

Larval development in Oligocene palaeobatrachid frogs

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A detailed account of the development of skeletal and some soft-tissue structures is based on 171 fossil tadpoles and metamorphosing froglets of *Palaeobatrachus* sp. from the Late Oligocene of the Czech Republic (locality Bechlejovice). Their exceptionally good preservation resulted from fossilization in diatomites. The fossil developmental series was compared with normal development of the contemporary anuran *Xenopus laevis* (Pipidae) represented by cleared and stained (alizarin/toluidin-blue) whole-mount specimens. The comparison revealed that in spite of differences in the sequence of ossification and its timing (e.g., ossification of the otic capsules and ribs was retarded in *Xenopus* whereas dermal ossification was retarded in *Palaeobatrachus*), in the number of free ribs, and in composition of the sacral region (the synsacrum in *Palaeobatrachus* involves two posterior presacrals, whereas there is a single sacral in *Xenopus*), both genera were similar in great number of anatomical features that appear during development. The most important difference is the shape of vertebral centrum (procoelous in *Palaeobatrachus*, opisthocelous in all Pipidae) which is formed in comparatively early developmental stages. A view that could result from anatomical comparisons is that *Palaeobatrachus* could be derived from the Pipidae, but this is doubtful due to biostratigraphic and palaeogeographic discrepancies. The earliest palaeobatrachids were recorded from the Late Cretaceous of Europe but pipids could not invade northern continents after the Early Cretaceous when the Tethys Sea prevented interchanges of anuran faunas. Also, all palaeobatrachids retain primitive anatomical features (e.g., five pairs of ribs) that were more derived even in the earliest pipids from the Lower Cretaceous of Israel.

Key words: Anura, Palaeobatrachidae, larval development, Oligocene, Czech Republic.

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Introduction

Fossil tadpoles (including those belonging to the Palaeobatrachidae) were reported as early as in the middle of the 19th century from the Upper Oligocene of Rott near Bonn, from other localities in Germany, and from Bohemia which is today the western part of the Czech Republic (e.g., Reuss 1855; Meyer 1860). They were reported as “anuran larvae” only, but with sufficiently accurate descriptions and illustrations. Moreover, Meyer (1860) described them in a section of his paper dealing with *Palaeobatrachus goldfussi* and *P. bohemicus*, so this can be taken as an indirect generic identification. Špinar (1972), in his monograph on the Tertiary frogs of Central Europe, made an attempt to follow larval development of palaeobatrachids and defined his own eight stages on the basis of features preserved in fossils. A single palaeobatrachid metamorphosing tadpole (described as *Palaeobatrachus vicetinus*) from the Middle or Upper Oligocene of Ponte, Italy, was described by Peters (1877). Palaeobatrachid tadpoles are also known from the ?Early Oligocene of Monte Viale, Italy (Vergnaud-Grazzini and Hoffstetter 1972). A large tadpole from the Upper Vindobonian (Miocene) of Randecker Maar, Germany, was briefly mentioned by Roček and Rage (2000).

The earliest known tadpoles are pipids from the Lower Cretaceous (Hauterivian) of Shomron region, Israel (Nevo

1968). They were described as *Shomronella jordanica* by Estes et al. (1978) and recently redescribed by Chipman and Tchernov (2002); adults are unknown. The large number of well preserved individuals in a series (about 270) allowed them to reconstruct skeletal development between (disregarding youngest larvae 4 mm in length, without any skeletal structures) Nieuwkoop’s and Faber’s (1967) (NF in following text) stage 51 defined by presence of parasphenoid but no ossified vertebrae, to about stage NF 60 characterized by ossification of forelimbs that did not yet reach terminal elements beyond metacarpus and distal metatarsus, and by limited dermal ossification of skull. Staging was arbitrarily defined based on the increasing length of the femur but this at least allows comparisons with those NF stages that are defined on the basis of relative length of extremities. No adults were found at the locality. In the slightly younger (Barremian) locality Makhtesh Ramon, Negev Desert, Israel, about 850 adult articulated pipid skeletons were recovered, among them only one tadpole (Nevo 1968). Some tadpoles and metamorphosing larvae attributed to *Eoxenopoides reuningi* from the Upper Eocene or Oligocene of South Africa were briefly mentioned by Estes (1977). Tadpoles were found also associated with adults of *Xenopus hassaunus* from the Lower Oligocene of Libya (Špinar 1980). Another pipid tadpole (genus *Saltenia*), from the Upper Cretaceous of northwestern Argentina, was illustrated by Báez (1981).

Although less numerous than mentioned palaeobatrachid and pipid tadpoles, there is also a series of pelobatid (*Eopelobates bayeri*) tadpoles from the Late Oligocene of the Czech Republic which allows a study of morphogenetic changes during larval development (Špinar 1972). A series of about thirty pelobatid tadpoles (*Pelobates* cf. *P. decheni*) was recently described by Maus and Wuttke (in press) from Upper Oligocene of Enspel, Germany. Besides this developmental series, single but sometimes well preserved pelobatid tadpoles have been reported from the Lower Oligocene of Sieblos, Germany (Gaudant 1985), and from the Miocene of Turkey (Paicheler et al. 1978; Wassersug and Wake 1995).

Information on developmental stages always represents a useful addition to data on adult morphology which is mostly taken as the only basis for comparative analyses and thus for taxonomic considerations. Comparisons of whole ontogenies may be even more useful because developmental morphology may clarify the history (and polarity) of characters used in taxonomy. Fossil tadpoles sometimes provide information not only on development of bones but of cartilaginous and soft-tissue parts as well. This makes it possible to use criteria applied to contemporary species, including criteria for staging. Moreover, comparisons of corresponding developmental stages can provide information on rate and timing of developmental processes.

The principal aim of this study is to define developmental stages of *Palaeobatrachus* sp. in accordance with criteria used for contemporary *Xenopus laevis* and to compare both ontogenies. Results of this comparison may provide information that can contribute to solving the problem of the relationships between the Pipidae and Palaeobatrachidae, although taxonomic conclusions are beyond the scope of the present paper.

Material and methods

Determination of developmental stages was based on the table of normal development of *Xenopus laevis* presented by Nieuwkoop and Faber (1967). These stages, 66 in total and covering the development from the fertilized egg until the end of metamorphosis, are based on various external and internal criteria. For practical reasons, determination of stages after external criteria (mainly development of limbs and reduction of tail) is preferred in this paper because development of internal criteria (including degree of ossification) may vary among individuals of the same species (see also Estes et al. 1978). Besides, the sequence of ossification in the Nieuwkoop and

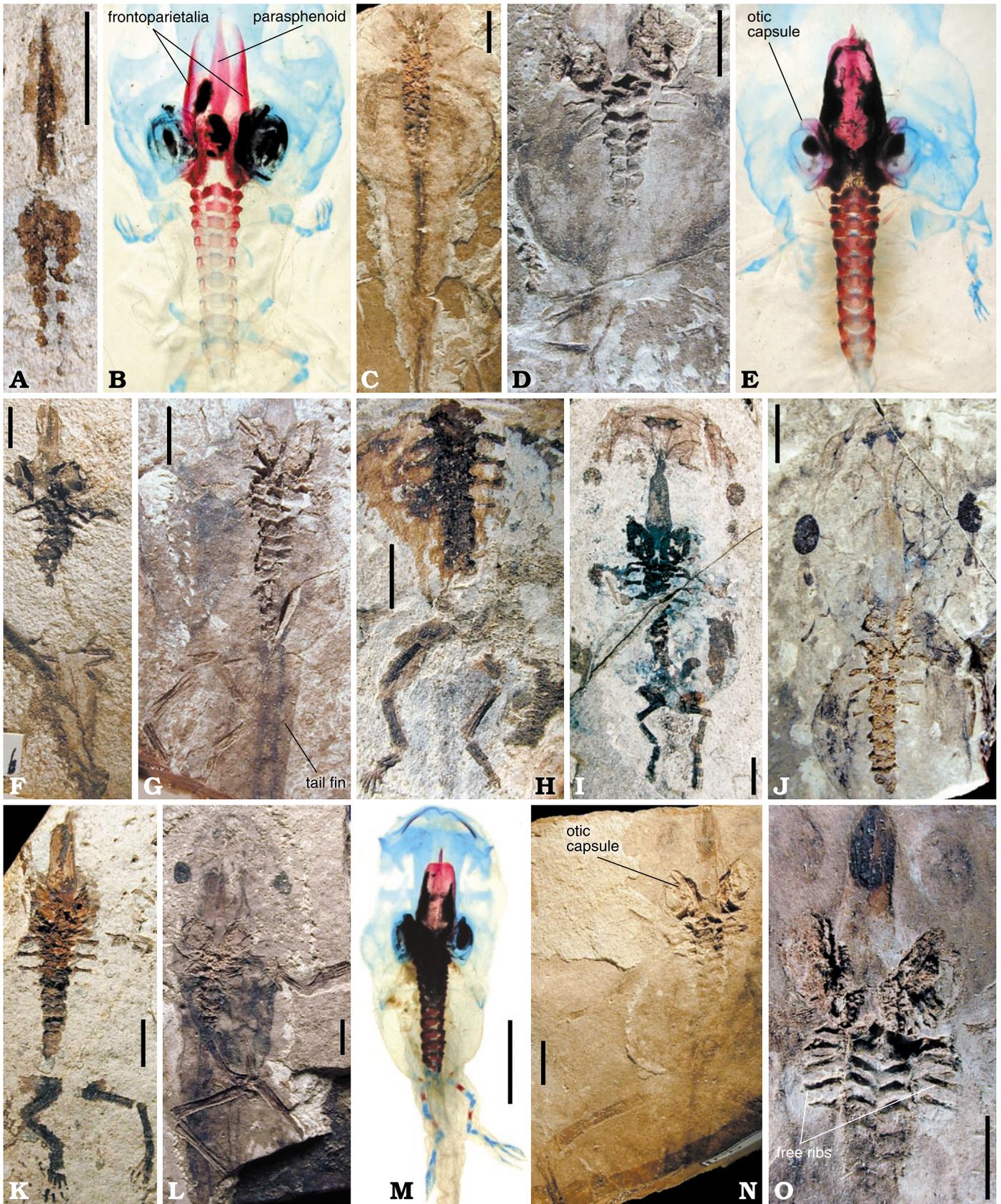
Faber's table was based on investigation of histological sections which allowed them to recognize earlier stages of ossification than in cleared-and-stained whole mounts. Hence, external criteria defined by Nieuwkoop and Faber are used for staging, and cleared-and-stained whole mounts of *Xenopus* covering the period between stages 46 and 66 (deposited in the Department of Zoology, Charles University, Prague) were used for comparisons with fossil tadpoles of *Palaeobatrachus*. Alizarin was used for staining calcified/ossified tissues, and toluidin blue for staining cartilage. Where some intermediate stages were recognized between those defined by Nieuwkoop and Faber, they were marked by low case letters (e.g., NF 59a, 59b, etc.). Hence, they do not mean subdivision of Nieuwkoop and Faber stages.

Even if it is suspected that several *Palaeobatrachus* species might be present in Bechlejovice (Špinar 1972), the larval characters do not allow to determine tadpoles taxonomically at the species level, and I refer to them as *Palaeobatrachus* sp. This may be inferred from developmental series of the larvae of closely related Recent species (e.g., *Bombina bombina* and *B. variegata*) in which morphological diversification begins only in advanced stages of metamorphosis (Sedláčková 1999).

In the earliest preserved stages of *Palaeobatrachus*, external characters cannot be recognized yet and their relative development can be assessed exclusively after skeletal structures. Ossified elements may be fossilized or can at least leave three-dimensional imprints in matrix. Calcified or sometimes even soft-tissue parts (eye pigments, nerves, tail fins, skin including colour strips) are preserved in Bechlejovice tadpoles too, in contrast to cartilaginous parts of their skeleton (larval cranial structures, epiphyses of the long bones) that are rare.

Altogether 171 specimens of larval, metamorphic and postmetamorphic stages were used in this survey. The earliest developmental stage is larva with first dermal ossifications (frontoparietals, parasphenoid) and calcification of cartilage in neural arches of several foremost vertebrae, presumably with rudiments of limbs with cartilaginous skeleton; this stage approximately corresponds to Nieuwkoop and Faber's stage 58. The terminal stage of development is documented by fully developed and ossified ("gerontic" according to Špinar 1972) adults. The material was recovered from the fossil site Bechlejovice near the town of Děčín, Czech Republic during the period 1950–1976 by Zdeněk V. Špinar and Zbyněk Roček. The geological age of the site is now considered the Late Oligocene (24.5–26.8 Ma; Bellon et al. 1998; Jean Gaudant personal communication November, 2000). Further information on the site may be found in Špinar (1972). All the fossil specimens are deposited in the

Fig. 1. Larval stages of Oligocene *Palaeobatrachus* sp. (A, C, D, F–L, N, O) in comparison with Recent *Xenopus laevis* (B, E, M). A. The earliest preserved larva (DP NMP Pb 1316), supposedly stage NF 58. B. *Xenopus laevis*, DZ FN5P XL59-ex4, stage NF 59 (stage NF 54 according to ossification sequence) for comparison. C. Larva with first rudiments of posterior limbs (Pb 326), stage NF 59. D. Larva with 3 pairs of ribs and advanced posterior limbs (Pb 354), stage NF 59. E. *Xenopus laevis*, XL60-ex1, stage NF 60 for comparison. F. Larva with the earliest rudiments of anterior limbs (Pb 358), stage NF 59. Note the distance between the most posterior ossified vertebrae and posterior limbs. G. Larva with first rudiments of ilia (Pb 382), stage NF 59. H. Larva with advanced posterior limbs, including ossified metatarsals (Pb 361), stage NF 59. I. Larva with rudiments of extremities, showing proportions of the ossified and cartilaginous skull (Pb 1696), stage NF 59. J. Larva with 5 pairs of free ribs, showing details of cartilaginous skull (Pb 1697), stage NF 59. K. Larva with



posterior limbs nearly in contact with the posterior end of ossified axial skeleton (Pb 378), stage NF 59. **L.** Larva with complete posterior and anterior extremities, still with well developed tail (Pb 331), stage NF 59. **M.** *Xenopus laevis*, XL60-ex2, stage NF 60 for comparison. **N.** Larva with 3–4 pairs of ribs and posterior and anterior limbs (Pb 372), stage NF 59. **O.** Counterpart of the same specimen (Pb 373). Scale bars 5 mm.

Department of Palaeontology, National Museum, Prague (abbreviated DP NMP); specimens of extant *Xenopus* are deposited at the Department of Zoology, Faculty of Natural Sciences, Charles University, Prague (abbreviated DZ FNŠP). For the sake of brevity, the Museum's and Faculty's abbreviations are omitted throughout the text and figure captions. In the description of stages, referred material represented by counterparts has catalogue numbers separated by slashes.

Description of stages

Palaeobatrachid tadpoles from Bechlejovice may be divided into 16 developmental stages, some of them representing additions to original Nieuwkoop and Faber's stages.

Stage NF 58 (Fig. 1A).—This is the earliest preserved developmental stage of *Palaeobatrachus* sp. Although external characters are not preserved, based on skeletal features it immediately precedes stage 59. Otic capsules do not show any sign of ossification yet (although they were no doubt present, as were other chondrocranial structures). Parasphenoid is developed nearly up to the cranio-vertebral articulation, whereas the frontoparietals (still paired) only in their anterior part. The vertebral column consists of rudiments of about 6 anterior vertebrae; the neural arches of 4–5 posterior ones are still widely separated from one another (DP NMP Pb 1315/1316, Fig. 1A).

Stage NF 59 (Fig. 1F–H).—In *Xenopus laevis*, this stage is defined by “stretched forelimb reaching down to base of hindlimb” (Fig. 1B). In contrast to external criteria, the osteological criteria of Nieuwkoop and Faber (“perichondral ossification as well as calcification of cartilage starting in vertebral arches”) suggest a much earlier stage (stage 54). In *Palaeobatrachus*, the otic capsules begin to ossify medially (but may be still entirely cartilaginous in some specimens). Frontoparietals of both sides are either still separated or may be fused with one another (as in DP NMP Pb 1232; in *Xenopus*, this is characteristic of stage 56, according to Nieuwkoop and Faber 1967). The parasphenoid is lanceolate in shape, reaching anteriorly beyond the level of the frontoparietals; its length is about the same as that of the ossified vertebral column. The axial skeleton may be taken as the principal criterion of this stage: 8–10 vertebrae are ossified or at least calcified in anterior-posterior gradient, their centra (if present) are still separated from neural arches. The transverse processes of the anterior three vertebrae begin to ossify, similar to rudiments of three pairs of ribs that are, however, not yet in contact with the processes; the 1st pair of ribs is present on the atlas (DP NMP Pb 312/313; Pb 315; Pb 316/317; Pb 328; Pb 332; Pb 335; Pb 338; Pb 348; Pb 358,

Fig. 1F; Pb 361, Fig. 1H; Pb 379; Pb 382, Fig. 1G; Pb 1232/1233).

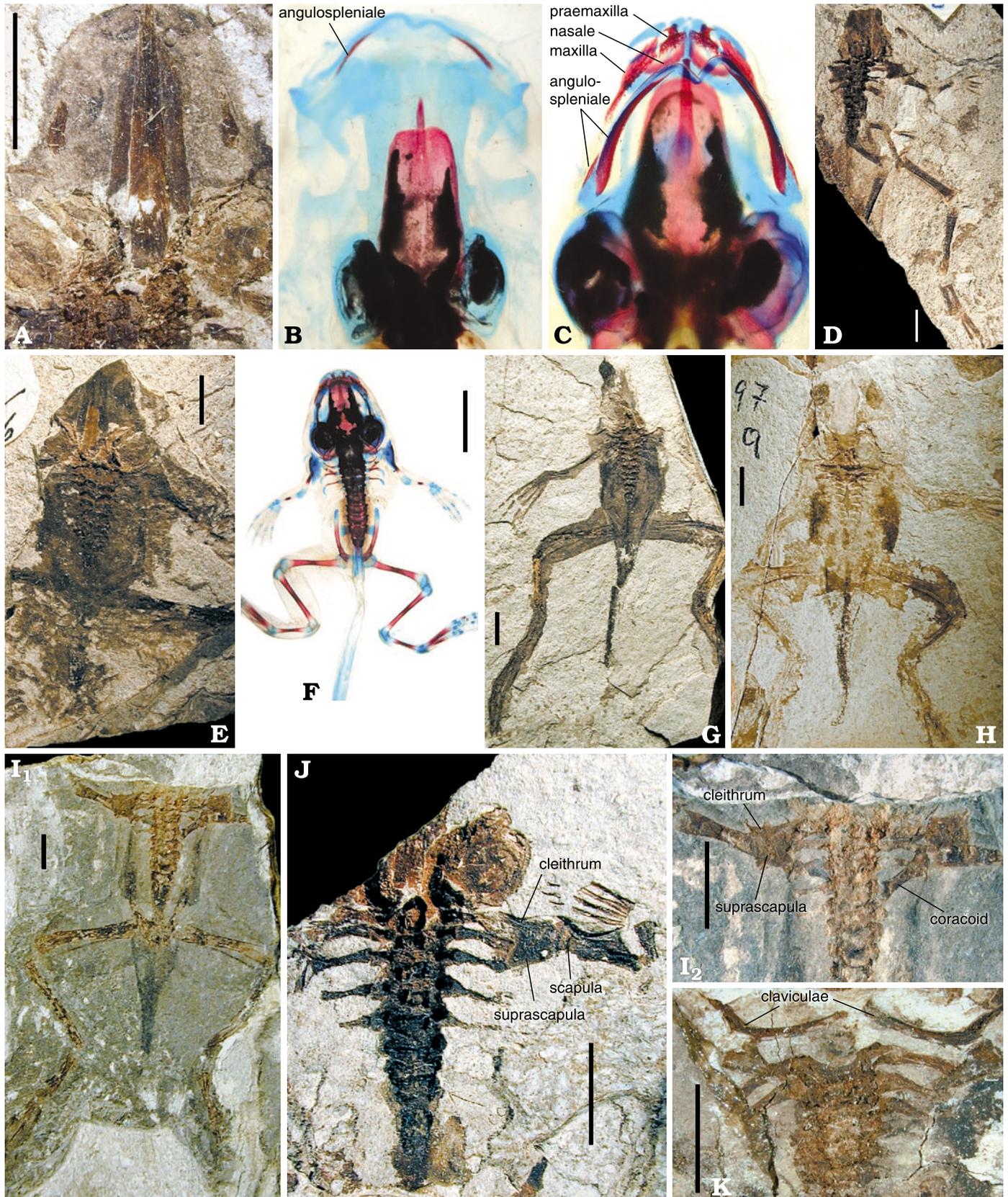
Stage NF 59a (Fig. 1C).—Basically the same as the previous stage but with tiny early rudiments of perichondral ossification of the femur, tibia and fibula (DP NMP Pb 325/326, Fig. 1C; Pb 330; Pb 342; Pb 1633/1634).

Stage NF 59b (Figs. 1J, L, N, O, 4H).—This stage does not differ substantially from the basic features of stage 59. However, the number of ribs increases to five pairs, and vertebral centra are clearly procoelous (Fig. 4H). Another significant advance is the initial perichondral ossification of the diaphyses of long bones of the forelimb including all four metacarpals and proximal phalanges of all four fingers; similarly, diaphyses of the femur and tibiofibula are well ossified. In *Xenopus laevis* specimens with limb proportions corresponding to stage 59 in *Palaeobatrachus*, using the internal osteological criteria of Nieuwkoop and Faber (“frontoparietalia fused; beginning of ossification of vertebral portions of perichordal tube; coracoid slightly ossified perichondrally; ossification extended to forearm; perichondral ossification of iliac processes; ossification extended distally to tibiale and fibulare”) would suggest stages 55–56 (DP NMP Pb 327; Pb 331, Fig. 1L; Pb 333; Pb 341; Pb 372/373, Fig. 1N, O; Pb 383; Pb 384; Pb 659/660; Pb 1045; Pb 1282, Fig. 4H; Pb 1392; Pb 1697, Fig. 1J; perhaps also Pb 1293).

Stage NF 59c (Fig. 1D, F–I, K).—Otic capsules are ossified for the most part. The parasphenoid is lanceolate in shape and complete, reaching anteriorly beyond the cartilaginous postnasal walls, as can be judged by specimens with preserved eye pigments and outlines of cartilaginous cranial structures (Fig. 1I). The vertebral column consists of nine ossified vertebrae (leaving 3-dimensional imprints in matrix); the 10th vertebra is calcified. There are regularly four pairs of ribs on four anterior vertebrae (including the atlas), separated only by a comparatively narrow zone from the transverse processes; in some specimens, the fifth pair of ribs may still be rudimentary. The scapula is ossified and suprascapular calcification is also discernible. All proximal elements of the forelimb are ossified to various degrees; diaphyses of the bones of the hind limb are ossified up to the metatarsals. Tiny rudiments of the ilia may appear close to the proximal end of the femora (DP NMP Pb 314; Pb 334; Pb 344; Pb 345; Pb 351/352; Pb 353/354, Fig. 1D; Pb 357/358, Fig. 1F; Pb 359/360; Pb 361/362, Fig. 1H; Pb 378, Fig. 1K; Pb 382, Fig. 1G; Pb 653; Pb 1413/1414; Pb 1589; Pb 1696, Fig. 1I; Pb 1945).

Stage NF 59d.—The vertebral column consists of 11 vertebrae, anterior 4–5 vertebrae are ossified, bearing five pairs of

Fig. 2. Larval stages of Oligocene *Palaeobatrachus* sp. (A, D, E, G–K) in comparison with Recent *Xenopus laevis* (B, C, F). A. Head of an advanced metamorphosing larva in ventral view (DP NMP Pb 388), stage NF 60. Ossifications below the posterior part of the orbits may belong to angulosplenials. B. *Xenopus laevis*, DZ FNŠP XL60-ex2, stage NF 60; skull in dorsal view. Note medial ossification centre of the angulosplenial. C. *Xenopus laevis*, XL62-ex1, stage NF 62; skull in ventral view. D. Advanced metamorphosing larva (Pb 1362), stage NF 60. E. Advanced metamorphosing larva in dorsal view, with not-yet-developed urostyle (Pb 389), stage NF 60. F. *Xenopus laevis*, XL63-ex3, stage NF 63; dorsal view. G. Larva before the end of external →



metamorphosis (Pb 401), stage NF 64. **H.** Metamorphosing larva with vestigial tail (Pb 376), stage NF 64. **I.** Nearly completely metamorphosed froglet with vestigial tail (Pb 1699), stage NF 64; general dorsal view (I₁), closeup of pectoral girdle (I₂). **J.** Metamorphosing larva with still limited dermal ossification (Pb 368), stage NF 60. Note absence of ossified carpus. **K.** Ventral view of the pectoral girdle of a nearly completely metamorphosed individual (Pb 1702), stage NF 65. Scale bars 5 mm.

ribs, the 5th is still only moderately calcified (DP NMP Pb 1130/1131).

Stage NF 60 (Figs. 2A, D, E, 4A).—This stage is defined in relation to stage 59c, principally after the degree of ossification, and size and proportions of limbs, although some osteological criteria used by Nieuwkoop and Faber (1967) for definition of stage 60 in *Xenopus laevis* (“formation of praemaxillae; appearance of dentale; 13th pair of vertebral arches fused with urostyle”) do not yet occur in *Palaeobatrachus*. In *Xenopus*, the beginning of ossification of hindlimb phalanges marks stage 57 and appearance of the maxillae and nasals, and fusion of both halves of the pelvic girdle, mark stage 58 (Nieuwkoop and Faber 1967). In *Palaeobatrachus*, otic capsules are ossified although their most lateral parts may still remain cartilaginous (i.e., incomplete in fossils) in some specimens. Dermal ossification of the skull is still restricted to the frontoparietal (already unpaired) and parasphenoid. The only exception is well delimited, symmetrically located ossification below the posterior part of the orbit; it may be interpreted as lateral ossification centre of the angulosplenic (Fig. 2A). Similar isolated ossification occurs in DP NMP Pb 1362/1363 (Fig. 2D). There are 9–11 vertebrae (10th and 11th may be present as calcified rudiments); those which are ossified have clearly procoelous centra. The hypochord appears, located by its narrow anterior part underneath the postsacral (10th and 11th) vertebrae and judging by its 3-dimensional imprint in matrix it was apparently ossified (Fig. 4A₂). Five pairs of ribs (although the 5th may still be rudimentary) are articulated with transverse processes of corresponding (1st–5th) vertebrae. The clavicle is present and both endochondral elements of the pectoral girdle (scapula, coracoid) and most elements of forelimb (humerus, ulna, radius, metacarpals and proximal digits) are ossified. Both halves of pelvic girdle are in contact with each other, but still isolated from vertebral column. Iliac are ossified, except for their anterior tips. Femur, tibia and fibula (in contact along the whole their length, but still distinguishable by their diaphyses), astragalus, calcaneum, and proximal phalanges are ossified (DP NMP Pb 320/321; Pb 322/323; Pb 324; Pb 336/337; Pb 385; Pb 386/387; Pb 388/389, Fig. 2A, E; Pb 1287/1288; Pb 1362/1363, Fig. 2D; Pb 1465/1466; Pb 1526).

Stage NF 60a (Fig. 2J).—Otic capsules are completely ossified. The total number of ossified vertebrae is 9–10, the neural arches of the posteriormost vertebrae can still be separated from each other. There are five pairs of completely ossified ribs on the 1st through 5th vertebrae, ribs are articulated with the transverse processes. The cleithrum is formed. A nearly complete anterior extremity (except for carpus) is

developed including the proximal two phalanges (Fig. 2J) (DP NMP Pb 343; Pb 346; Pb 368/369, Fig. 2J; Pb 1213/1214; Pb 1312; Pb 1393/1394; Pb 1545/1546).

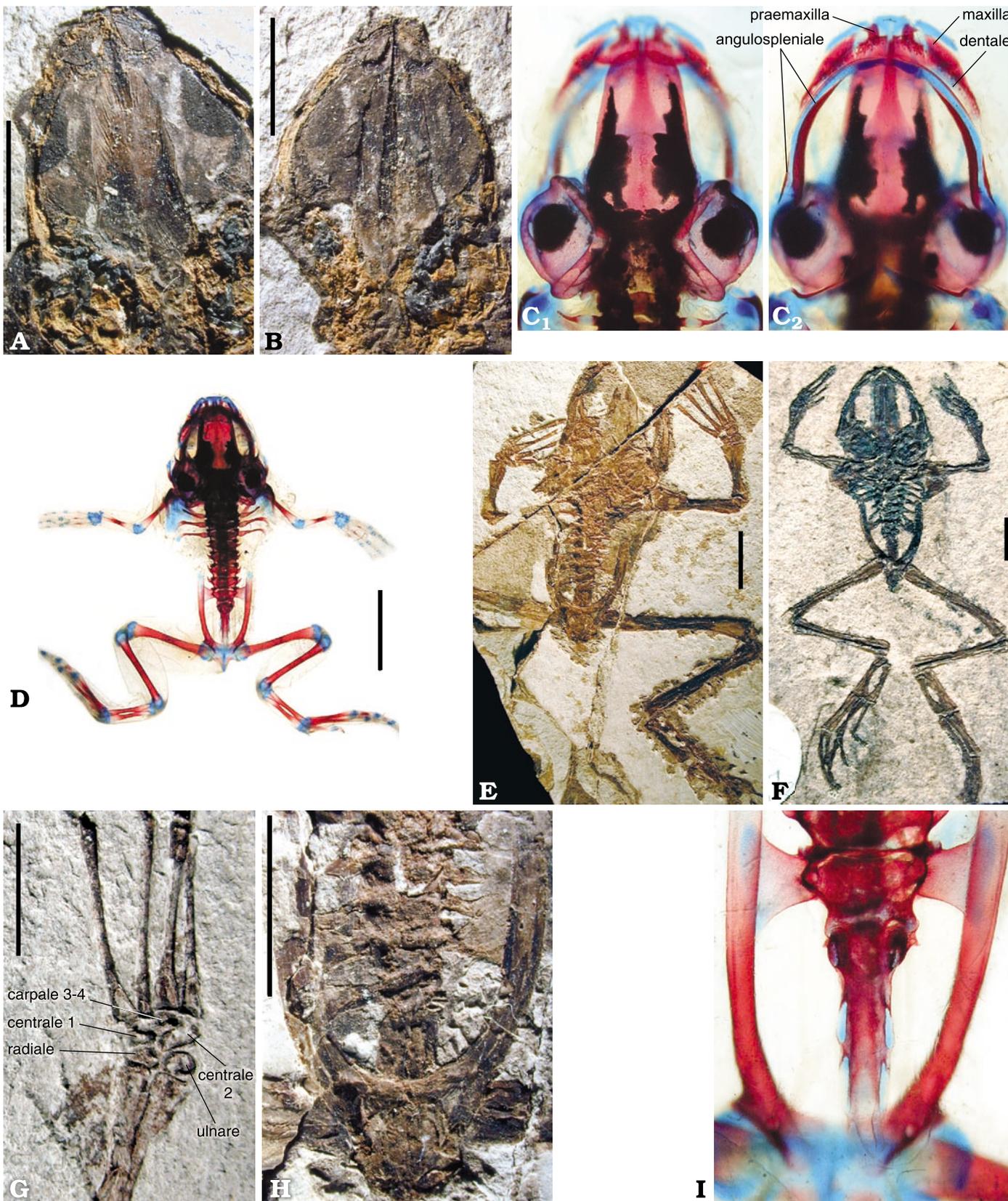
Stage NF 63.—This stage is based on relative length of the tail which is still of about the same length as body (the latter measured in fossils as a distance between the tip of the parasphenoid and acetabulum). The parasphenoid becomes bifurcated posteriorly but the degree of dermal ossification of the skull is still low (similar to specimens illustrated in Fig. 2G, H, although these represent more advanced stage in other anatomical aspects). The number of ossified vertebrae is increased to 10–11. Ribs are firmly articulated with transverse processes. The pectoral girdle and forelimb are ossified except for the carpus, although the ulna and radius are still separate. Although complete ilia are parallel to the posterior part of the vertebral column, the pelvis is still free because of absence of sacral transverse processes. Judging by stable position of the ilia in all specimens, both halves of the pelvis are probably coalesced with one another. The hind limb is ossified up to the tips of toes, although the tibia and fibula (and tibiale and fibulare) are still free from each other (DP NMP Pb 355; Pb 370/371; Pb 396; Pb 1321/1322; Pb 1631/1632).

Stage NF 64 (Fig. 2G, H, I).—The tail still present, but shorter than the hind limbs. The postnasal wall and nasal septum are visible (possibly still cartilaginous) but the vomers are not yet formed, as can be observed in DP NMP Pb 392. The anterior (preorbital) part of the maxillary is formed, and rudiments of the nasals appear. The humerus and femur are still without epiphyses. The ischia begin to ossify (DP NMP Pb 339/340; Pb 365; Pb 366/367; Pb 376/377, Fig. 2H; Pb 392; Pb 1129; Pb 1324).

Stage NF 64a.—The tail still reaches at least the level of the distal end of the tibiofibula. Skeletal features are basically the same as in the previous stage but posterior to the 9th ossified vertebra there is a proximal part of the urostyle in which 10th and 11th vertebrae are fused. The hypochord is still distinguishable. The sacro-urostyler articulation is loose. Transverse processes of three posterior presacrals are distinct but sacral transverse processes are still lacking. The carpus and tarsus are present as calcified primordia, leaving no 3-dimensional imprints yet. The radioulna and tibiofibula are fused to single bones. Left and right halves of the pelvis were still connected by cartilage which is suggested by the fact that in some specimens they are separated (DP NMP Pb 395; Pb 1328).

Stage NF 64b (Fig. 3A, B).—The nasals, praemaxillae, maxillae, pterygoids, dentaries, and angulosplenicals appeared. Typical striae of palaeobatrachids are already present on the

Fig. 3. Larval stages of Oligocene *Palaeobatrachus* sp. (A, B, E–I) in comparison with Recent *Xenopus laevis* (C, D). A. Head of a metamorphosing larva with advanced dermal ossification (dorsal view) (DP NMP Pb 397), stage NF 64. Note the tip of parasphenoid exceeding beyond the anterior margin of the frontoparietal. B. Ventral view of the same individual (Pb 398, counterpart of Pb 397). C. *Xenopus laevis*, DZ FNSP XL63-ex1, stage NF 63. C₁. Skull in dorsal view; note ossification of well developed semicircular canals which is a typical feature also in palaeobatrachids. C₂. Skull in ventral view; black areas indicate extent of the endolymphatic sacs filled with not transparent calcareous mass. D. *Xenopus laevis*, XL66-ex1, stage NF 66; dorsal view. Note degree of



ossification at the end of external metamorphosis. **E.** Fully grown adult, with completely ossified carpals (Pb 390), stage NF 66. **F.** Specimen with completely preserved and articulated skeleton after reaching terminal stage of somatogenesis (Pb 404), stage NF 66. **G.** Carpus of an adult (Pb 1691), stage NF 66. **H.** Posterior part of the vertebral column (Pb 390) in ventral view. Note asymmetrical synsacrum, stage NF 66. **I.** *Xenopus laevis*, XL66-ex1, stage NF 66; ventral view of the sacrum and pelvis. Note persisting segmentation of the urostyle indicated by cartilage. Scale bars 5 mm.

frontoparietal (Fig. 3A). Neural arches of the postsacral vertebrae are still separated in the midline although they are already included in the urostyle. The hypochord is still separated from the dorsal part of the urostyle. Carpal elements may be still absent in some individuals (DP NMP Pb 393/394; Pb 397/398, Fig. 3A, B; Pb 1719/1720).

Stage NF 64c (Figs. 2I, 4A, C).—The tail is still present. Dermal bones of the posterolateral cranium (squamosals, posterolateral rami of the pterygoids) are formed. Postsacral vertebrae fuse to form the dorsal part of the urostyle; the hypochord remains separated. Epiphyses within the hind limb ossify (DP NMP Pb 380/381, Fig. 4A; Pb 545; Pb 1210; Pb 1527; Pb 1698/401, Fig. 2G; Pb 1699, Fig. 2I; Pb 1713/1714, Fig. 4C).

Stage NF 65 (Figs. 2K, 4E).—The tail is preserved as a triangular vestige. The transverse processes of sacral vertebrae are dilated to various degree and begin to fuse with much narrower transverse processes of the 8th and later 7th presacrals (Fig. 4D–F) along their distal margin, giving rise to the synsacrum in which the vertebral centra are still distinguishable. Consequently, the number of articulated presacrals decreases and the iliac shafts reach first the posterior margin of the synsacral transverse processes, later expanding beyond their anterior margins, joining them ventrally. The hypochord is still distinguishable (DP NMP Pb 349; Pb 399/400; Pb 1489; Pb 1583; Pb 1692, Fig. 4E; Pb 1702/1703, Fig. 2K; Pb 1711; Pb 1723/1724; Pb 1739/1740).

Stage NF 66 (Fig. 3E–H).—The froglet is completely tailless. The sphenethmoid is ossified. Six procoelous praesacral vertebrae, the synsacrum consisting of up to three vertebrae, including 9th, sacral, which is firmly articulated but not coalesced with the urostyle. The synsacral transverse processes are confluent laterally but still separated by fenestrae medially. Five pairs of well ossified ribs are firmly articulated with the transverse processes. The four carpal elements are ossified (radiale, ulnare, centrale 1, centrale 2, carpale 3–4; Fig. 3G). The ischia are completely ossified. The tibiale and fibulare remain separated. The distal tarsals are ossified (DP NMP Pb 390/391, Fig. 3E, H; Pb 404/405, Fig. 3F; Pb 1120/1121; Pb 1365; Pb 1691, Fig. 3G; Pb 1712).

Stage NF >66 (Fig. 4D, F, I).—The completely developed frog in which, however, ribs are still articulated, but not coalesced with transverse processes (Fig. 4F, I₁); ribs coalesce with transverse processes only in fully grown individuals. The parasphenoid reaches the level or even beyond the level of the symphysis of the lower jaw. The urostyle, even in large individuals, may still consist of a hypochord separated from the dorsal part. Tibiale and fibulare are not fused, even in

fully grown individuals (DP NMP Pb 296/297; Pb 308; Pb 310; Pb 311; Pb 522; Pb 525/526; Pb 544, Fig. 4F; Pb 1124, Fig. 4I; Pb 1242/1243; Pb 1471/1472; Pb 1535/1536; Pb 1537/1538; Pb 1693; Pb 1715, Fig. 4D; Pb 1730/1731; Pb 1738; Pb 1749/1750).

Review of development

Although cartilaginous and soft tissue parts are often preserved in more advanced tadpoles (e.g., Figs. 1G, I, J, 2H, I₁), the early period of the development is not recorded because of absence of ossified structures.

The earliest ossifications of the skull are the parasphenoid and pair of narrow strips representing anterior parts of the frontoparietal (i.e., frontals). These strips of dermal ossification expand posteriorly and medially, fuse with one another, and ultimately give rise to a single frontoparietal. The anterior tip of the parasphenoid extends beyond the anterior margin of the frontoparietal. Only later are these dermal ossifications followed by ossification of the otic capsules (stage NF 59) that begins along their anterior and posterior semicircular canals, and only later spreads laterally. The parasphenoid, frontoparietal, and otic capsules are completely ossified as early as in stage NF 59 (Fig. 1I). Shortly afterwards (stage NF 60), the parasphenoid expands close to the anterior margin of the head (it expands also posteriorly to form a bifurcated posterior end in stage 63). At the same time (stage NF 60), another dermal ossification appears (the identity of which is discussed below), which is located on the posterior part of Meckel's cartilage (Fig. 2A). Then, ossification of the skull is interrupted until stage 64 when the posterior part of the lower jaw, maxillae, premaxillae, and pterygoids appear, followed by the squamosals and vomers. The latter bones were not yet recorded in the stage 64 specimen, though its nasal septum and postnasal walls could be recognized, most probably as cartilaginous structures (the sphenethmoid, which involves ossified part of the septum nasi and ossified parts of the postnasal walls, was recorded only in completely metamorphosed frog of stage 66).

The vertebral column develops in anterior-posterior direction. The earliest recognizable parts of vertebrae are neural arches, followed by centra. The centra and arches soon fuse together (also in anterior-posterior sequence). Then, ossification within the arches proceeds dorsomedially to form a roof over the vertebral canal. Completely ossified anterior vertebrae were present as early as in stage 58, followed posteriorly by neural arches separated in the midline, i.e., without ossified vertebral centra. New vertebrae (represented by additional pairs of rudimentary neural arches) were added

Fig. 4. Larval stages of Oligocene *Palaeobatrachus* sp. (A, C–F, H, I) in comparison with Recent *Xenopus laevis* (B, G). A. Larva with pelvic girdle still widely separated from vertebral column (DP NMP Pb 380), stage NF 64 in ventral view (A₁). A₂. Detail of the same specimen; note independent hypochord. B. *Xenopus laevis*, DZ FNSP XL66-ex1, stage NF 66; posterior part of the vertebral column in lateral (sinistral) view. C. Completely metamorphosed individual, still without sacral transverse processes (Pb 1714), stage NF 64 in ventral view (C₁) and closeup of the sacral region (C₂). D. Pelvic region of a completely ossified adult with sacral transverse processes. Note still isolated hypochord (Pb 1715). E. Nearly completely metamorphosed individual with



arising synsacrum (Pb 297), stage NF 65. **F.** Fully grown adult with ankylosed ribs and synsacrum consisting of 3 vertebrae (Pb 308), stage NF 66. **G.** *Xenopus laevis*, XL66-ex1, stage NF 66; posterior part of vertebral column in ventral view. Note single sacral transverse processes and opisthocelous vertebral centra. **H.** Early larva with well developed procoelous centra (Pb 1282), stage NF 59. **I.** Fully grown adult (Pb 1124). **I₁**. Closeup of vertebral column with clearly procoelous centra. **I₂**. General view of the specimen. Scale bars 5 mm.

posteriorly, and this process of posterior expansion of the vertebral column was simultaneous with morphological completion of anterior vertebrae. The total number of vertebrae (including tiny posterior rudiments) recorded in the course of larval development (stages 60, 63) was 12 (although rudimentary neural arches of the 13th vertebra were recorded by Špinar 1972). The vertebral centra soon (in advanced stage 59) become procoelous (Fig. 4H).

Also, transverse processes (the latest developing parts of vertebra) appear first in anterior vertebrae, reflecting gradual anterior-posterior appearance of ribs. The first pair of ribs appears on the 1st vertebra (i.e., on the atlas) and the ribs are widely separated from corresponding neural arches (obviously, transverse processes and both ends of ribs were still cartilaginous). Then, ribs appear on the 2nd through 5th vertebrae (no ribs were recorded yet in stage 58, whereas 3–5 pairs in stage 59). Five pairs of ribs are invariably present in stage 60. Then, ossified ribs expand against transverse processes so that at the end of metamorphosis ribs articulate with processes and in fully grown individuals they fuse together.

The 9th vertebra is sacral. The dorsal part of the urostyle develops from the 10th through 12th vertebrae that fuse together at the end of metamorphosis (stage 64), but the 13th vertebra may also be incorporated as evidenced by its transverse processes projecting from the urostyle (Špinar 1972). The hypochord appears in stage 60 and was no doubt ossified, broad posteriorly but tapering anteriorly. It appears even before the full set of postsacral vertebrae is developed. The hypochord can be recognized on the ventral surface of the urostyle even in fully metamorphosed individuals (Fig. 4D).

The presacral part of the vertebral column becomes shortened at the very end of metamorphosis when the 8th and often also 7th vertebrae are incorporated into the synsacrum. Transverse processes of the original sacral (9th) vertebra appear only in advanced stages of metamorphosis (stage 65), become dilated anteroposteriorly and joined by posteriorly declined transverse processes of the two most posterior presacrals. Fenestrae between the proximal parts of synsacral transverse processes become closed only in gerontic individuals (Špinar 1972). Because two presacrals are incorporated into the synsacrum, the pre-synsacral column of adults consists only of six vertebrae. If the most anterior two vertebrae fuse with one another, which is often accompanied by lateral fusion of 1st and 2nd ribs, the pre-synsacral column consists of only five free vertebrae. This low number of vertebrae is the reason why the anterior tips of ilia reach far beyond the anterior margin of synsacral transverse processes and the trunk is extremely short in adult palaeobatrachids.

It seems that development of the hind limbs precedes that of the anterior extremities, as can be judged from presence of tiny transverse processes of the femur, tibia and fibula in early stage 59 (Fig. 1C) and absence of the anterior limb. However, this might only reflect the sequence of perichondral ossification, as can be judged from posterior-anterior ossification sequence of limbs in *Xenopus* (Figs. 1M, 2F). In advanced stage 59, the scapula appears as the first ossified element of the pec-

toral girdle, accompanied by calcified suprascapula; small diaphyses of the proximal bones of the limbs (humerus, ulna and radius) are also present. At this stage, posterior extremities are ossified up to the metatarsals. Only when transverse processes of femora, tibiae and fibulae have reached their nearly final length (without epiphyses), tiny ilia appear close to the proximal ends of femora (Fig. 1G).

In the pectoral girdle, the scapula is followed by the coracoid and clavicle (in stage 60); the cleithrum is formed as the last element of the girdle, in advanced stage 60. Ossification of the limb extends distally up to proximal phalanges. The forelimb is ossified up to the tips of fingers in stage 63, except for the carpus which ossifies only at the end of metamorphosis (in stage 66).

As mentioned above, the pelvic girdle begins to develop as early rudiments of the ilia. Both halves of the early pelvic girdle are widely separated both from each other and from the most posterior vertebrae (Fig. 1H, K). In those specimens in which the pelvic region is preserved in lateral aspect (Fig. 1G), it is obvious that iliac shafts were perpendicular to the vertebral column. Later (stage 64), both halves of the pelvis come in contact and later co-ossify in the region of ischia. The pubis is ossified in fully grown adults (Špinar 1972) and because of its small size it is difficult to determine when its ossification begins. As regards the posterior limbs, ossification of their diaphyses extends from the femur towards the tips of toes, including the tibiale and fibulare, but leaving distal tarsals cartilaginous. Ossified epiphyses of the long bones appear in stage 64, whereas distal tarsals ossify at the very end of metamorphosis (stage 66).

Discussion

As was mentioned above, external criteria of *Xenopus laevis* were used as a basis for determination of developmental stages in *Palaeobatrachus* sp. so that larvae of corresponding morphology could be used for comparison of the two genera. However, it soon became clear that considerable variation exists in appearance (timing) of internal characters in *Xenopus laevis* (see also Estes et al. 1978: 388). For instance, stage 59 is defined externally by “stretched forelimb reaching down the base of hindlimb” (Nieuwkoop and Faber 1967: 184, pl. 9) and individuals of this stage should osteologically demonstrate the appearance of the maxillae and nasale; scapula, metacarpals and phalanges should be ossified perichondrally; membrane bones of the pectoral girdle (cleithrum and clavicle) should be formed; pelvic girdle should be fused ventrally; and ossification of ischia should be recognizable. In nearly all these characters the development of our laboratory-reared *Xenopus* larvae is delayed (Fig. 1B), although proportions of forelimb and hindlimb correspond to Nieuwkoop’s and Faber’s definition. This may be due to the fact that material used in Nieuwkoop and Faber’s tables of normal development was obtained from wild populations (which was also confirmed by Brown 1980, ex Trueb and Hanken 1992) and

that degree of ossification was assessed from histological sections in which osteogenesis may be recognized in earlier stages than in cleared-and-stained whole mounts. It is obvious that if only ossified skeletal elements would be used for determination of stages, external appearance of larvae would be different and thus different developmental stages would be compared.

Disregarding variation in timing and sequence of ossification in a single taxon one can infer the following facts from the comparison between *Xenopus* reared in laboratory (then cleared-and-stained), and *Palaeobatrachus*. In *Palaeobatrachus*, paired frontoparietals, parasphenoid, and anterior vertebrae appear before ossification of the otic capsules begins, and before ribs and limbs begin to ossify (stage 58, Fig. 1A). Ossification of the otic capsules begins when both frontoparietals fuse together and ribs appear, simultaneously with the earliest rudiments of the femur, tibia and fibula (stage 59, Fig. 1C, F). Ossification begins in the medial parts of the capsules and spreads laterally. On average, ossification of the otic capsules is complete very early, in advanced stage 59. Also, in *Xenopus*, the ossification of the otic capsules starts along the lateral and anterior semicircular canals (Fig. 1E) but complete ossification of the capsules is delayed until stage 64 (Fig. 3C₁), which means that it is completed much later than in *Palaeobatrachus*. Similarly delayed in *Xenopus* is development and ossification of ribs.

In contrast, development of the vertebral column seems to be delayed in *Palaeobatrachus* sp. which is evidenced by the fact that despite similar rate of ossification in the earliest compared stages (cf. Fig. 1A, B), the number of ossified vertebrae increases later in *Xenopus* (Fig. 1E) whereas it remains the same or increases slowly in *Palaeobatrachus* (Fig. 1K, N).

In both genera, the ilium appears only when perichondral ossification of the femur, tibia and fibula is advanced (in *Palaeobatrachus* even proximal metatarsals begin to ossify), the pectoral girdle begins to ossify later than the pelvic girdle, and the scapula ossifies only after diaphyses of humerus, ulna and radius are clearly discernible. Hence, the ossification sequence within the postcranial skeleton is mostly the same in both genera.

The ossification sequence in the skull differs in details although also here the basic sequence is similar. In stage 60 (both in *Xenopus* and *Palaeobatrachus*), the dermal bones of the lower jaw are first to follow the parasphenoid and frontoparietal whereas the medial ossification of the angulosplenial (*sensu* Trueb and Hanken 1992) appears first in *Xenopus* (Fig. 2B), but in *Palaeobatrachus* the first ossification is located below the posterior part of the orbit, in the area of jaw joint (Fig. 2A). This might suggest that this is the lateral ossification of the angulosplenial. It should also be remembered that the otic capsule is completely ossified when the first dermal bones of the lower jaw appear in *Palaeobatrachus*, whereas the capsules only begin to ossify medially in *Xenopus* of this stage (Fig. 1C, see also Trueb and Hanken 1992: fig. 3). Then, in *Palaeobatrachus* the degree of dermal

ossification remains the same until stage 64 when the dermal bones of the anterior part of the skull eruptively appear (maxilla, premaxilla, nasal and complete angulosplenial), whereas all these bones appear as early as in stage 62 in *Xenopus*. The last dermal bone of the skull is the squamosal, obviously because of the final building of the palatoquadrate connections with the otic capsule, and the last endochondral ossification (disregarding minute elements that cannot be recognized in the studied material) is the sphenethmoid which can be recognized in stage 66. It is therefore obvious that dermal ossification of the skull is retarded in *Palaeobatrachus* relative to *Xenopus*.

Both in *Xenopus* and *Palaeobatrachus*, the sacral transverse processes ossify late (stage 64), simultaneously with fusion of the anterior postsacral (= caudal) vertebrae. It is worthy of note that the urostyle begins to form at the time when the larval tail begins to reduce (stage 63–64). However, identity of the hypochord may be recognized even after completion of metamorphosis in *Palaeobatrachus*, whereas it fuses with the block of postsacral vertebrae in earlier stages of *Xenopus* (see also Trueb and Hanken 1992).

A remarkable feature in *Palaeobatrachus* (and *Pliobatrachus*; see Fejérváry 1917; Roček and Rage 2000: fig. 9) is shortening of the presacral column due to regular fusion of the 8th and 7th presacral with the sacral, to form the synsacrum (first discussed by Wolterstorff 1886 and Portis 1885). As a deviation from the normal development, such fusion (often asymmetrical) may occasionally be found in the extinct pipoids *Thoraciliacus* (Nevo 1968), *Saltenia* (Báez 1981), and *Eoxenopoides* (Estes 1977), as well as in *Ascaphus* (Ritland 1955), *Rana* (Howes 1886; Kovalenko 1992), *Bombina*, *Pelobates* (personal observation), and some others.

However, the synsacrum which would regularly involve one or two presacral vertebrae has been recorded neither in *Xenopus* nor in other pipoids (except, probably, in *Eoxenopoides*; Estes 1977: 60, 62, fig. 7). Instead, the fusion occurs between the 9th and 10th pairs of arches in *Xenopus* (Smit 1953), and the transverse processes of the sacral (9th) and the first postsacral (10th) vertebrae fuse along their distal margins in *Pipa* (Trueb et al. 2000). Similar fusion between the sacral and the first postsacral may also be found in all other pipoids—Upper Cretaceous *Saltenia* (Báez 1981), Paleogene *Eoxenopoides* (Estes 1977), *Xenopus arabiensis* (Henrici and Báez 2001), *X. libycus* (Špinar 1980), *Shelania* (Báez and Trueb 1997), and in some non-pipid anurans (e.g., *Pelobates*; Ramaswami 1933; Böhme et al. 1982). In *Palaeobatrachus*, the sacrum and urostyle remain unfused until very late post-metamorphic stages.

Fusion of two posterior presacrals with the sacral into the synsacrum results in a final number of six free presacral vertebrae in postmetamorphic *Palaeobatrachus*. Occasionally, the first two vertebrae (including distal ends of their ribs) may also fuse with one another which reduces the number of free presacrals to five. Occasional fusion of the first two vertebrae was recorded also in *Xenopus* (Ridewood 1897), and regular fusion of these vertebrae in *Pipa* (though in early

precartilaginous stages) was observed by Smit (1953); this explains the fact that *Pipa* has seven free presacrals. Also, in *Hymenochirus*, the first two vertebrae fuse with one another, so the number of free presacrals is six (Báez and Trueb 1997: fig. 15). In *Eoxenopoides*, there are six free presacral vertebrae but the first of them represents in fact the fused first two, which is also evident in tadpoles (Estes 1977: 60, fig. 6). Other pipoid frogs (*Saltenia*, *Shelania*) have the regular number of eight free presacrals.

In spite of some differences in structure of the sacral region it seems probable that the iliosacral articulation functioned similarly in *Palaeobatrachus* and *Xenopus* (van Dijk 2002), judging from various positions of iliac shafts relative to synsacral transverse processes in adult *Palaeobatrachus* (compare Fig. 4D with Figs. 4E and 3H).

Development of the urostyle does not differ substantially in *Palaeobatrachus* and *Xenopus*. In the former it develops from the pairs of neural arches of the 10th, 11th, and 12th vertebrae which in stage 64 fuse to form a dorsal part of the urostyle, and which is later, in postmetamorphic development, completed by the rudiment of the 13th vertebra indicated by lateral transverse processes (Špinar 1972). This corresponds to the condition in *Xenopus* in which 10th–13th vertebrae were recorded as pairs of cartilaginous arches, and even procartilaginous rudiment of the 14th vertebra could be distinguished which, however, becomes resorbed and does not contribute to the urostyle (Smit 1953). The same number (3) of caudal vertebrae involved in the urostyle was found in *Xenopus* by Branham and List (1979), in *Leiopelma* by N.G. Stephenson (1951) and E.M. Stephenson (1960), and in *Alytes* by Hodler (1949). Judging by number of myomeres adjacent to developing urostyle, from which the pyriform muscle arises, three are also present in *Ascaphus* (van Dijk 1960). As regards the hypochord, it is considered a vestige of ventral arch elements (haemal arches) fused into a block (Mookerjee and Das 1939; Smit 1953). It ossifies as a separate element but fuses with dorsal part of the urostyle (in stage 66 in *Xenopus*; Trueb and Hanken 1992, but much later in *Palaeobatrachus*, in old postmetamorphic individuals).

Palaeobatrachus displays five pairs of ribs that develop in an anterior-posterior direction on the 1st to 5th vertebra, and fuse to the transverse processes only in fully grown postmetamorphic individuals. A slightly reduced number of free ribs (four, on 2nd to 5th vertebra, the 1st vertebra bears no ribs) may be found only in Lower Cretaceous pipoids (*Thoraciliacus*, *Cordicephalus*) from Negev (Nevo 1968) and in *Shomronella* tadpoles 3–4 pairs of ribs were recognized (Estes et al. 1978). In all Recent anurans in which free ossified ribs are preserved during the development, their number is reduced to three pairs.

If all characters available in the development of *Palaeobatrachus*, from early preserved through gerontic stages, are compared with other anurans, then the closest forms appear to be *Xenopus* and *Eoxenopoides*, i.e., representatives of the family Pipidae. There is a considerable number of striking similarities, sometimes comprising astonishing details (e.g.,

slender anterior tip of the parasphenoid reaching up to level of the symphysis of the lower jaw, origin of the angulosplenial from two ossification centers), that would suggest a close relationship between *Palaeobatrachus* and *Xenopus*. Differences between them may be found in sequence and timing of ossification, in the number of ribs (only three pairs in *Xenopus* and *Eoxenopoides*), composition of the sacral region, and a few other characters. However, the most important anatomical difference is the shape of vertebral centra which are procoelous in *Palaeobatrachus*, but opisthocelous in all the Pipidae. Also, the paleogeographic and biostratigraphic context contradicts the view that the Palaeobatrachidae could be directly derived from the Pipidae. The Tethys Sea opened completely as early as the Late Jurassic and prevented interchanges of anuran faunas between the African platform and Eurasia (only Jones et al. 2003 speculated on possible relations of an Early Cretaceous anuran from Morocco to basal palaeobatrachids). It should be emphasized that the earliest Palaeobatrachidae are known only from the Late Cretaceous (Campanian) of France (Buffetaut et al. 1996) and the Late Cretaceous (Maastrichtian) of Spain (Astibia et al. 1990). Moreover, even the Early Cretaceous pipoids from Israel (which represent the earliest known fossil record of the Pipidae) are more derived in some characters (e.g., number of ossified ribs) than the Palaeobatrachidae which still retained these primitive characters in the Tertiary. Relations between the Palaeobatrachidae (*Palaeobatrachus*) and Pipidae (*Xenopus*, *Eoxenopoides*) cannot be clarified unless these facts will be taken into consideration.

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