Amphibian Biology

Edited by

Harold Heatwole

and

Robert L. Carroll

Volume 4

Palaeontology
The Evolutionary History of Amphibians

Proanuran Stages (*Triadobatrachus, Czatkobatrachus*)

Zbyněk Roček and Jean-Claude Rage

I. INTRODUCTION

WHEREAS the ancestry of the Anura among primitive Palaeozoic amphibians is still a matter of discussion, the evolutionary stage preceding that of modern frogs is documented by *Triadobatrachus massinoti* (Figs 1–6) (Piveteau 1936a). This unique early Triassic fossil amphibian was discovered more than sixty years ago. It is known from only a single specimen found in northern Madagascar and deposited in the collections of the Museum d'Histoire Naturelle in Paris (MNHN, No. MAE 126). The specimen is represented by a natural mold enclosed in a nodule which, split open, shows the dorsal and ventral faces of the fossil (Fig. 1). The anterior part of the skull, the manus and parts of the hind limbs are lacking. On the split surface of the nodule outlines of the soft parts of the body are distinguishable. The nodule was found near the village of Betsieka, Madagascar by an amateur, A. Massinot, who gave it to J. Piveteau. It comes from shales that have yielded numerous fishes (also enclosed in nodules), ammonites, labyrinthodont amphibians and some plant fragments. These beds are of marine, more precisely littoral, origin but several other fossils besides *Triadobatrachus* are of continental origin (benthosuchid amphibians, plants). These marine levels are equated with the base of the middle part of the continental Sakamena group (outcropping in southwestern Madagascar) and therefore are equivalent to the local Gyronitian stage (Besairie and Collignon 1960). The Gyronitian corresponds to the Induan or Scythian, i.e., early Triassic.

The fossil was first described by Piveteau (1936a, 1936b, 1937) under the name *Protobatrachus*. Because this name was preoccupied, Kuhn (1962) replaced it by the name *Triadobatrachus*. After the first descriptions by Piveteau the specimen was reinvestigated

Fig. 1. *Triadobatrachus massinoti.* Left: Part of a nodule with an imprint of the dorsal side. Right: Part of a nodule with an imprint of the ventral side. Photo courtesy of the Laboratoire de Paleontologie, Museum national d'Histoire Naturelle, Paris.

and/or discussed by Watson (1940), Griffiths (1956, 1963), Hecht (1960, 1962), Estes and Reig (1973), Jarošová (1974), and Rage and Roček (1986, 1989). Its systematic position is as follows:

Order: Salientia Laurenti, 1768

Suborder: Proanura Romer, 1945

Family: Triadobatrachidae Kuhn, 1962

Genus: *Triadobatrachus* Kuhn, 1962
       Triadobatrachus massinoti (Piveteau, 1936)

II. DESCRIPTION OF *TRIADOBATRACHUS*

The whole animal had a total length (estimated from the presumed tip of snout to the presumed end of the tail; see below) slightly exceeding 10 cm.

The details of the skull are portrayed in Figure 3. The anterior part of the frontoparietal has low irregular rugosities on its dorsal surface that tend to be oriented anteroposteriorly. The posterior part is divided by a median suture that is also manifest
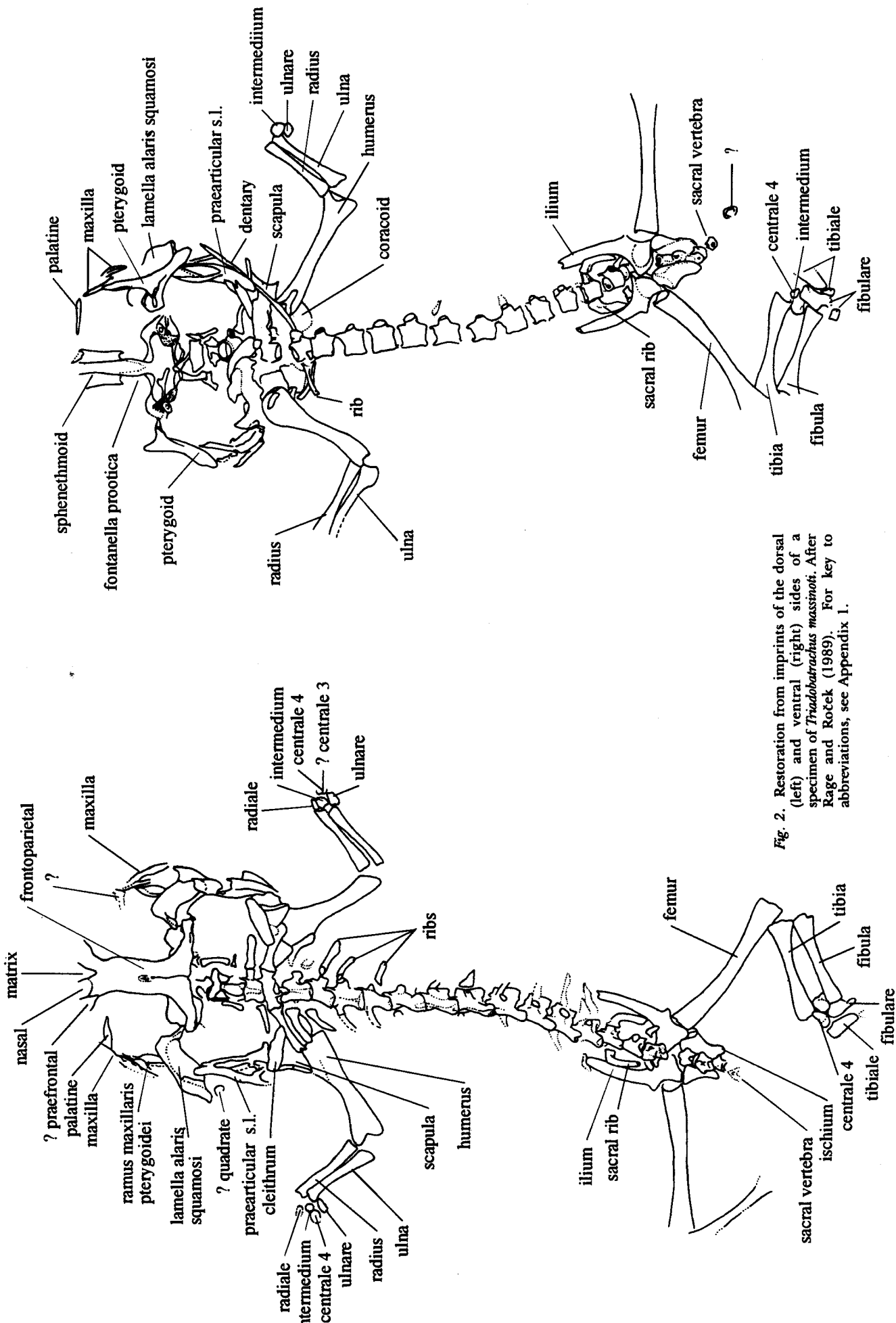
Fig. 2. Restoration from imprints of the dorsal (left) and ventral (right) sides of a specimen of *Triadobatrachus massinoti*. After Rage and Roček (1989). For key to abbreviations, see Appendix 1.
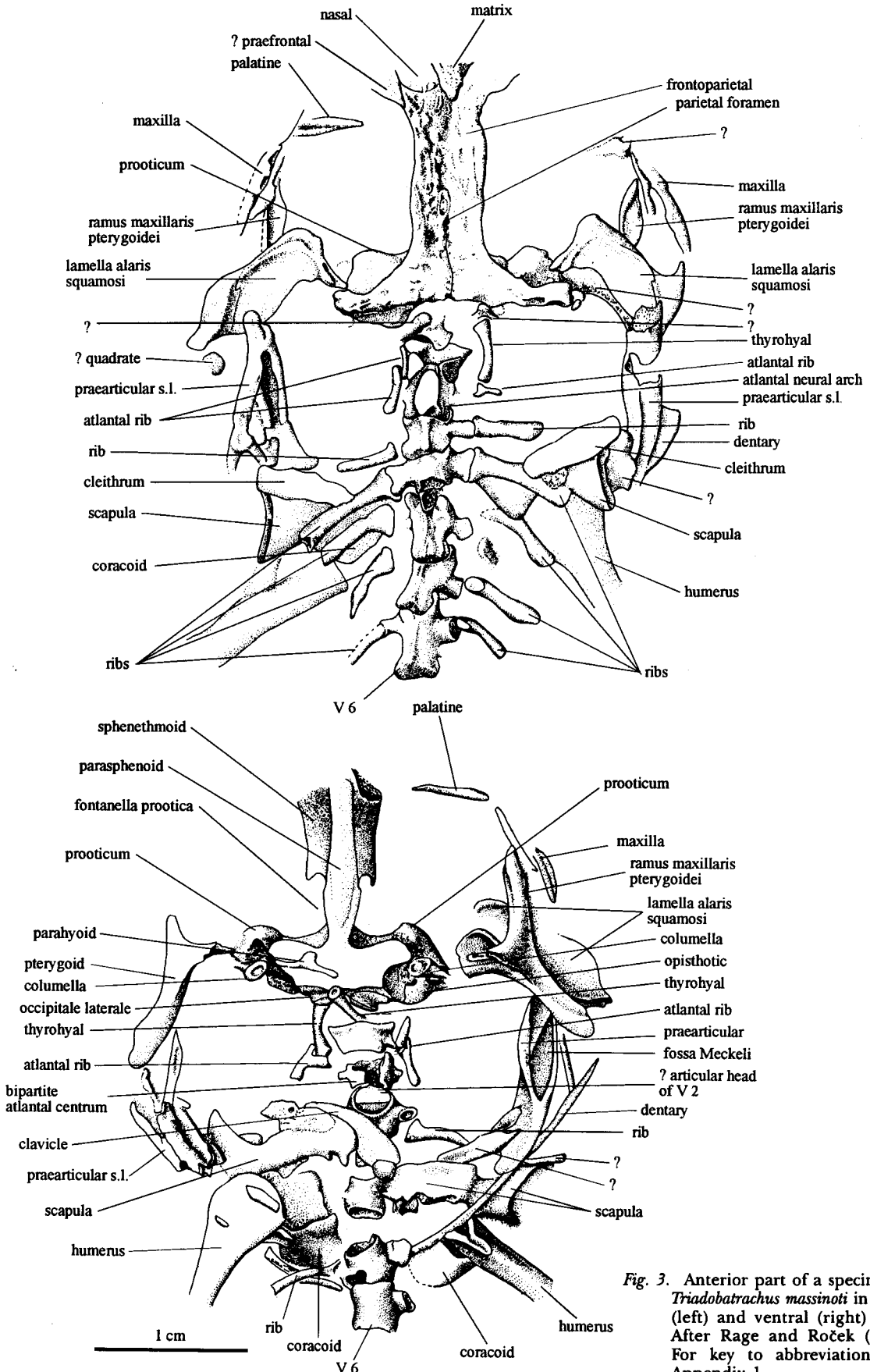
Fig. 3. Anterior part of a specimen of *Triadobatrachus massinoti* in dorsal (left) and ventral (right) views. After Rage and Roček (1989). For key to abbreviations, see Appendix 1.

V 12

proc. transversus

proc. spinosus

ribs

ilium

sacral rib

caudal rib

caudal rib

femur

ischium

vertebra

rib

ilium

sacral rib

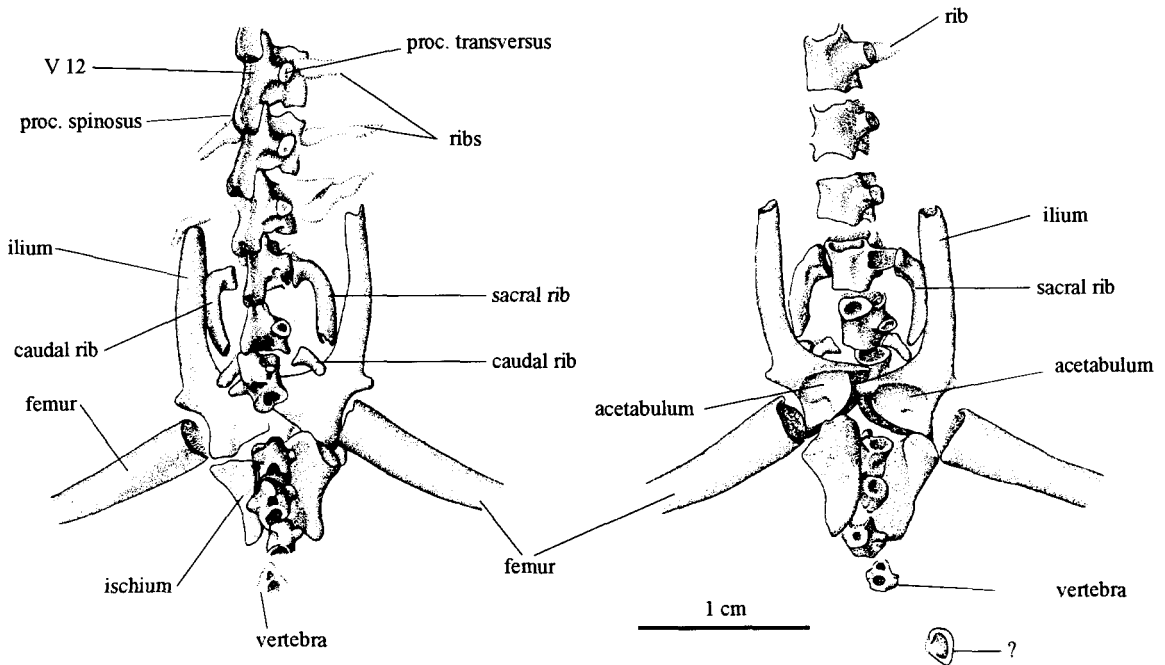acetabulum

acetabulum

femur

vertebra

1 cm

?

Fig. 4. Sacral and caudal regions of *Triadobatrachus massinoti* in dorsal (left) and ventral (right) views. After Rage and Roček (1989). For key to abbreviations, see Appendix 1.

prooticum

nasal

? praefrontal

frontoparietal

maxilla

lamella alaris squamosi

atlantal rib

cleithrum

radiale

intermedium

centrale 4

? centrale 3

ulnare

radius

ulna

scapula

suprascapula

ribs

sacral rib

ilium

caudal rib

ischium

femur

tibia

fibula

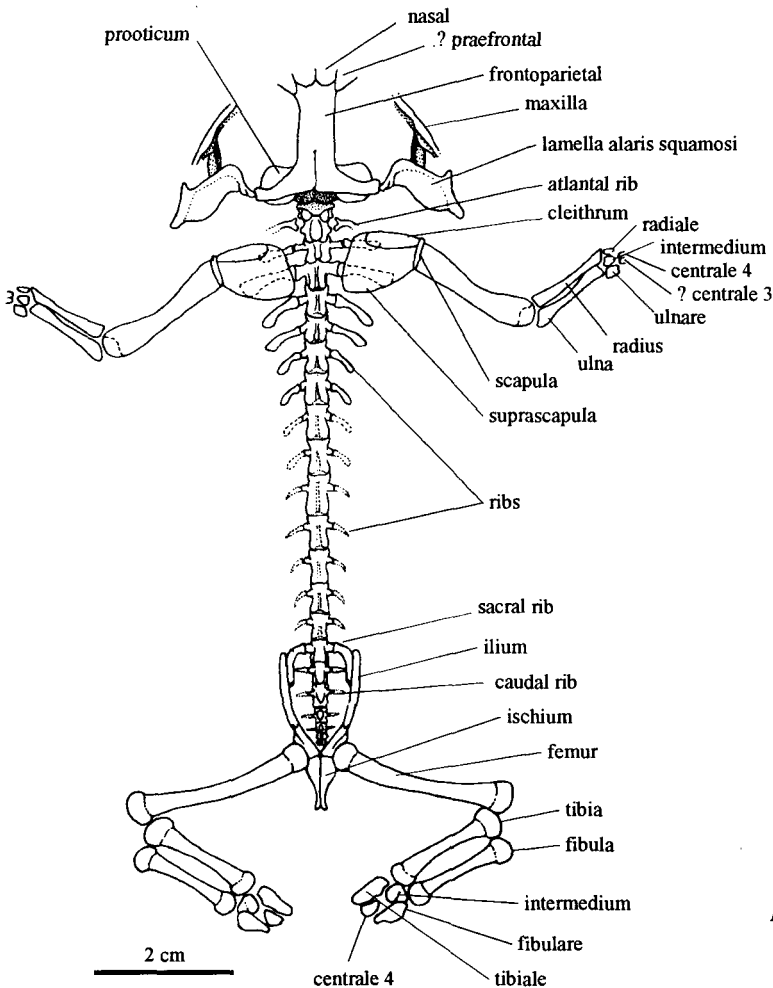intermedium

fibulare

centrale 4

tibiale

2 cm

Fig. 5. Restoration of known parts of *Triadobatrachus massinoti.* After Rage and Roček (1989). For key to abbreviations, see Appendix 1.
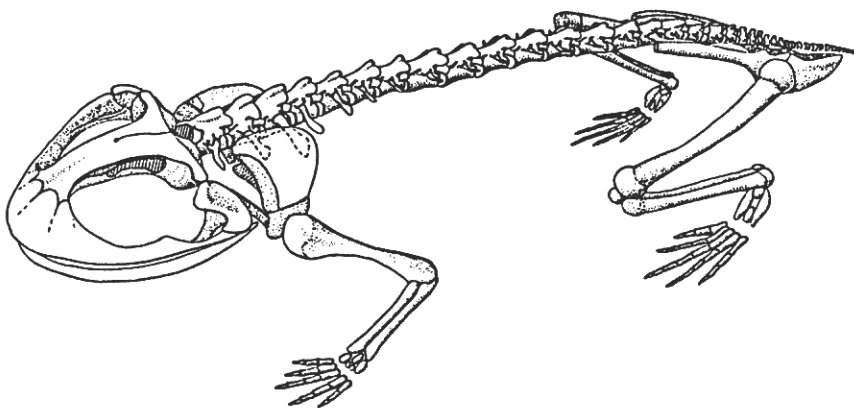
Fig. 6. Hypothesized restorations of the whole animal (upper) and skeleton (lower) of
Triadobatrachus massinoti. Skeletal reconstruction after Rage and Roček (1989);
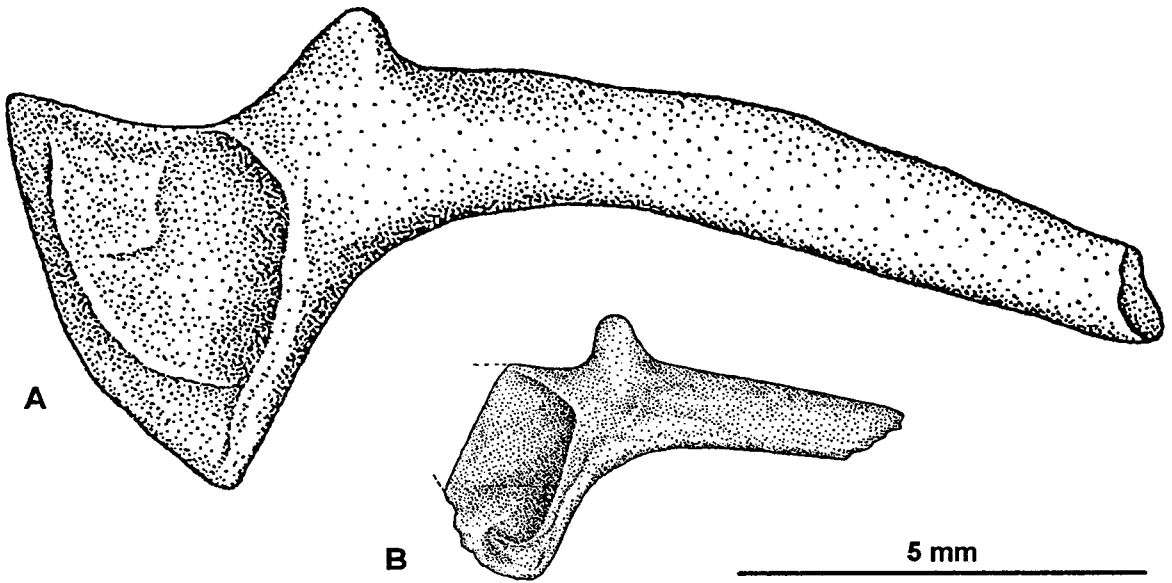drawing by J. Berger.

Fig. 7. Right ilium of *Triadobatrachus massinoti* (A) and of *Czatkobatrachus polonicus* (B). From Evans and Borsuk-Białynicka (1998).

on the margin of the bone. In the anterior half of the frontoparietal, no conspicuous suture is discernible, but the table is markedly depressed along the median longitudinal axis. This suggests that the bone was paired, or had been paired in earlier ontogenetic stages (Roček 1988). Slightly posterior to the mid-length of the frontoparietal, the parietal foramen is represented by a small depression in the midline through which the median suture passes. Laterally, the frontoparietals form short ventral flanges. Posteriorly, these flanges form strongly projecting lateral wings that cover the posterior margin of the otic capsules; laterally, the wings project slightly beyond the capsules (i.e., over the crista parotica) and articulate with the squamosals. A markedly raised, triangular area anterior to the frontoparietal complex — considered paired nasals by Piveteau (1937), possibly the sphenethmoid by Estes and Reig (1973), and surface contact between the skeleton and matrix by Hecht (1962) — is a sedimentary structure.

A semi-circular fragment of bone to the left of this sedimentary structure is probably the posteromedial part of the nasal. Another, more laterally incomplete bone bordering the anteromedial section of the orbit was considered the prefrontal by Piveteau (1937) and Sedra (1949), the frontal process of the maxilla by Estes and Reig (1973), and a supraorbitotectal by Jarvik (1942). The identity of this structure remains questionable. In any case, it is not a broken part of the nasal because limits of both bones are very distinct and do not fit one another.

Both squamosals are disarticulated from the frontoparietals. Since the lamellae alares are pressed into the horizontal plane and do not retain their original position, corresponding to the vaulted dorsolateral surface of the head, their lateral extent is greater than in the living animal. Hence, the head was not so broad as is commonly portrayed. When the original position of the squamosals is reconstructed, the orbitotemporal vacuities display a wide anterior part, prolonged posterolaterally by a narrower portion. The anterior marginal part of the dorsal surface of the lamella alaris squamosi is slightly ornamented; posteriorly, there is a large, smooth, semilunar depression that undoubtedly served for insertion of the cervical muscles (m. rhomboideus ant., m. sternocleidomastoideus). The processus posterolateralis squamosi is either broken off or hidden in the space between the lamella alaris and the pterygoid.

Only the posterior sections of the maxillae, including their laminae horizontales, are preserved, but no teeth are apparent.

The parasphenoid shows the T-shaped morphology that occurs in nearly all anurans. Its posterolateral corners display curved emarginations that bordered the fenestra ovalis. This suggests that the fenestra faced somewhat ventrally.

The pterygoid is triradiate. In dorsal view, its rami maxillares display grooves that housed cartilaginous parts of the palatoquadrate. Deep and thin lamellae extend ventrally from the rami interiores; these structures are lacking in modern frogs.

The palatine is exposed within the left orbit, and is apparently displaced posteriorly from its original location on the ventral surface of the postnasal wall. As in frogs, it has an elongate shape. It is not attached to the maxilla.

The lower jaw was reflected back against the ventral surface of the thorax and shifted somewhat anteriorly onto the dorsal surface of the lamella alaris squamosi. Each half of the jaw consists of two disarticulated parts, the prearticular (*sensu lato*) and the dentary. There is no evidence of teeth. The groove on the prearticular that housed Meckel's cartilage is open ventrolaterally and in its original state was covered by the dentary. The fossa Meckeli is preserved in the prearticular; in modern frogs this fossa is lacking. According to Carroll and Holmes (1980) the m. adductor mandibulae externus is small or absent in modern frogs, and the longus head of the m. adductor mandibulae posterior had its area of origin on the otic capsule.

In contrast to Piveteau's (1937) statement, the quadratojugal cannot be discerned.

The ethmoidal part of the sphenethmoid, including the postnasal wall, is lacking but its posterior margin is well preserved. The visible part of the sphenethmoid is quite reminiscent of that in modern frogs. Between the sphenethmoid and the prootic the braincase wall consisted of cartilage and membrane. Cranial nerves III-V passed from the braincase through foramina in this part of the braincase.

The otic capsules consist of three elements (the prooticum, opisthoticum, and the occipitale laterale). As is clearly seen on the ventral cast, the opisthotic and lateral occipital were probably separated from one another by a slender strip of cartilage, whereas in adult stages of modern frogs they are fused. Estes and Reig (1973) misinterpreted the posterior wall of the otic capsule (the opisthoticum) as the operculum.

The columellae are well preserved, although not retaining their original position. The proximal section of each columella is far more stout than the distal one, and was probably completed by a cartilaginous ring. The columellae were somewhat flattened.

A small ovoid bone behind the posterolateral end of the left squamosal might be the quadrate. The parahyoid bone, preserved on the posterior part of the parasphenoid, is widely bifurcated posteriorly. Two small, elongate and rather curved bones preserved in the cervical region are probably thyrohyalia.

There are 14 presacral vertebrae (including the atlas), one sacral and six exposed caudal vertebrae that make up the vertebral column (Figs 2, 5). All (except perhaps the second) are amphicoelous, and probably all (atlas included) bear free ribs.

The centrum of the atlas is composed of separate anterior and posterior parts, but its neural arch is single. Perhaps the two parts of the centrum were connected by cartilage in the living animal. Two cervical cotyles are clearly, although not widely, separate. On both sides of the anterolateral surface of the neural arch, there are small distinct areas that took part in the craniovertebral articulation. Atlantal ribs are bicapitate. One articulation process is borne on each part of the bipartite centrum, both processes being located in an almost horizontal plane. The second vertebra displays a distinct semilunar element that is convex anteriorly. It might be the remnant of an intervertebral disc or a slightly displaced articulating process. If the latter interpretation is correct, this vertebra

would be the only one within the whole column to be opisthocoelous. Both ribs of this vertebra, similar to those of the two more posterior vertebrae, are single-headed. The third vertebra is short with stout transverse processes; its ribs are the longest and strongest in the entire vertebral column. The centrum of the fourth vertebra is amphicoelous; its neural arch is long (about twice as long as the centrum) with a low median keel occupying the posterior two-thirds of its length. The prezygapophyses have flat, oval articular surfaces. Up to the fourteenth vertebra, the morphology is similar to that of vertebra four. In as far as the lateral surfaces are visible, foramina for the spinal nerves are lacking throughout the trunk. The fifteenth vertebra is the sacral. It is comparatively short but strong and its neural arch seems to be narrow. It is provided with stout transverse processes that articulate with strong and posteriorly recurved sacral ribs. Six caudal vertebrae are exposed. The section of the neural canal of the posteriormost visible vertebra is still well formed, which suggests that this vertebra was not the last one and that the tail was probably substantially longer. Only one pair of short, stout and nearly straight caudal ribs is apparent, but as they possess marked transverse processes it seems that all visible caudal vertebrae could have borne ribs.

The pectoral girdle (Figs 3, 5) is badly crushed but a curved, flat and elongate bone, that is most probably the clavicle, can be distinguished. The curved shape of this bone suggests that the girdle was not firmisternal. Large flat elements may be interpreted as the scapulae. There is no trace of suprascapulae; they were apparently cartilaginous. Massive, flat and arched bones on either side of the column might be fragments of the coracoids. Thus, the scapula and coracoid seem to be separate elements. Both cleithra are partially visible on the dorsal cast but their exact shape cannot be discerned.

Compared with the pectoral girdle, the pelvic girdle (Figs 4, 5) is only slightly disarticulated. The ilia are elongate and in the living animal they were completed by cartilaginous anterior tips as demonstrated by their hollowed out extremities. The ossified shaft of the ilium extends anteriorly and corresponds to about the length of the last three presacral vertebrae. There is no trace of an interiliac tubercle on the medial face of the acetabular area. There is a distinct tuber on the dorsal border of both bones. The articulation between the ilium and sacral rib was unlike that of modern frogs. Because the sacral rib was recurved, most of its length was in contact with the medial surface of the shaft of the ilium. The ischia stretched posteriorly and were connected with the ilia either syndesmotically or synchondrotically. Both pubes are lacking and it is probable that they were cartilaginous, as in modern anurans. The acetabula were comparatively large.

The anterior limbs are represented by both humeri, each of which displays a well developed ventral crest. Their distal end is wide with two epicondyles, and the epiphyses on both humeri are lacking, suggesting that they were cartilaginous. The ulna and radius are separate and markedly shorter than the humerus. The right limb displays the proximal row of the carpus, which consists of three elements (probably the radiale, intermedium, and ulnare) plus centrale 4 (centrale 1 in other terminology) and perhaps centrale 3 (centrale 4 in other terminology). The number of fingers remains unknown.

The posterior limbs are represented by long, cylindrical, slightly sigmoid femora, the epiphyses of which are lacking and were probably cartilaginous. The tibia and fibula are separate and markedly shorter than the femora. Four tarsal elements are known, the tibiale and fibulare being less elongate but more massive than in the restorations by Piveteau (1937), Estes and Reig (1973) and Jarošová (1974). A further two bones are small and may be identified (Estes and Reig 1973; Jarošová 1974) as the intermedium and centrale 4 (centrale 1 of Jarošová who used a different terminology).

Although Griffiths (1956, 1963) expressed the view that *Triadobatrachus* was a larva, several characters suggest that this is not the case. Full ossification of the dermal bones, definitive size of the columella, and complete ossification of the parahyoid and thyrohyals support the view that the specimen represents a postmetamorphic animal (Fig. 6). On the

other hand, the absence of epiphyses of the long bones suggests that it had not yet concluded its growth. For a discussion of the characters used by Griffiths to support his view see Rage and Roček (1986, 1989).

III. THE RELATIONS OF *TRIADOBATRACHUS* WITH ANURANS AND THE CONSTITUTION OF THE ANURAN STRUCTURAL SCHEME

Judging by its structure, *Triadobatrachus* may be regarded as an intermediate between primitive amphibians and anurans. It is now generally agreed that similarities between *Triadobatrachus* and anurans reflect their true phylogenetic relationships, although there is a gap in the fossil record of about 40 million years.

Several advanced features of *Triadobatrachus* are characteristic of anurans, namely the fusion of the frontals and parietals, a T-shaped parasphenoid, deeply triradiate pterygoids, a reduced palate, transversely situated palatine bones, anteriorly projecting ilium, cartilaginous pubis, and possibly also the morphology of the hyoid and the probable absence of teeth (at least on the lower jaw). Thus, most anuran features of *Triadobatrachus* appear in the skull, whereas those few on the postcranial skeleton are associated with the pelvic girdle (but not with the hind limbs, which are of approximately the same length as the front ones). One may thus conclude that the sequence of changes leading to anurans did not start with the elongation of the posterior extremities (i.e., with saltatorial locomotion), but with the skull. In other words, jumping cannot be considered as the initial stimulus in anuran evolution (see also Jenkins and Shubin 1998).

From the biomechanical point of view, the anuran skull structure of *Triadobatrachus* (as a starting point of anuran evolution) could be the result of the strengthening of the longitudinal axis required by enlarged cervical muscles for firm but nearly immovable connection of the head with the trunk. These muscles insert into extensive orbitotemporal vacuities and, in *Triadobatrachus*, also may have inserted on the posterodorsal surface of the lamella alaris squamosi. The fusion of the frontals and parietals with each other also serves to strengthen the longitudinal axis. The co-ossification of the frontoparietal complex may have evolved in association with the extreme reduction of the bony palate. This, in turn, can be correlated with enlargement of the eyes that in anurans bulge into the mouth cavity.

The posterolateral extent of the frontoparietal complex, reaching the level of the crista parotica, may also include other elements situated lateral to the parietal in the Palaeozoic ancestors of *Triadobatrachus* (see also Hecht 1962) and thus may be considered a primitive feature. The presence of a bone tentatively interpreted as a prefrontal on the anterior margin of the orbit, the lack of fusion between the opisthotic and prootic, and the retention of a well defined fossa Meckeli are other primitive characters of the skull in *Triadobatrachus*.

In contrast with the advances in the skull, the postcranial skeleton retains many of the structures and proportions seen in amphibamid dissorophoids such as *Eoscopus* and *Doleserpeton*, which are thought to be the closest sister-taxa of anurans (see Chapter 7 this volume). The trunk retained a comparatively high number of presacral vertebrae, each of them bearing ribs. The anterior and posterior limbs are of nearly the same length. This, together with the fact that the tibia and fibula were much shorter than the femur, indicate that there were few if any changes that would have facilitated jumping. The radius and ulna, and the tibia and fibula remain separate. The only advanced characters are the fully cylindrical configuration of the centra and the moderately elongated, anteriorly oriented ilia, and the cartilaginous pubes.

The question arises as to the reason for the elongation of the ilia and why the pubes lost their ability to ossify. Major muscles inserting onto the ala ossis ilii (iliac shaft) in anurans are the m. obliquus externus and m. transversus (both taking part in the formation of the body flanks), m. iliacus externus (running to the trochanter femoris, i.e., to the proximal part of the hind limb), m. tensor fasciae latae (not very important for

locomotion), m. iliacus internus (abductor of the femur), and m. coccygeo-iliacus (connecting the ilium and urostyle). It is obvious that several of these muscles belong to the trunk and, among muscles inserting onto the ilium, only the iliacus internus muscle plays a significant role in locomotion. It should be noted that it originates close to the acetabulum, within the complex of other muscles responsible for locomotion, not on the anterior elongate part of the ilium. All other locomotor muscles of the posterior limb surround the acetabulum. Arguing from the pattern of the muscles in modern anurans, one may deduce that elongation of the shaft of the ilium was caused by other factors than the requirement for altered areas of muscle insertion area associated with jumping.

Since the most anterior muscles of the iliac shaft in modern anurans belong to the flank and the acetabulum is located lateral to the urostyle (i.e., to the former caudal section of the vertebral column), the acetabular level obviously shifted posteriorly in respect to the sacral vertebra. The posterior shift of the acetabulum (and corresponding elongation of the ilium) can be associated with, and was probably caused by, simultaneous shortening of the presacral part of the vertebral column. The posterior shift of the acetabular region appears to be in contradiction with the reduction of the number of presacral vertebrae. This paradox is explained by the need for rigidity of the body axis (Gans and Parsons 1966) and by the requirement for maintaining a certain minimum distance between the forelimbs and hind limbs, thereby preventing uncontrolled rotations while jumping (see also Jenkins and Shubin 1998).

In *Triadobatrachus* the ilia are only moderately elongated and the number of presacral vertebrae is still comparatively high. This may indicate an early stage in the evolution of saltation, but the similar length of the anterior and posterior extremities suggests that this was not the prevailing mode of locomotion.

It may be concluded that *Triadobatrachus* displays evolutionary trends toward anurans, but the impetus that caused their origin was not associated with saltatorial locomotion. On the other hand, the shortening of the vertebral column and modification of the pelvic girdle in *Triadobatrachus* illustrates a condition from which saltatory adaptation subsequently evolved.

IV. *CZATKOBATRACHUS*

Recently, disarticulated postcranial bones (vertebrae, humeri, and ilia) have been discovered from karst deposits of the Early Triassic (Scythian) at the Czatkowice locality in Poland (Evans and Borsuk-Białynicka 1998). All bear distinct salientian characters. The material was described as *Czatkobatrachus polonicus*. *Czatkobatrachus* is approximately five million years younger than *Triadobatrachus*, but is more derived in features of the vertebrae and elbow joint. It is smaller than *Triadobatrachus*, about 50 mm in snout-vent length, as inferred from isolated bones. *Czatkobatrachus* may be characterized by the following combination of characters: ilium with very prominent tuber superius (Fig. 7); atlantal centrum single and without rib facets; anterior cotyles well spaced and slightly divergent; most or all presacral vertebrae bearing long slender transverse processes; sacral rib robust, posterolaterally curved, fused to vertebral centrum. The sacrum of *Czatkobatrachus* appears to be intermediate between that of *Triadobatrachus* and that of anurans. The sacral ribs are fused to the sacral vertebra, but sacral diapophyses are not yet developed. The humerus is slender with a distinct olecranon scar and a well ossified single distal humeral condyle, the width of which equals or exceeds 60% of the width of the distal humeral head. The medial epicondyle is larger than the lateral one.

Triadobatrachus and *Czatkobatrachus* provide evidence of a wide geographic distribution of early salientians, and suggest that their origin should probably be sought in the Permian (Evans and Borsuk-Bialynicka 1998).

V. REFERENCES

Besairie, H. and Collignon, M., 1960. Madagascar. Pp. 1–93 *in* "Lexique stratigraphique international", Vol. 4 "Afrique". *Centre national Rech. Scient.* **11** (Supplement).

Carroll, R. L. and Holmes, R., 1980. The skull and jaw musculature as guides to the ancestry of salamanders. *Zool. J. Linn. Soc.* **68**: 1–40.

Estes, R. and Reig, O. A., 1973. The early fossil record of frogs. A review of the evidence. Pp. 11–63 *in* "Evolutionary Biology of the Anurans", ed by J. L. Vial. Univ. Missouri Press, Columbia.

Evans, S. E. and Borsuk-Białynicka, M., 1998. A stem-group frog from the Early Triassic of Poland. *Acta Palaeont. Polon.* **43**: 573–580.

Gans, C. and Parsons, T. S., 1966. On the origin of the jumping mechanism in frogs. *Evolution* **20**: 92–99.

Griffiths, I., 1956. The status of *Protobatrachus massinoti*. *Nature* **177**: 342–343.

Griffiths, I., 1963. The phylogeny of the Salientia. *Biol. Reviews* **38**: 241–292.

Hecht, M. K., 1960. The history of the frogs. *Anat. Record* **138**: 365.

Hecht, M. K., 1962. A reevaluation of the early history of the frogs. Part I. *Syst. Zool.* **11**: 39–44.

Jarošová, J., 1974. The components of the tarsus in *Palaeobatrachus* and their development in related species. *Acta Univ. Carol.- Geologica* **1**: 119–144.

Jarvik, E., 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zool. bidr.* **21**: 235–675.

Jenkins, F. A. Jr. and Shubin, N. H., 1998. *Prosalirus bitis* (Shubin and Jenkins 1995) and the anuran caudopelvic mechanism. *J. Vert. Paleon.* **18**: 495–510.

Kuhn, O., 1962. Die vorzeitlichen Frösche und Salamander, ihre Gattungen und Familien. *Jb. Ver. vaterl. Naturkunde Württemberg* **117**: 327–372.

Piveteau, J., 1936a. Une forme ancestrale des Amphibiens Anoures dans le Trias inférieur de Madagascar. *C.R. Acad. Sci.* **102**: 1607–1608.

Piveteau, J., 1936b. Origine et evolution morphologique des Amphibiens Anoures. *C. R. Acad. Sci.* **103**: 1084–1086.

Piveteau, J., 1937. Paleontologie de Madagascar. XXIII. Un Amphibien du Trias inférieur. *Ann. Paleontol.* **26**: 135–177.

Rage, J.-C. and Roček, Z., 1986. *Triadobatrachus* revisited. Pp. 255–258 *in* "Studies in Herpetology", ed by Z. Roček. Charles University, Prague.

Rage, J.-C. and Roček, Z., 1989. Redescription of *Triadobatrachus massinoti* (Piveteau, 1936) an anuran amphibian from the early Triassic. *Palaeontographica* A **206**: 1–16.

Roček, Z., 1988. Origin and evolution of the frontoparietal complex in anurans. *Amphibia-Reptilia* **9**: 385–403.

Sedra, S. N., 1949. On the homology of certain elements in the skull of *Bufo regularis* Reuss (Salientia). *Proc. Zool. Soc. Lond.* **119**: 633–641.

Watson, D. M. S., 1940. The origin of the frogs. *Trans. Roy. Soc. Edinb.* **60**: 195–231.