

# Amphibian Biology

Edited by

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and

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Volume 4

Palaeontology

The Evolutionary History of Amphibians

Published by

Surrey Beatty & Sons

# Anatomical Transformations in the Transition from Temnospondyl to Proanuran Stages

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## I. INTRODUCTION

**B**ECAUSE the only palaeontologically documented proanurans are from the Lower Triassic (*Triadobatrachus* and *Czatkobatrachus*), the origin of the phylogenetic lineage that ultimately led to the Anura should be sought among the late Palaeozoic through Lower Triassic amphibians. Of these, the Aïstopoda generally are excluded from the possible ancestry of the Anura. This also holds for the Nectridea, although Gardiner (1982, 1983) and Parsons and Williams (1963) suggested a possible lissamphibian-nectridean relationship. Cox (1967) proposed the Microsauria as ancestors of the entire Lissamphibia (including anurans) and more recently Laurin and Reisz (1997) argued that lepospondyls in general include the immediate ancestors of all modern amphibian orders. Only McDowell (1958) has suggested the Anthracosauria (namely Seymouriamorpha) as ancestral to the Anura. No Aïstopoda or Microsauria are known after the Early Permian and the last remaining nectridean appeared in the Upper Permian.

In contrast, similarities between the anurans and temnospondyls were recognized as early as the nineteenth century and were even taken as evidence for including the labyrinthodonts in the Class Amphibia (Quenstedt 1850). Gadow (1933), Säve-Söderbergh (1934), and Schmalhausen (1968), following Cope (1889), suggested direct evolutionary links between extant amphibians and those amphibians with rachitomous vertebrae (see Chapter 7 this volume). Evolutionary links between the anurans and Temnospondyli were proposed as early as the 1930s, namely: the Trematosauridae from the Lower Triassic (Säve-Söderbergh 1936), the dissorophid *Amphibamus* from the Upper Carboniferous (Watson 1940; Romer 1945; Bolt 1979) (however, Gregory 1950 and Shishkin 1973 denied these relationships), *Doleserpeton* (Fig. 1) from the Lower Permian (Bolt 1969, 1977), the Dissorophidae in general (Estes 1965; Shishkin 1973; Rage and Janvier 1982; Bolt and Lombard 1985), and the Branchiosauridae (Fig. 2) (Bolt 1969, 1977; Boy 1981).

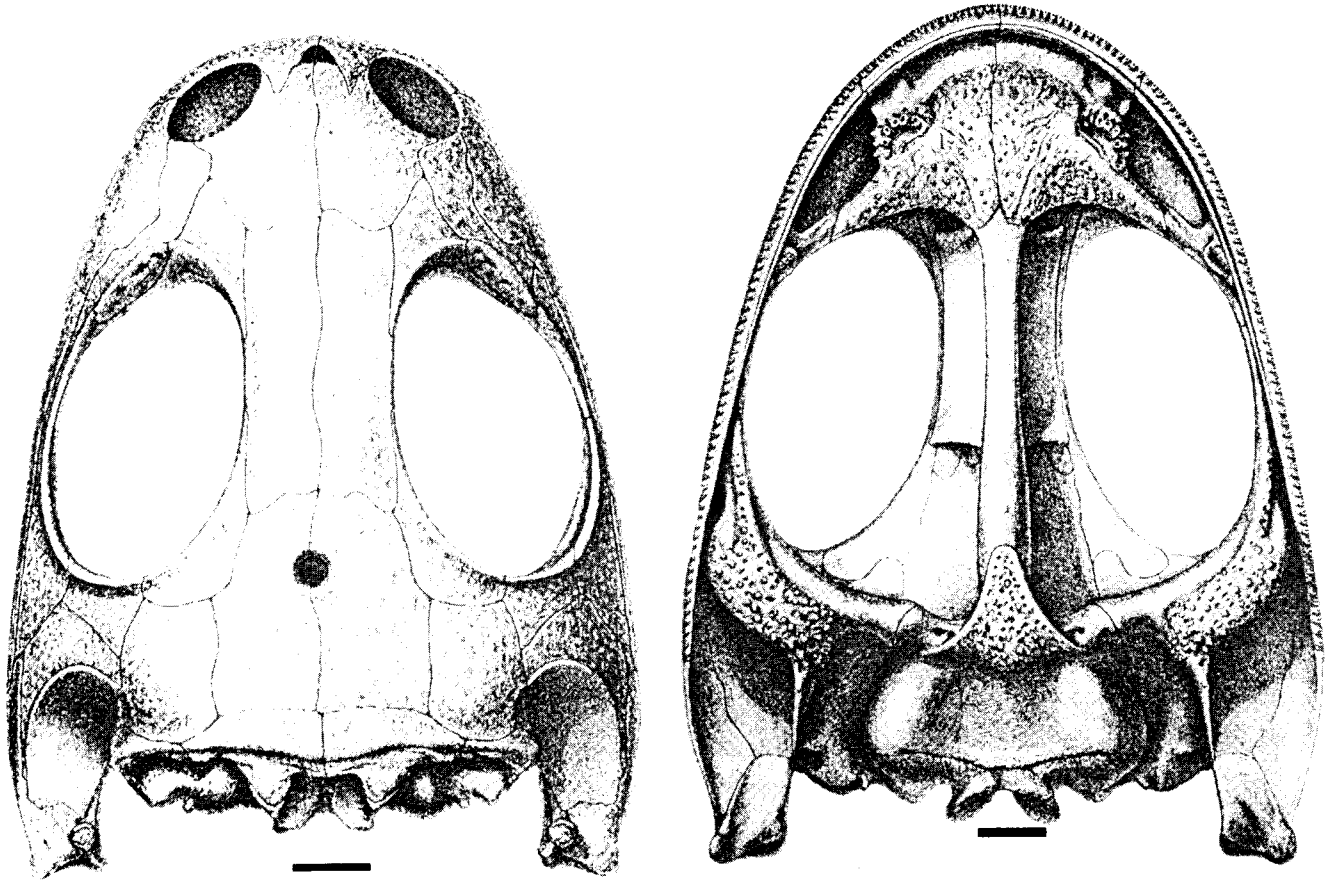


Fig. 1. Dorsal (left) and ventral (right) views of the skull of *Doleserpeton annectens*, an Early Permian labyrinthodont amphibian with pedomorphic features. Scale equals approximately 1 mm. From Bolt (1969).

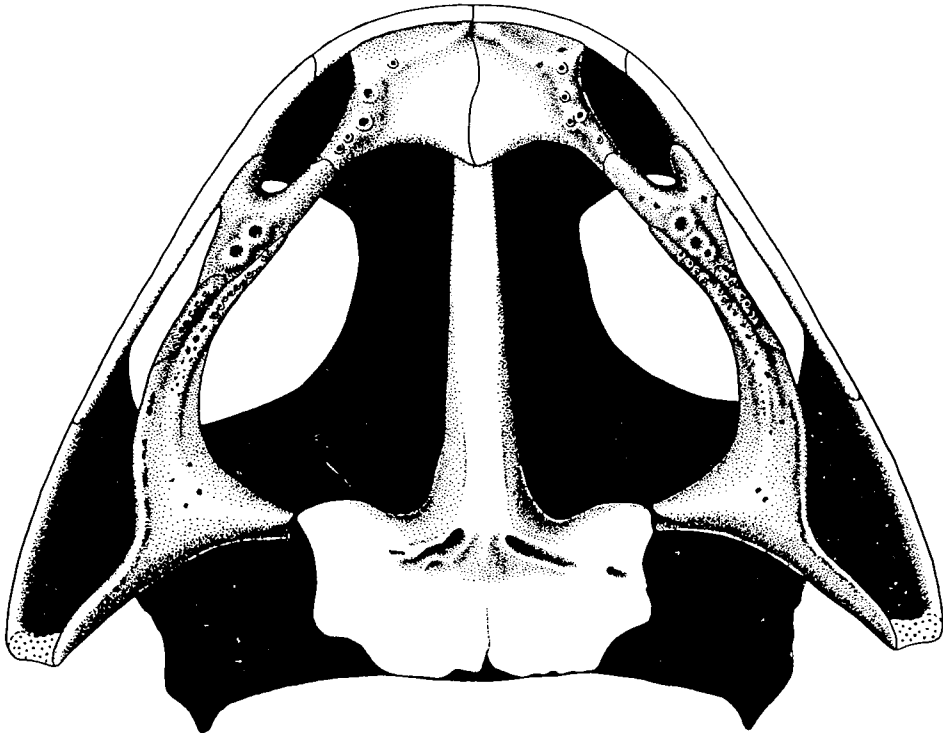


Fig. 2. Ventral view of the skull of *Branchiosaurus* cf. *petrolei*, an Early Permian labyrinthodont amphibian with pedomorphic features. Length of skull approximately 14 mm. From Boy (1978).

According to Milner (1988, 1993) and Trueb and Cloutier (1991), branchiosaurids may be even closer to anurans than is *Dolesempeton*, or they may represent convergent paedomorphosis. All of these authors suggested a direct evolutionary link between these presumed ancestral taxa and either the Anura, or the entire Lissamphibia although it is not clear yet whether the Lissamphibia are monophyletic (see e.g., Lehman 1968; Shishkin 1973: 217–225; Carroll and Holmes 1980; Bolt and Lombard 1985). Nevertheless, it is now generally agreed that the ancestors of the Anura evolved from temnospondyl amphibians.

Shishkin (1973) was the first to propose that anurans evolved from temnospondyls by means of somatic underdevelopment, primarily of cranial structures. This conclusion was based specifically on his studies of various species, including paedomorphic forms, of the Late Permian *Dvinosaurus*. Later, when *Dolesempeton* and *Amphibamus* were assessed within the context of the normal development of temnospondyls (Bolt 1977, 1979), it was found that they, too, correspond to a late larval or early postmetamorphic stage. This led to the conclusion, now generally accepted (e.g., Milner 1988; Boy 1992; Schoch 1995), that paedomorphosis was a principal evolutionary mechanism in the origin of the modern groups of the Amphibia. However, this phenomenon, interpreted as “morphological degeneration”, was recognized previously by Evans in 1944, and similarities between the structure of the skull in adult anurans and in labyrinthodont larvae (“Phyllospondyli”) were recognized by Noble (1931), Watson (1940), Reig (1964). Although paedomorphosis is the most significant process, it is not the only factor that led to the origin of the Anura. Progressive evolution (manifested by developmental additions) and modifications at premetamorphic stages also contributed.

The paedomorphic nature of anurans becomes obvious if growth series of temnospondyl amphibians are compared to the cranial structure of *Triadobatrachus* and with modern Anura. Evolutionary changes between temnospondyls and anurans are usually interpreted as miniaturization, lightening, fenestration, reduction or loss. However, it should be emphasized that these processes can be considered as resulting from somatic underdevelopment, i.e., that somatic development in anurans is blocked at an earlier developmental stage than in temnospondyls. The problem is that paedomorphosis could have been manifested in various phylogenetic lineages independent of one another but with the same anatomical expression (convergence). This is why it is easier to recognize general anatomical transformations associated with the transition from temnospondyls to the anurans than to determine the specific phylogenetic ancestry of the Anura.

## II. PAEDOMORPHOSIS: A PRINCIPAL PHENOMENON IN THE ORIGIN OF ANURA

Comparisons of growth series of Early Permian branchiosaurids (Boy 1974; Schoch 1992), archegosauroids and trimerorhachoids (Boy 1990), the Late Permian dvinosaurids (Shishkin 1973), the Early Triassic capitosaurid *Parotosuchus* (Warren and Hutchinson 1988a; Warren and Schroeder 1995), and the small stereospondyl *Lapillopsis* (Warren and Hutchinson 1988b, 1990) reveal that the following evolutionary trends that occurred in the transition between the temnospondyls, *Triadobatrachus*, and modern anurans were paedomorphic in nature (see also Smirnov 1999):

1. *Shift to small size with retention of juvenile shape and proportions of the skull.* Usually, such changes are described as miniaturization (e.g., Milner 1988; Schoch 1995), because the animals did not grow to the large size of adult stages of the ancestral lineage. The preorbital part of the skull remained short with a broad, rounded snout, and the orbits remained comparatively large. The tabular horns remained weakly projecting and the otic notches were not deeply incised. The degree of miniaturization can be assessed by a comparison between the metamorphic stages of *Parotosuchus galiciae* (skull length barely greater than 10 mm; Warren and Hutchinson 1988a) and the adults (skull length about 200 mm; Warren and Schroeder 1995) (Fig. 3).

2. *Shortening the ossification sequence.* Comparison of the full sequence of ontogenetic ossification in branchiosaurs, from the earliest stage recorded when bones retained independent ossification centres to late postmetamorphic stages (Boy 1974; Schoch 1992), with equivalent stages of anurans (e.g., Trueb and Alberch 1985) reveals that some elements that appear in the late larval or postmetamorphic periods in branchiosaurs (e.g., ectopterygoid, prefrontal, postfrontal, postorbital, jugal), are absent in anurans (see also Shishkin 1973: 215) or (e.g., sclerotic ring) they are blocked at the stage of cartilage. This is also true for sensory lines, ornamentation, and the infolding of the dentine. By contrast, the bones that appear in premetamorphic stages of branchiosaurs (e.g., parasphenoid, pterygoid, palatine, maxilla, nasal, frontal, parietal, dentary) are retained in anurans, although they may be part of developmentally complex units.

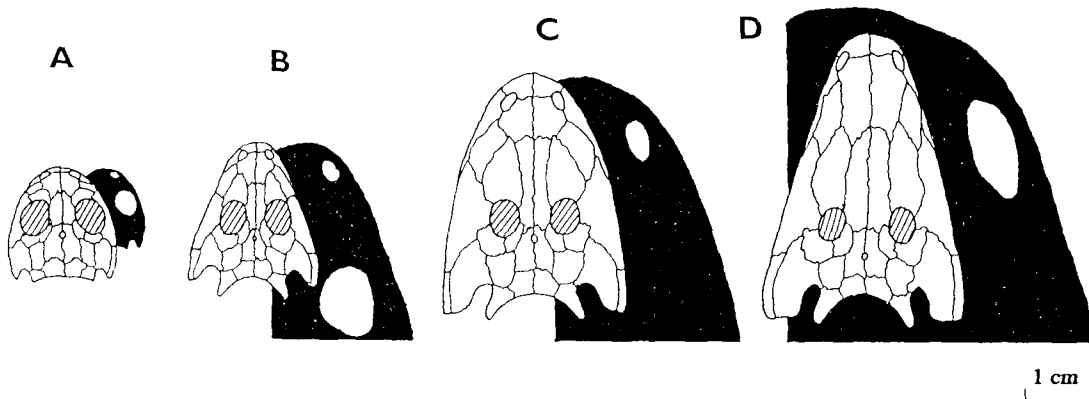


Fig. 3. Changes in skull roof proportions of the roof of the skull during postmetamorphic growth of a capitosaurid amphibian, *Parotosuchus aliciae*, from the Early Triassic (Scythian A1) of Queensland. **A:** At metamorphosis. **B, C:** Intermediate growth stages. **D:** Adult. All specimens are drawn to the same orbital length. Actual sizes are indicated by black silhouettes. Modified from Warren and Hutchinson (1988).

3. *Reduction in size of dermal bones.* Reduction occurs mainly in the squamosal, transversum (palatine), and dorsal margin of the otic notch (Shishkin 1973).
4. *Loss of dermal bones.* In the Anura, the prefrontals and postfrontals were entirely lost, permitting the frontal part of the frontoparietal complex to enter the margin of the orbit (the prefrontal is preserved in *Triadobatrachus*, lost in anurans). The lacrimal, jugal and postorbital disappeared, resulting in the formation of the contiguous orbito-temporal fenestra. The coronoids were lost from the lower jaw.
5. *Progressive reduction of the palate.* This involves increasing fenestration of the palate, associated with deepening of the embayments of the triradiate pterygoid (which remains movably articulated with the parasphenoid), loss of the ectopterygoid, reduction and anterior movement of the palatine (Shishkin 1973).
6. *Shift of metamorphosis to earlier stages of somatogenesis.* Modern anurans reach metamorphosis far earlier with respect to overall osteogenesis than is true of temnospondyls (Boy 1974; Schoch 1995; also see Chapter 9 this volume). Trends 3, 4, 6 and probably 5, are all correlated with 2.
7. *Shift of the pineal organ anteriorly.* In *Triadobatrachus* and in the primitive Anura in which this organ is still preserved (*Xenopus*, *Hymenochirus*), the pineal organ is located anterior to the level of the basicranial articulation; this position corresponds to the larval, rather than to the adult condition in temnospondyls (Shishkin 1973).
8. *Appearance of pedicellate, bicuspid teeth.* Bolt (1977, 1979) argued that pedicellate bicuspid teeth were present in juvenile dissorophoids, while adults developed labyrinthodont teeth. In late developmental stages of branchiosaurs the enamel is folded in a normal

- labyrinthodont way, but it is not folded in earlier stages (Schoch 1992, his figures 16, 29). Carroll and Holmes (1980) suggested that the evolution of pedicellate teeth may be associated with tongue-feeding out of water. According to Smirnov and Vasil'eva (1995), the presence of non-pedicellate teeth in some anurans (e.g., *Pipa carvalhoi*) results from incomplete tooth development due to paedomorphosis. However, not all non-pedicellate anurans (e.g., *Pyxicephalus*) lost their pedicellate teeth in this way.
9. *Tympanum becomes located posterior to the squamosal and lateral to the otic process of the palatoquadrate.* This condition is typical of early developmental stages of the middle ear in temnospondyls (Shishkin 1973, fig. 79g).
  10. *Shallow otic notch.* This condition corresponds to the early developmental stages of temnospondyls.
  11. *Ventrolaterally facing foramen ovale:* This condition occurs in paedomorphic temnospondyls (Shishkin 1973, his figures 48, 50).
  12. *Shift of the processus oticus.* In temnospondyls, the connection of the palatoquadrate with the otic capsule in the area of the anterior semicircular canal disappears during ontogeny and is replaced by another one posterior to the periphery of the lateral semicircular canal. This connection also ultimately disappears (Shishkin 1973). These two connections, respectively called the *processus oticus larvalis* and the *processus oticus adulti* (Plasota 1974), appear sequentially in the Anura during larval and postmetamorphic development; the latter is the definitive connection in adult anurans.
  13. *Shift of the basipterygoid articulation.* As seen in paedomorphic *Dvinosaurus primus*, the basipterygoid (= basitrabecular) articulation of the palatoquadrate (pterygoid) is established with the parachordal section of the neural endocranium by means of the *processus basalis* (= *pseudobasalis*), and only later in development does it move on to the trabecular section (Shishkin 1967, 1973, his figures 67, 74). In anurans, the condition remains as in *D. primus*.
  14. *Shift of the arteria carotis interna.* The *arteria carotis interna* (internal carotid artery) passed below the parasphenoid in larval and paedomorphic temnospondyls, whereas in adults it was included within this bone. In the anurans the condition resembles that of temnospondyl larvae (Shishkin 1973, his figures 57–58, 59 left).
  15. *Reduction and ultimate loss of the adductor mandibulae externus.* This feature is correlated with reduction of the surface area of the squamosal and with the large size of the otic notch and tympanum (Carroll and Holmes 1980).
  16. *Loss of the interclavicle.* An ossified interclavicle was present in adult temnospondyls. Its loss in the Anura is a striking feature but of similar importance is the occurrence in anurans of two distinct types of pectoral girdle (arciferal, firmisternal). It is not known which of these conditions might be the more primitive. Neither in *Triadobatrachus* (see below) nor in the Jurassic *Notobatrachus* (Stipanovic and Reig 1956) are there the median elements typical of firmisternal girdles. Thus, the firmisternal girdle must have been absent in these early evolutionary stages of anurans (Eaton 1959). Whether the median "sternum" of the firmisternal girdle with one or two bony pieces plus cartilage is a vestige of the interclavicle, or evolved *de novo* in association with axillary amplexus, as suggested by Cope (1889), remains obscure. The clavicle and the cleithrum are closely connected to the underlying procoracoid and suprascapular cartilages (Schmalhausen 1917). Transformation of the shoulder girdle may have evolved through paedomorphosis or it may be an adaptation related to jumping.

In summary, somatogenesis was abbreviated through retardation and/or elimination of particular developmental pathways. Consequently, a number of features of adult temnospondyls were lost in their descendants. However, because these changes occurred against the background of a complete ontogenetic cycle (i.e., larva → metamorphosis → adult), some other somatogenic processes (e.g., those associated with air-breathing) were

accelerated and rapidly reached a mature stage. This may explain why the transition from temnospondyls to anurans was associated with more pronounced adaptation for life on dry land.

### III. CHANGES DUE TO PROGRESSIVE EVOLUTION

In addition to the paedomorphic features mentioned above, there were changes that occurred through progressive evolution. These were manifested as more derived structures than those found in adult temnospondyls. Among these are:

17. *Fusion of dermal bones.* The postparietal, supratemporal and tabular were present in temnospondyls as independent elements. In anurans they are present as independent ossification centres only in early developmental stages but in adults they fuse with the frontals and parietals to form the frontoparietal complex (Roček 1988; Smirnov 1995). Similarly, the preopercular and squamosal fused in anurans to give a composite element termed the "squamosal" (Lebedkina 1979, her figure 99), and the palatine (still independent in *Triadobatrachus*) fused either with the maxilla or with the vomer (Roček 1981, his figure 59).
18. *Miniaturization of the stapes (= plectrum) and loss of contact of its processus externus with the hyoid* (Shishkin 1973). The principal morphological features of the ossified part of the stapes were present at the temnospondyl stage, as seen by its similarities with anurans, including the presence of a straight ventral margin on the stapedial footplate (= *pars interna plectri* Gaupp), absence of any process from either the shaft or the footplate that might have articulated with the skull (see, however, Eaton 1959), presence of a posterior notch, and an antero-posteriorly compressed stapedial shaft (Bolt and Lombard 1985). Miniaturization of the stapes in most modern anurans made possible the transfer of sound waves from the tympanic membrane to the membrane of the *fenestra ovalis* via the stapes. In this process vibrations of large amplitude and low intensity are amplified by conversion to vibrations of small amplitude and high intensity (Schmalhausen 1957).
19. *Changes in the connection of the palatoquadrate with the nasal capsule.* In temnospondyls, the *processus pterygoideus palatoquadrati* is connected medially with the *lamina orbitonasalis* by means of the *commissura quadratocranialis anterior*, and laterally via the *processus maxillaris posterior*. In anurans, the medial connection no longer exists and the palatoquadrate is connected with the nasal capsule only through the posterior maxillary process. However, the temnospondyl developmental stages are recapitulated in the development of anurans (Shishkin 1973, his figures 47–50, 73; Roček 1993, his figure 6).
20. *Shift of the arteria palatina anterior into the cranial cavity.* In temnospondyls, the *arteria palatina anterior* splits from the *arteria carotis interna anterior* to the *arteria palatina proper* beneath the endocranium (see Shishkin 1973, his figures 52–54, 56). In the Anura, division of these vessels beneath the endocranium occurs in the premetamorphic stages but in adults the origin of the *arteria palatina anterior* is moved into the cranial cavity (Millard 1944).
21. *Loss of the arteria stapediales.* The *arteria stapediales* is progressively reduced in temnospondyls and it is entirely absent in the Anura; consequently, the *arteria temporalis*, which originally split from the *arteria stapediales* in temnospondyls, became a branch of the *arteria occipitalis* in anurans (Shishkin 1973).
22. *Establishment of a connection of the adductor muscles and the hyoid with the otic capsule* (Shishkin 1973).
23. *Secondary resorption of the cartilaginous epipterygoid* (Shishkin 1973).
24. *Fusion of the foramen of the arteria carotis with that of cranial nerve III* (Shishkin 1973).
25. *Development of nearly monospondylous vertebrae in which the main central element is the pleurocentrum* (Shishkin 1973). According to Eaton (1959), this condition in the Anura

is a simplification of the pattern of the Temnospondyli. *Doleserpeton* (Bolt 1977) shows progressive ossification of the vertebrae during ontogeny that approaches the condition in primitive frogs.

26. *Reduction and simplified articulation of the ribs with the transverse processes.* Very much reduced unicipital ribs are already present in *Triadobatrachus*. This animal was not capable of jumping (Rage and Roček 1989) and hence this reduction was not a saltational adaptation. In contrast with reduction in size of the individual ribs, all of those in the trunk and some of those in the tail were retained.

It should be noted that the transverse processes together with the development of the *pars labyrinthica* (*sensu* Gaupp) of the exoccipital also occurred in some Triassic labyrinthodonts, and continued into some lineages of frogs (Shishkin 1973: 217). It is difficult to decide what function these changes had, except that the reduction of the ribs and simplification of their articulations may be related to the elaboration of cutaneous respiration.

#### IV. CHANGES ASSOCIATED WITH SPECIAL MODE OF LOCOMOTION

The following changes may be associated with the mode of locomotion, although the major anatomical transformations relating to jumping (fusion of the tibia and fibula and ulna and radius, as well as elongation of the two proximal bones of the tarsus) did not occur until later, beyond the level of *Triadobatrachus*:

27. *Reduction in number of vertebrae, accompanied by formation of the urostyle.* This process started in the proanuran stage and reached its maximum later.
28. *Elongation of the pelvis posteriorly relative to the sacrum.* This change was achieved by anterior elongation of the ilia. Elongation of the pelvis may have compensated for shortening of the vertebral column so that some minimum distance between the anterior and posterior limbs was retained. This modification may have functioned in stabilizing the body during movement through the air (see Jenkins and Shubin [1998] for a more detailed discussion of the evolution of the jumping apparatus in the ancestry of frogs).
29. *Shortening of the tail.* Although the total length of the tail in *Triadobatrachus* remains uncertain, it is clear that substantial shortening had already occurred.

Obviously, all of the locomotory adaptations were intimately correlated.

#### V. TRANSFORMATIONS IN PREMETAMORPHIC STAGES

Besides transformations in the anatomical structure of adults, there were also striking morphological changes in the larval stages. These were:

30. *Caenogenetic adaptations associated with extensively necrobiotic metamorphosis* (Shishkin 1973). The anatomical structure of larval anurans differs extensively from that of larval temnospondyls (e.g., shape of the body, jaw apparatus). The developmentally earliest known larvae of temnospondyls that bear distinct external gills (Boy 1974, his figures 1–3) are salamander-like in shape. Evolution of the generalized tadpole structure includes closure of the gill-chamber by the opercular (= gill) folds, and associated retardation of development of the anterior limbs (both gills and anterior limbs are entirely covered by the folds), expansion of the lips, and growth of parallel rows of horny teeth. These features could evolve in association with suctorial feeding (Eaton 1959; Schmalhausen 1968). The larval oral opening takes the form of a funnel which serves for sucking, and is invested by vestigial elements of the premandibular branchial arches (Roček 1981). In anuran larvae, external gills of the same type as those present in temnospondyls and urodeles are developed first, but with development of the opercular folds the gills are reduced. Under the folds new “internal” gills are developed



that are not homologous either with those of urodeles or those of fish (Schmalhausen 1955, 1968). A change from predation to feeding on plants is another feature that appeared during the transition from the temnospondyl larva to the anuran tadpole.

## VI. ECOLOGICAL IMPETUS FOR THE ORIGIN OF ANURA

The appearance in the Early Triassic of transitional forms between temnospondyls and modern anurans (such as *Triadobatrachus*) may be related to some climatic event at the end of the Permian. Some such event is generally considered to have been responsible for the massive extinction of the earth's biota, including 75% of amphibian and 80% of reptilian families (Nevo 1995). This was also a period when metabolic thermoregulation (i.e., endothermy) first appeared in the evolutionary history of vertebrates (in the lineage leading to mammals). Thermoregulation was probably an adaptation to a sustained period of global aridity. Bolt (1979) suggested that increasing aridity in the Late Permian and Triassic played a role in the origin of modern Amphibia. It is known that aridity can cause a rapid shift to neoteny in living urodeles (e.g., Balkan populations of *Triturus alpestris* after deforestation during medieval times). Thus, either a drop in temperature or an increase in aridity could have been a major impetus for pedomorphosis and the origin of the Anura.

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