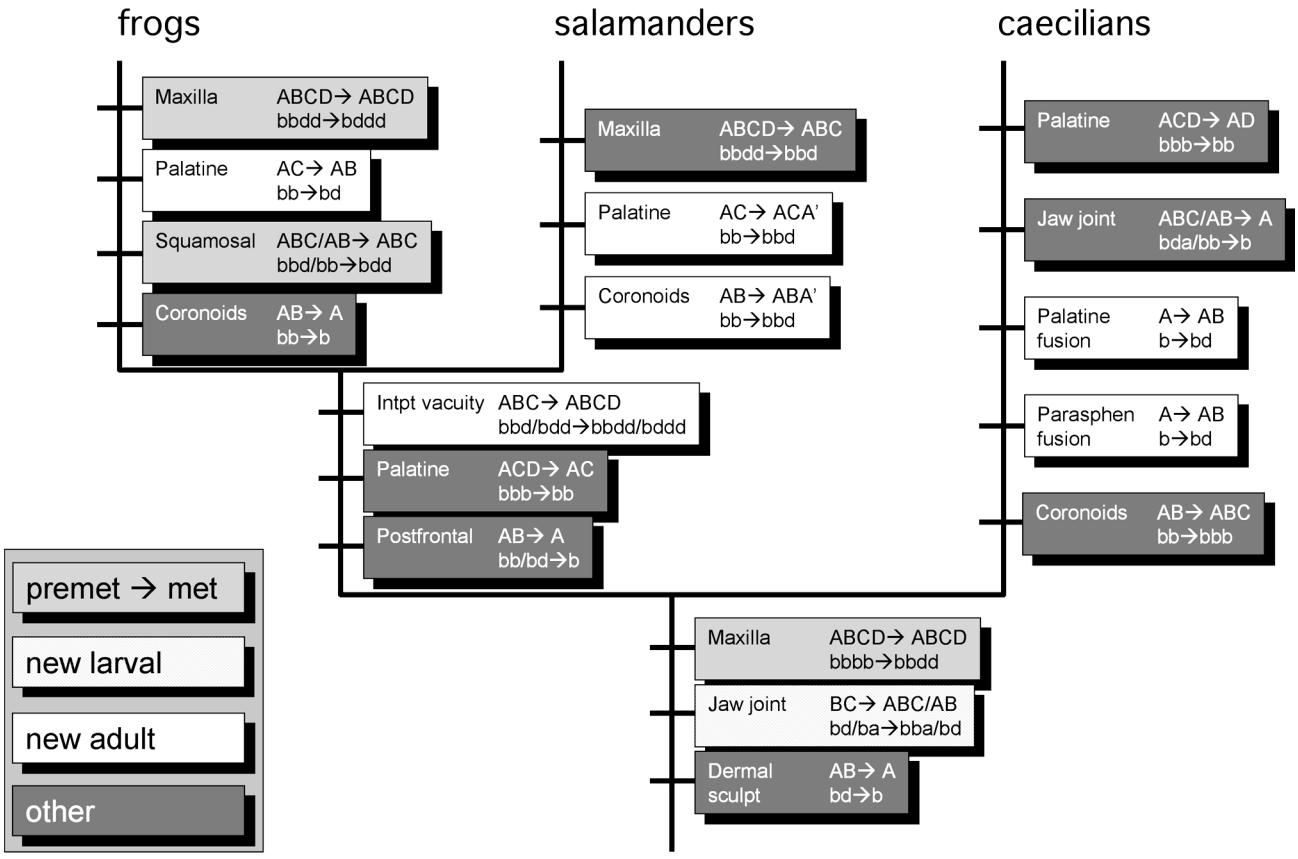

Fig. 8. All unambiguous changes reconstructed for the ingroup (lissamphibians). For each feature, the change (if any) in the transformation sequence character is shown above, and that in the corresponding event sequence characters below. For example, on the branch leading to frogs, the maxilla undergoes no change in transformation sequence (ABCD → ABCD) but the associated event sequences change from bbdd → bddd. In other words, event B is delayed to occur during (d) rather than before (b) metamorphosis. In cases where it is clear that a change occurred, but the precise change is unclear, alternatives are given. For example, on the branch leading to frogs, it is unclear whether the ancestral transformation sequence of the squamosal was ABC or AB. The shading of the boxes for each character corresponds to the different classes of change indicated by the legend; see text for further discussion.

mation sequences, in the sense that transformation sequences can be read directly from event sequences. The redundancy in coding is a problem if one is trying to reconstruct phylogeny, but it is not a problem if one is only trying to reconstruct character evolution on a known phylogeny. Although it might seem that the transformation sequence coding could be discarded entirely, in practice the reconstructed transformation sequence character states can be useful in deciding among unresolved event sequence characters.

For the preliminary analysis here, I examined 12 transformation sequence characters, all from the skull (Appendix 1). These included the interpterygoid vacuity and the maxilla; the remainder were chosen to represent the variety of changes seen. I performed an analysis of character evolution with these characters and five taxa (frogs, salamanders, caecilians, temnospondyls and discosauriscids). Data on character states in each terminal taxon were gathered from the literature (see references in Reiss, 1996), and represent my best estimate of the primitive condition within each group. I assumed a phylogeny that can be represented as follows: (discosauriscids + (temnospondyls + (caecilians + (frogs + salamanders)))). In other words, within the Lissamphibia frogs and salamanders were considered each other's closest relatives, with temnospondyls and discosauriscids successive outgroups to the Lissamphibia. Importantly, reconstructions of character evolution above the outgroups did not depend on the relative position of the two outgroups. 48 total characters were used, including the 12 transformation sequence and 36 associated event sequence characters. Character evolution was analyzed using McClade 3.0 (Maddison and Maddison, 1992) and PAUP* 4.0b8 (Swofford, 2001).

Results and discussion

Figure 8 shows the phylogenetic tree of ingroup taxa with all reconstructed unambiguous changes. Not surprisingly, there are many autapomorphies, representing unique features in the metamorphosis of each group. However, some synapomorphies of the groups are also present. For the Lissamphibia, synapomorphies include a shift in the lengthening of the maxilla from before to during metamorphosis, an anterior shift in the jaw joint in larvae, and the loss of dermal sculpturing in postmetamorphic animals. For the clade of frogs and salamanders (Batrachia of some authors) synapomorphies include a widening of the interpterygoid vacuity during metamorphosis, the loss of a Y-shaped stage in the development of the palatine, and the loss of the postfrontal.

Focusing on the evolution of individual characters reveals some interesting patterns (Fig. 9). Of the two main characters mentioned earlier, the maxilla (Fig. 9A) has a fully resolved history. The ancestor has the transformation sequence state ABCD, all of which occurs before metamorphosis. On the branch leading to lissamphibians static states C and D are relatively delayed, to occur during metamorphosis. This condition is retained by caecilians, in frogs there is a further delay of state B, while in salamanders there is a truncation of the developmental sequence.

The evolution of the interpterygoid vacuity is less clearly reconstructed (Fig. 9B). There is great uncertainty about the ancestral state, and no unambiguous change on the branch leading to lissamphibians (though there is a change on the branch leading to frogs and

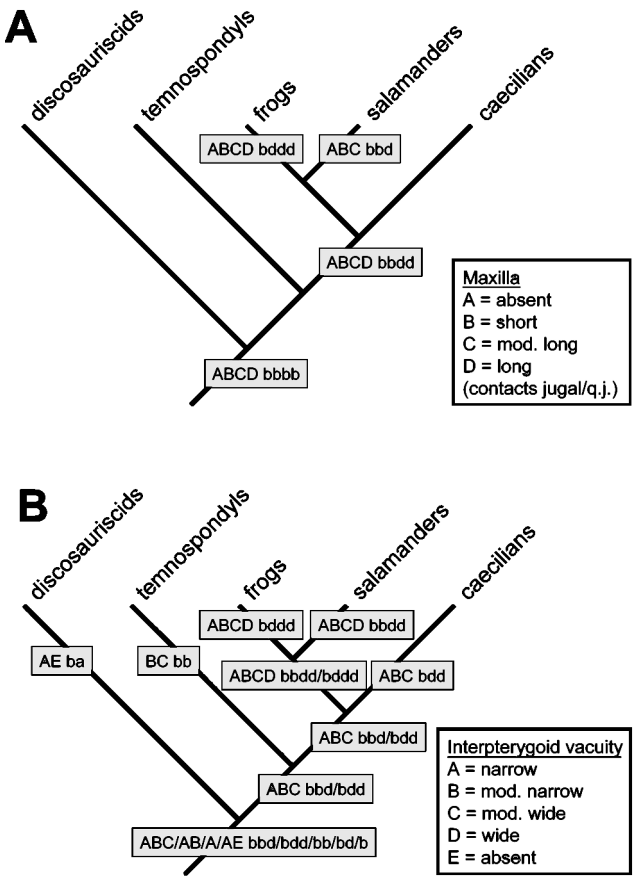

Fig. 9. Reconstructed evolution of the maxilla and the interpterygoid vacuity on the full tree. The boxes show the transformation sequence and event sequence character states present on each branch. Ambivalent character states are indicated as in Fig. 8. The evolution of the maxilla is well-resolved, that of the interpterygoid vacuity is not. See text for discussion.

salamanders). The poor resolution of the evolution of this character is clearly due to the great variation in transformation sequence between the two outgroup taxa, as well as the wide variation in event sequence in lissamphibians. The difference between temnospondyls and discosauriscids is critical. For example, if one forces the common ancestor of temnospondyls and lissamphibians to have the state seen in temnospondyls, as the "traditional" phylogeny would suggest, then the interpterygoid vacuity does have an unambiguous change from BC to ABC on the branch leading to lissamphibians, representing a narrowing of the interpterygoid vacuity in larvae.

The reconstruction of character evolution (Fig. 8) can also be used to examine the phylogeny of metamorphosis in a more theoretical context. Alberch (1989) pointed out two types of evolutionary change that could be involved in the origin of metamorphosis from a non-metamorphic ontogeny: 1) the concentration of developmental events into a short time period (heterochrony), and 2) the insertion of new larval specializations (caenogenesis), creating divergence between larva and adult. The present study has been concerned with the *elaboration* of metamorphosis, not its origin, but a parallel distinction between two classes of changes that could have led to this elaboration can be made. First, existing developmental events may be *concentrated* into a metamorphic period via heterochrony. This can be caused either by a *delay* of ancestral premetamorphic events to the metamorphic period, or by *precocious onset* of ancestral postmetamorphic events. Second, the larva and adult may *diverge* morphologically. This can either be caused by *new larval specializations* (caenogenesis) or *new adult specializations* (terminal addition). Given the reconstructed character phylogeny, we can ask to which of these classes the changes reconstructed belong.

In Figure 8, I have coded the tree of unambigous changes according to this classification. Two examples fall into the category of character states that are delayed from the premetamorphic to the metamorphic period: the lengthening of the maxilla for all lissamphibians and again for frogs, and the ossification of the squamosal in frogs (because frogs are almost entirely unossified prior to metamorphosis, many more bones could be added that would display a similar pattern). There is no example of a character state shifted from the postmetamorphic to metamorphic period; perhaps this is an artifact of character selection. The category of new larval characters includes the anterior position of the jaw joint in all lissamphibian larvae, whereas the category of new adult characters includes the widening of interpterygoid vacuity in frogs and salamanders, as well as various autapomorphies scattered among the terminal taxa. A number of changes do not fit any of these categories. These include the loss of dermal sculpturing in adult lissamphibians (synapomorphic loss of an ancestral adult character) and the fusion of coronoids with other lower jaw bones before metamorphosis in caecilians (new adult character appearing in larvae). Such changes contribute to evolutionary diversification, but do not contribute to elaboration of metamorphosis.

Conclusions

The analysis in this paper was based on the assumption that if the Lissamphibia are monophyletic, we should expect to find features of anuran metamorphosis uniquely shared by other lissamphibians, indicating the path by which some of the changes of anuran metamorphosis evolved. The reconstruction of character evolution showed that the lengthening of the maxilla at metamorphosis in lissamphibians is a shared derived feature not seen in the outgroup taxa. The interpretation of this depends on the phylogeny adopted. If we accept the "traditional" phylogeny (Fig. 3A), it is of great interest that one of the dissorophoid temnospondyls, *Amphibamus grandiceps*, which has been considered especially close to lissamphibians on other grounds (Bolt, 1991; Milner, 1988, 1993), may share such a change (Schoch, 2001). The anterior position of the jaw joint in lissamphibian larvae, reconstructed as a further synapomorphy of the group, may also be approximated in *Amphibamus*. Conversely, if Laurin and Reisz' (1997) phylogeny (Fig. 3B) is correct, the ontogeny of "lepospondyls", which is largely unknown, becomes of great interest. It is even possible that an extreme metamorphosis might characterize the entire lepospondyl + lissamphibian + amniote clade; we know virtually nothing about the ontogeny of stem amniotes either. Regardless of their phylogenetic relationships, the analysis presented above provides some support for the idea that lissamphibians as a group are distinguished among "amphibians" by having a relatively extreme metamorphosis (Reiss, 1996; Boy and Sues, 2000; Schoch, 2001).

The present study primarily has been an exploration of a method for analyzing ontogenetic evolution and not an attempt to provide the final word on the subject of the evolution of amphibian metamorphosis. It is clear that a combined approach using both transformation and event sequences can reconstruct ontogenetic evolution with at least some degree of confidence, and can allow one to examine questions that can not be addressed by methods analyzing one or the other independently. A strength of the method is that unique shared features of ontogeny (e.g., the enlargement of the interpterygoid vacuity during metamorphosis in lissamphibians) are not always reconstructed as synapomor-

phies, for reasons that seem justified when plausible paths of ontogenetic evolution are considered.

To better understand the origins of anuran metamorphosis, it would obviously be desirable to expand the present study to include more characters, both skeletal and soft tissue. It would also be good to include many more taxa; there is significant variation *within* each of the five terminal taxa I have treated here (Schoch, 2001 provides an excellent discussion of variation among the temnospondyls). At the theoretical level, it would be good to examine more carefully the question of the reliability of the reconstructed states. This is really a question of how labile ontogenies are, which is a general issue in the reconstruction of ancestral character states. If ontogenies are very labile, as one might fear based on the wide diversity of life histories seen among living forms, then our taxonomic sampling is probably not dense enough to recover the relevant information. Ontogenies would have to be at least as conserved as morphology, because at present our sampling is not dense enough to fill the morphological gap between lissamphibians and extinct groups (Carroll, 2000). On the other hand, if ontogenies are relatively stable, then we have a good chance of successfully reconstructing the relevant states. As more data on ontogenies of fossil amphibians accumulate, we should be able to better judge the reliability of the reconstructed ontogenies, and thus the reliability of the reconstructed path of ontogenetic evolution.

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Appendix I. Character definitions and data matrix

Transformation sequence character definitions:

1) Interpterygoid Vacuity

Static states:	Possible ontogenies:
A = narrow	0: ABCD
B = moderately narrow	1: ABC
C = moderately wide	2: AB
D = wide	3: A
E = absent	4: BCD
	5: BC
	6: AE
	7: E

Step matrix of distances between ontogenies:

	0	1	2	3	4	5	6	7
0	0	1	2	3	1	2	4	5
1	1	0	1	2	2	1	3	4
2	2	1	0	1	3	2	2	3
3	3	2	1	0	4	3	1	2
4	1	2	3	4	0	1	5	4
5	2	1	2	3	1	0	4	3
6	4	3	2	1	5	4	0	1
7	5	4	3	2	4	3	1	0

2) Maxilla

Static states:	Possible ontogenies:
A = absent	0: ABCD
B = short	1: ABC
C = moderately long	
D = long (contacts jugal or quadratojugal)	

3) Quadratojugal

Static states:	Possible ontogenies:
A = absent	0: AB
B = present	1: A

4) Palatine

Static states:	Possible ontogenies:
A = absent	0: AB
B = transverse only (on lamina orbitonasalis)	1: ACA’
	2: AC
C = longitudinal (anterior tip on lamina orbitonasalis)	3: AD
	4: ACD

D = Y-shaped (transverse and longitudinal components)
A' = secondarily absent

Step matrix of distances between ontogenies:

	0	1	2	3	4
0	0	3	2	2	3
1	3	0	1	3	2
2	2	1	0	2	1
3	2	3	2	0	1
4	3	2	1	1	0

5) Postfrontal

Static states:	Possible ontogenies:
A = absent	0: A
B = present	1: AB

6) Squamosal

Static states:	Possible ontogenies:
A = absent	0: ABC
B = elongate (along quadrate process)	1: AB
C = elongate, with anteroventral projection	

7) Jaw Joint Level

Static states:	Possible ontogenies:
A = anterior to otic capsule	0: ABC
B = at level of otic capsule	1: AB
C = posterior to otic capsule	2: A
	3: BC

Step matrix of distances between ontogenies:

	0	1	2	3
0	0	1	2	1
1	1	0	1	2
2	2	1	0	3
3	1	2	3	0

8) Palatine Fusion to Maxilla

Static states:	Possible ontogenies:
A = unfused	0: A
B = fused	1: AB

9) Dermal Bone Sculpturing

Static states:	Possible ontogenies:
A = not sculptured	0: A
B = sculptured	1: AB

10) Exoccipital Ossification

Static states:	Possible ontogenies:
A = unossified	0: AB
B = ossified	1: A

11) Parasphenoid Fusion with Neurocranium

Static states:	Possible ontogenies:
A = not fused	0: A
B = fused	1: AB

12) Coronoids

Static states:	Possible ontogenies:
A = absent	0: A
B = present, independent	1: AB
C = present, fused to other jaw elements	2: ABC
	3: ABA'
A' = secondarily absent	

Step matrix of distances between ontogenies:

	0	1	2	3
0	0	1	2	2
1	1	0	1	1
2	2	1	0	1
3	2	1	1	0

Event sequence character definition (same for all):

Possible states:
0: b – before metamorphosis
1: d – during metamorphosis
2: a – after metamorphosis
3: i – inapplicable

Step matrix of distances between states:

	0	1	2	3
0	0	1	2	3
1	1	0	1	3
2	2	1	0	3
3	3	3	3	0

Data matrix:

Taxon	Interpter Vac	A	B	C	D	E	Maxilla	A	B	C	D	Quadjug	A	B
frogs	ABCD	b	d	d	d	i	ABCD	b	d	d	d	AB	b	d
salamanders	ABCD	b	b	d	d	i	ABC	b	b	d	i	AB	b	b
caecilians	ABC	b	d	d	i	i	ABCD	b	b	d	d	AB	b	d
temnospondyls	BC	i	b	d	i	i	ABCD	b	b	b	b	AB	b	b
discosauriscids	AE	b	i	i	i	a	ABCD	b	b	b	b	AB	b	b

Data matrix (cont.):

Taxon	Palatine	A	B	C	D	A’	Postfrontal	A	B	Squamosal	A	B	C
frogs	AB	b	d	i	i	i	A	b	i	ABC	b	d	d
salamanders	ACA’	b	i	b	i	d	A	b	i	AB	b	b	i
caecilians	AD	b	i	i	b	i	AB	b	d	ABC	b	b	d
temnospondyls	ACD	b	i	b	b	i	AB	b	b	AB	b	b	i
discosauriscids	ACD	b	i	b	b	i	AB	b	b	AB	b	b	i

Data matrix (cont.):

Taxon	Jaw Joint Level	A	B	C	Pal Fusion	A	B	Derm Bone Sculpt	A	B	Exocc Oss	A	B
frogs	ABC	b	d	a	A	b	i	A	b	i	AB	b	b
salamanders	AB	b	d	i	A	b	i	A	b	i	AB	b	b
caecilians	A	b	i	i	AB	b	d	A	b	i	AB	b	b
temnospondyls	BC	i	b	d	A	b	i	AB	b	d	AB	b	a
discosauriscids	BC	i	b	a	A	b	i	AB	b	d	AB	b	b

Data matrix (cont.):

Taxon	Parasphen Fusion	A	B	Coronoids	A	B	C	A’
frogs	A	b	i	A	b	i	i	i
salamanders	A	b	i	ABA’	b	b	i	d
caecilians	AB	b	d	ABC	b	b	b	i
temnospondyls	A	b	i	AB	b	b	i	i
discosauriscids	A	b	i	AB	b	b	i	i