ACTA UNIVERSITATIS CAROLINAE - BIOLOGICA 1980: 1—164 3. 1981

Department of Palaeontology, Charles University, Prague

CRANIAL ANATOMY OF FROGS OF THE FAMILY PELOBATIDAE STANNIUS, 1856, WITH OUTLINES OF THEIR PHYLOGENY AND SYSTEMATICS

ZBYNĚK ROČEK

Received April 5th, 1981

Abstract: The skull of an adult *Pelobates fuscus* is described including the topographical and functional relations of the exocranium to the endocranium, as well as the development of the skull before and during metamorphosis. On the basis of these data the homologization of the cranial structures of a tadpole with those of an adult frog was carried out, and of *Eusthenopteron* (which is representative of the group considered ancestral to amphibians) with a tadpole and with an adult frog. Comparison of the homologous structures has served as a basis for the determination of the main changes occurred during the evolution of frogs from their fish ancestors (through transitional forms corresponding to some types of stegocephalians), and for the determination of the main evolutionary trends within the group of frogs itself. The data obtained by the study of *Pelobates fuscus* has been compared with some Cretaceous and Tertiary frogs hitherto considered to be pelobatids, and with other representatives of the genus *Pelobates.* This comparison permitted a redefinition of the family Pelobatidae (*Macropelobates osborni,* American and Asian representatives of the genus *Eopelobates,* as well as forms hitherto assigned to the subfamilies Megophryninae and Scaphiopinae are excluded). The independent position of the Scaphiopinae is emphasized by re-attributing it the rank of the family Scaphiopodidae. The analysis of the embryonic development of the frontoparietal complex reveals that two different modes of the frontoparietal embryogenesis exist within frogs, and that both had to arise at an evolutionary level lower than *Triadobatrachus.* In connection with this a modified macrosystem of frogs is proposed in which both main evolutionary lines of frogs are classified as Archaeosalientia (frogs whose frontoparietal complex develops with the participation of an unpaired median element adjoining the *tectum synoticum*) and Neosalientia (frogs whose frontoparietal complex develops from paired elements only). *Triadobatrachus* (Proanura) is classified as an evolutionary stage in the lineage of *Neosalientia.*

Résumé: Le crâne de *Pelobates fuscus* adulte est décrit, avec les relations entre l'exocrâne et l'endocrâne, ainsi que son développement avant la métamorphose. A partir de ces données, sont proposées des homologies entre les structures crâniennes du têtard, de la grenouille adulte et d'*Eusthenopteron* (un représentant du groupe considéré comme l'ancêtre des amphibiens). Une comparaison entre les structures homologues a servi de base pour la détermination des changements principaux survenus pendant l'évolution des grenouilles à partir de leurs ancêtres poissons (à travers des formes intermédiaires correspondant à quelques types de Stégocéphales), ainsi que pour la détermination des principales tendances évolutives à l'intérieur du groupe des grenouilles lui - même.

Les données obtenues par l'étude de *Pelobates fuscus* ont été comparées avec quelques grenouilles crétacées et tertiaires jusqu'alors considérées comme des Pelobatides, et avec d'autres représentants du genre *Pelobates*. Cette comparaison a permis de redéfinir la famille des Pelobatidae (dont sont exclus les *Macropelobates osborni*, représentants asiatiques et américains du genre *Eopelobates*, ainsi que les formes jusqu'alors attribuées aux sous-familles des Megophryninae et Scaphiopinae). La position indépendante des Scaphiopinae est soulignée en les élevant au rang de famille des Scaphiopodidae. L'analyse du développement du complexe fronto-pariétal révèle que deux différents modes embryogénétiques du fronto-pariétal existent chez les grenouilles, et que tous les deux ont dû apparaître à un niveau évolutif inférieur à celui de *Triadobatrachus*. En rapport avec cela, un macrosystème modifié des grenouilles est proposé, dans lequel les deux principales voies évolutives sont représentées respectivement par les Archaeosalientia (grenouilles dont le complex fronto-pariétal se développe avec la participation d'un élement médian impair adjacent au *tectum synoticum*) et les Neosalientia (grenouilles dont le complexe fronto-pariétal ne se développe qu'à partir d'éléments pairs). *Triadobatrachus* (Proanura) est classé comme un stade de la lignée des Neosalientia.

1. INTRODUCTION

The family Pelobatidae is generally considered to be one of the most ancient anuran groups, and all fossil frogs which display some similarities with the genus *Pelobates* are almost automatically included in it. Among the most important characters serving for assignment to this family are the sculpture of the dermal cranial bones, the presence of upper jaw teeth, the broad transversal processes of sacral vertebra etc. Even Noble (1924 : 1), in his diagnosis of *Macropelobates osborni* curiously mentioned, as part of the evidence for its assignment to the pelobatids the absence of cartilaginous epiphyses on the long bones! Nor have diagnoses published later (for instance Špinar, 1972: 192—193; Lynch, 1973: 169—170; Duellman, 1975: 6) been so unequivocal as to define the pelobatids as a well limited group. Certain doubts have thus arisen whether or not the family in question presents a natural assemblage. It is not beyond consideration that characters which have been used hitherto in definitions of pelobatids (incidentally with a high degree of uncertainty) could have existed in different evolutionary lines, and could have changed with different intensity in them. In other words the possibility of convergent evolution must be taken into account. This is why the following study was carried out. Its main aim was to determine on the basis of cranial characters the main phylogenetic relations within the family Pelobatidae, and in connection with this to prove whether this family represents a natural group.

Thanks are due to Prof. Z. V. Špinar of the Department of Paleontology, Charles University, Prague, for valuable discussions on the topic, as well as for allowing me to study specimens found in Cretaceous of Mongolia which were placed at his disposal for detailed description by Dr. L. P. Tatarinov of the Paleontological Institute, Moscow. Prof. E. Jarvik of the Dept. of Palaeontology, the Swedish Museum of Natural History, Stockholm, kindly allowed me to study original specimens of *Eusthenopteron* and *Ichthyostega*, and I am also indebted to him for the photographs in figs 12 and 42. Dr. M. Borsuk-Bialynicka kindly lent me the original specimen of *Eopelobates leptocolaptus*. For the loan of *Macropelobates osborni* I am indebted to Dr. E. S. Gaffney of the Dept. of Paleontology, the American Museum of Nat. Hist., New York. I also wish to express my thanks to Dr. H. Bjerring of the Swedish Museum of Natural History in

Stockholm, for his valuable advice concerning the wax-model methods. The manuscript was critically reviewed by Prof. O. Slabý and Dr. V. Seichert, both of the Anatomical Institute, Charles University, Prague, Dr. K. Hensel of Faculty of Natural Science, Komenský University, Bratislava, and Dr. O. Fejfar of the Central Geological Service, Prague. Thanks are due also to Dr. J. Jarošová, Dr. M. Hodrová, Mrs V. Šilhanová and Miss J. Fuková, for their technical assistance.

2. MATERIAL*)

Pelobates fuscus fuscus - The study of the endocranium is based mostly on tadpoles in the stages 55—57**), 64, and on the adult specimen taken in the breeding season. The study of the ontogenetic development of the exocranium is based on 19 tadpoles in different stages of the ontogeny, and 3 adult specimens. In all these specimens the skeleton was stained with alizarin-red to determine the ossification centres and the original position of the bones. Detailed morphology of exocranial elements was studied on the following material:
1. DP FNSP 5826; 2. DP FNSP 5897; 3. DP FNSP 5898; 4. DP FNSP 6326; 5. DP FNSP 6333; 6. DP FNSP 6335; 7. DP FNSP 6339; 8. DP FNSP 6424; 9. DP FNSP 6425; 10. DP FNSP 6433; 11. DP FNSP 6438; 12. DP FNSP 6439; 13. DP FNSP 6440; 14. DP FNSP 6453; 15. DP FNSP 6454; 16. DP FNSP 6456; 17. DP FNSP 6459; 18. DP FNSP 6474; 19. DP FNSP 6475; 20. DP FNSP 6476; 21. DP FNSP 6477; 22. DP FNSP 6478.

All the above listed material was collected in Czechoslovakia.

Pelobates fuscus insubricus - 1. DP FNSP 6311.
Pelobates cultripes - 1. DP FNSP 10002.
Pelobates varaldii - 1. DP FNSP 2122; DP FNSP 6328.
Pelobates syriacus syriacus - 1. DP FNSP 2111; 2. DP FNSP 2117; 3. DP FNSP 2118; 4. DP FNSP 2120.
Pelobates syriacus balcanicus - 1. DP FNSP 6434; 2. DP FNSP 6455.
Pelobates syriacus boettgeri - 1. DP FNSP 3677.
Scaphiopus holbrooki - 1. DP FNSP 6462; 2. DP FNSP 6472.
Scaphiopus hurteri - 1. DP FNSP 6374.
Scaphiopus couchi - 1. DP FNSP 6408; 2. DP FNSP 6469.
Scaphiopus bombifrons - 1. DP FNSP 6334; 2. DP FNSP 6340; 3. DP FNSP 6341; 4. DP FNSP 6375; 5. DP FNSP 6381; 6. DP FNSP 6470; 7. DP FNSP 6471.
Scaphiopus hammondi - 1. DP FNSP 6412.
Eopelobates leptocolaptus - ZPAL MgAb III/1 (loc. Khermeen Tsav II, Mongolia).***)
Macropelobates osborni - AMNH 6252 (loc. Loh, Mongolia).***)
Hitherto undescribed form from the locality Khermeen Tsav, Mongolia***) - 3 specimens, coll. numbers are lacking.
Eopelobates bayeri adults - 1. DP FNSP 183 a, b; 2. DP FNSP 652 a, b; 3. DP FNSP 6874 a, b; 4. DP FNSP 7648 a, b; 5. DP FNSP 9641 a+); 6. DP FNSP 9641 b+); 7. DP FNSP 9648.
Eopelobates bayeri tadpoles - 1. DP FNSP 62; 2. DP FNSP 119; 3. DP FNSP 123; 4. DP FNSP 138; 5. DP FNSP 140 a, b; 6. DP FNSP 152; 7. DP FNSP 181; 8. DP FNSP 224; 9. DP FNSP

---

*) Abbreviations used:
DP FNSP — Department of Paleontology, Charles University, Prague;
ZPAL — Institute of Palaeobiology, Polish Academy of Science, Warsaw;
AMNH — Department of Paleontology, The American Museum of Natural History, New York.

**) Ontogenetic stages designated in accordance with Nieuwkoop and Faber (1967).

***) Further data on the geological age may be found in chap. 4.3: Comparison of *Pelobates fuscus* with some Cretaceous and Tertiary forms considered to be pelobatids, and with other representatives of the genus *Pelobates* (p. 113).

+) These specimens are not positive and negative imprints of the same animal.

365; 10. DP FNSP 461 a, b; 11. DP FNSP 586; 12. DP FNSP 589; 13. DP FNSP 861; 14. DP FNSP 1367 a, b; 15. DP FNSP 1369; 16. DP FNSP 1370; 17. DP FNSP 1374; 18. DP FNSP 1382 a, b; 19. DP FNSP 2034; 20. DP FNSP 4349; 21. DP FNSP 5083; 22. DP FNSP 5937; 23. DP FNSP 5993; 24. DP FNSP 6002; 25. DP FNSP 6003; 26. DP FNSP 6008; 27. DP FNSP 6045; 28. DP FNSP 6047; 29. DP FNSP 6074 a, b; 30. DP FNSP 6080 a, b; 31. DP FNSP 7644; 32. DP FNSP 7647; 33. DP FNSP 9640; 34. DP FNSP 9642; 35. DP FNSP 9643; 36. DP FNSP 9645; 37. DP FNSP 9650; 38. DP FNSP 9651; 39. DP FNSP 9652.

Besides this material, original specimens of the Upper Devonian osteolepiform lobe-fin fish *Eusthenopteron foordi* have also been studied (including a wax model of its endocranium constructed on the basis of serial grinding sections of the specimen No P 222 Stockh.; for further data see Jarvik, 1954: 6), and *Ichthyostega* both of which are deposited in the Swedish Museum of Natural History, Stockholm. *Triadobatrachus* has been studied on the original specimen in the Institut de Paléontologie, Paris.

3. METHODS

The endocranium as a whole was studied on the basis of wax-models which were constructed using approximately 33× multiplication. Besides, ossified parts of endocranium were also studied on these elements, isolated and prepared by maceration. The hyoid was prepared as a whole, and stored in a 4 % solution of formaldehyde. Only the topographical relations of distal part of *cornua hyoidei* were reconstructed on the basis of serial sections.

The study of the exocranium was based on the material prepared by maceration. Only in a few cases could a study not be made of both the complete skull and its disarticulated elements due to only one specimen being available. The ontogeny of the exocranium was studied on a series of tadpoles and adult specimens whose musculature was cleared by usual methods employing solutions of KOH or NaOH, and whose skeletons were stained with alizarin-red. Thus, data on the degree of ossification as well as on the intact bone topography were recorded.

As for terminology, the terms chondrocranium and desmocranium (eventually dermocranium, osteocranium etc.) are avoided, and the terms endocranium and exocranium are used instead. The chondrocranium is a term used in reference to those parts of the neurocranium consisting of bones preformed in cartilage and/or of persisting cartilage. The term endocranium includes also non-ossifying connective tissue which completes the walls of the braincase, to the extent of fontanelles. For the structure called the desmocranium (=dermocranium), the corrersponding term exocranium is used (dermal bones formed directly from mesenchyme). The term neurocranium is used for the part of the skull which does not arise by modification of visceral arches. The part of the skull arising in this way is called the viscerocranium. The endocranium may be distinguished into a neural endocranium and a visceral endocranium, and an exocranium may be distinguished similarly. However, as some visceral elements became incorporated to the neural endocranium in the course of phylogenetic development, it is sometimes rather difficult to distinguish the boundary between visceral and neural endocrania.

In the description of the mandibular arch the term Meckel's element is used instead of Meckel's cartilage, as in phylogenetically earlier forms this structure is ossified. The anatomical nomenclature used in this paper takes into account the terms used by earlier authors, although they are not quite correct in some cases. This resulted from the tendency not to extend the number of synonyms.

For practical reasons the simplified designations »before metamorphosis« and »after metamorphosis« are used, although the metamorphosis is actually a continuous row of modifications beginning in the early stages of larval development and resulting in the completion of the hyoid in adult specimens.

4. SKULL OF THE GENUS PELOBATES

4.1. Endocranium of Pelobates fuscus

The ethmoidal region was studied by BORN (1891); some data on the endocranium were also published by SEWERTZOW (1891).

For the purposes of description the endocranium is usually distinguished into the four regions:

a) The ethmoidal region (*regio ethmoidalis*) is situated in the most anterior part of the endocranium, which extends in the posterior direction up to the level of the foramen by which the *canalis pro ramus medialis n. ophthalmici* (seu *n. ophthalmicus* sensu GAUPP, 1896: 136, seu *medial nasal branch of n. profundus* sensu JARVIK, 1942: 245, seu *ramus ophthalmicus profundus sensu* JURGENS, 1971: 23, fig. 7) opens from the postnasal wall into the orbit.

b) The orbitotemporal region (*regio orbitotemporalis*) extends from the above mentioned boundary in the posterior direction up to the level of the opening through which the *n. trigeminus* leaves the braincase.

c) The otic region (*regio oticalis* seu *labyrinthica* sensu ORSKA 1976: 240 a) extends from the above mentioned boundary in the posterior direction up to the level of the opening through which the *n. vagus* leaves the braincase.

d) The occipital region (*regio occipitalis*) is situated in that part of the endocranium which is posterior to the opening for the *n. vagus*. In frogs, the shortening and lateral expansion of the posterior endocranial parts caused a transposition of the *occipitalia lateralia* into the position anterior to the level of the opening for the *n. vagus*. Hence the importance of this distinguishing line decreases in these animals.

4.1.1 Endocranium of adults

The ethmoidal region (figs 1—8)

(See also BORN 1876, tab. XXXIX/1—3)

This has the most complicated structure of all the endocranial structures. It serves as a paired case for protecting the olfactory organ, it takes part in the formation of the anterior orbital wall, and it also serves as a support for the most exposed exocranial bones. The material consists of both cartilaginous and bone tissues. The ossified part of the ethmoidal region belongs to the larger bone element called the *ethmoideum* in older literature (see GAUPP, 1896: 44 for instance); however, the term *os sphenethmoideum* is more convenient, as this element is situated both in the ethmoidal and orbitotemporal regions. It follows from this fact that the distinguishing of the endocranium listed above is to a considerable extent artificial and can be used only for topographical orientation.

The following description of the ethmoidal region is based on the general constructional scheme (i. e. paired case for the nasal sacs). The olfactory organ fills two nasal cavities (*cavitas nasalis* seu *cavitas capsulae nasalis*), situated alongside each other, separated by the median wall called the *septum nasi.*

The roof of *cavitas nasalis* is formed by *tectum nasi,* and its floor is formed by *solum nasi.* Laterally, the nasal cavity is incompletely closed by a wall of complicated structure, composed of several elements which will be described below. The anterior walls of both nasal cavities are attached medially to the *septum nasi*; this structural whole is considered an unpaired element (JARVIK, 1942: 245) called the *divisio praenasalis communis.* There is some confusion in the terminology concerning the wall separating the nasal cavity and the orbit. Regarding the fact that it forms a part of the nasal capsule and that it is situated entirely within the ethmoidal region (JARVIK op. cit.: 243), it is impossible to consider it as having some relation to the orbit. This is why terms such as »*planum antorbitale*« and »*processus* (*cartilago*) *antorbitalis*«

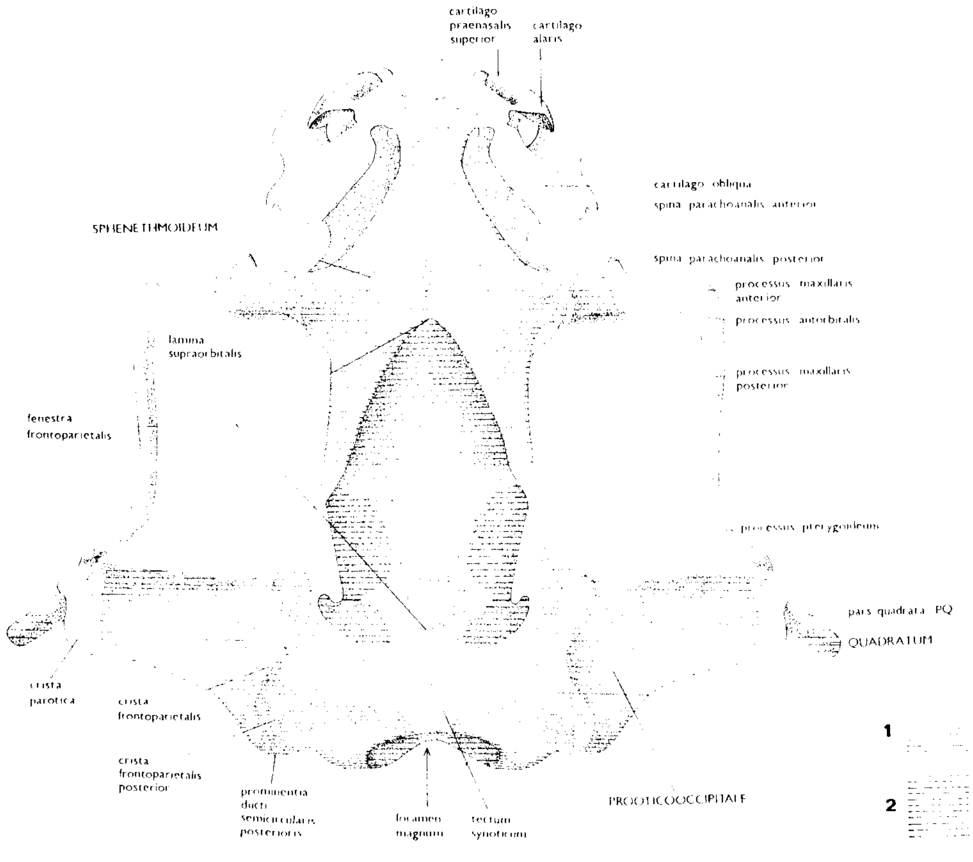


Fig. 1. Endocranium of an adult *Pelobates fuscus* in dorsal aspect. 1 - ossified parts; 2 - membranous parts (fontanelles). Free elements are omitted.

should be avoided. The term »*lamina orbitonasalis*« should be avoided also, as it designates only the larval structure taking part in the separation of the nasal cavity and the orbit, which is not, however, fully homologous with the structure of the same function occurring in adults. In this paper the term postnasal wall will be used.

Nasal cavities of the right and left sides (*cavitas nasalis dextra et sinistra*) contain the olfactory organ which is composed of two nasal sacs (*saccus nasalis dexter et sinister*). Their cavities are designated as cavities of the nasal sacs (*cavitas sacci nasalis*). Hence, the *cavitas nasalis* is the cavity in the endocranium, the *cavitas sacci nasalis* is a cavity in the olfactory organ. The *cavitas nasalis* is opened to the endocranial surface by the orifice called the *fenestra endonarina,* to the mouth cavity by *fenestra endochoanalis*. The cavity of nasal sac opens onto the body surface by the orifice *naris externa,* while with the mouth cavity it is connected by the *naris interna* or *choana*. This terminology taken from JARVIK (1942) is more precise than that used earlier.

The septum nasi (figs 7, 8) is well limited only in its posterior part by the margin of *foramen olfactorii*. Its limitation in other directions is not so clear, as dorsally and ventrally it continuously broadens into the *tectum* and *solum nasi,* and in the anterior direction it also continuously passes into the *divisio praenasalis communis*. It is impossible to take as its anterior limit the superficial boundary between the cartilage of the *divisio praenasalis communis* and the bone tissue composing the septum, because the bone greatly extends in the anterior direction into this praenasal wall. In spite of these difficulties concerning limitation it is possible to state that the septum of adult *Pelobates* is fully ossified. It is thinnest in its central part (a little more than 0.1 mm in the specimen investigated), while anteriorly and posteriorly it becomes considerably thicker, so that between both *foramina olfactorii* it is approximately five times thicker, at the level of the anterior margin of the *fenestra endonarina* even fifteen times thicker. With the exception of its thinnest parts it contains a system of irregular cavities.

The tectum nasi (figs 4, 5, 7, 8) is complete only in its posterior part close to the postnasal wall, while it considerably narrows in the anterior direction and broadens again close to the praenasal wall. It is mostly ossified; only a small part dorsally covering the anterior recess of the nasal cavity is composed of cartilage. A tiny bridge well developed on both left and right sides, however connects this part of the tectum with the *cartilago obliqua,* which to a certain extent takes part in the composition of the nasal cavity roof (however, this cartilage plays a more important role in the composition of the lateral wall of this cavity). Between the *cartilago obliqua* and the *tectum nasis* a large elongated opening, the *fenestra nasolateralis* which is covered only by the exocranial bones (esp. by nasal, see fig. 9). The ossified part of the tectum contains irregular cavities of different size, which are connected with a similar system of cavities within the *septum nasi.*

The solum nasi (figs 6, 8) passes medially into the *septum nasi,* posteriorly into the postnasal wall, posterolaterally it forms the margin of *fenestra endochoanalis,* anterolaterally it meets the lateral wall of the nasal capsule at a sharp angle and together with it runs out lateroventrally forming the *crista subnasalis.* Anteriorly, the *septum nasi* passes into *divisio praenasalis communis.*

The *solum nasi* is ossified posteromedial and medial to the *fenestra endochoanalis.* This stripe of bone passes into the *septum nasi*; it narrows in the anterior direction, while the lateral part of *solum nasi* composed of cartilage is broad. The ossified part is rather thin medially, but its lateral margin is considerably thickened (fig. 8; see also BORN 1876: 586). JURGENS (1971, figs 7A 8, 9B, C) designates the homologous thickening in *Scaphiopus intermontanus* as a »skeletal support of *eminentia olfactoria*«, RAMASWAMI (1936, fig. 4) as a »solar ossification of the *eminentia*«. In contrast to the osseous part, the cartilaginous lamina continuing anterolaterally is relatively thin. On both sides of the skull, one process called the *cartilago praenasalis inferior* (figs 6, 7) runs out ventrally from the cartilaginous parts of *solum nasi*, and is directed in close proximity to the ventral surface of the *divisio praenasalis communis* in the anterior direction.

The lateral wall (figs 2, 7) of the nasal capsule is considerably incomplete, and is composed namely of *cartilago obliqua* (see also BORN, 1876: 586, tab. XXXIX/2, 3, 4) (seu *lamina obliqua* sensu JARVIK, 1942: 311) which is connected by *planum terminale* (seu *pars terminalis* sensu JARVIK, op. cit: 312) with horizontal lamina. This lamina may be interpreted in two ways: regarding the fact that it separates the *recessus inferior* and the *recessus medius* of the nasal cavity, one may consider it as the *lamina inferior cristae intermediae* (this is the interpretation of STADTMÜLLER, 1936, fig. 415 d, for instance). JARVIK (1942: 312), on the other hand, considers this part a structure separating the *fenestra endonarina* from the *fenestra endochoanalis* (op cit.: 244, 245, 246), and according to him it is a structure called the *lamina nariochoanalis.* Jarvik's view was accepted by JURGENS (1971: 24). It is, however, more convenient to hold the first interpretation because the structure in question plays a considerable role in the inner arrangement of the nasal cavity. It is true that it separates the *fenestra endonarina* and the *fenestra endochoanalis,* but it refers, however, to that part of the *fenestra endochoanalis* which is filled by *diverticulum inferius sacci nasalis,* and thus again the more important role is that of dividing the nasal sac. The only adherence to the choana is displayed by the posterior part of this lamina because it forms a cartilaginous support of a short section of choanal margin.

It must be mentioned in connection with the inclusion of the *planum terminale* among the elements of the lateral wall of the nasal cavity that JARVIK (1942: 312) considers the *planum terminale* a structure belonging to the inner elements of the nasal capsule, not the elements of its lateral wall.

The *lamina inferior cristae intermediae* is sharply bent in its anterolateral portion, and then slants passing lateroventrally into the rather concave lamina called *paries nasi* (see DE JONGH, 1968, tab. XXVI) which terminates with the *crista subnasalis.* Medially to that lamina is attached the cartilaginous part of the *solum nasi.* Posteriorly, the *lamina inferior cristae intermediae* runs out with the tiny process *spina parachoana-*

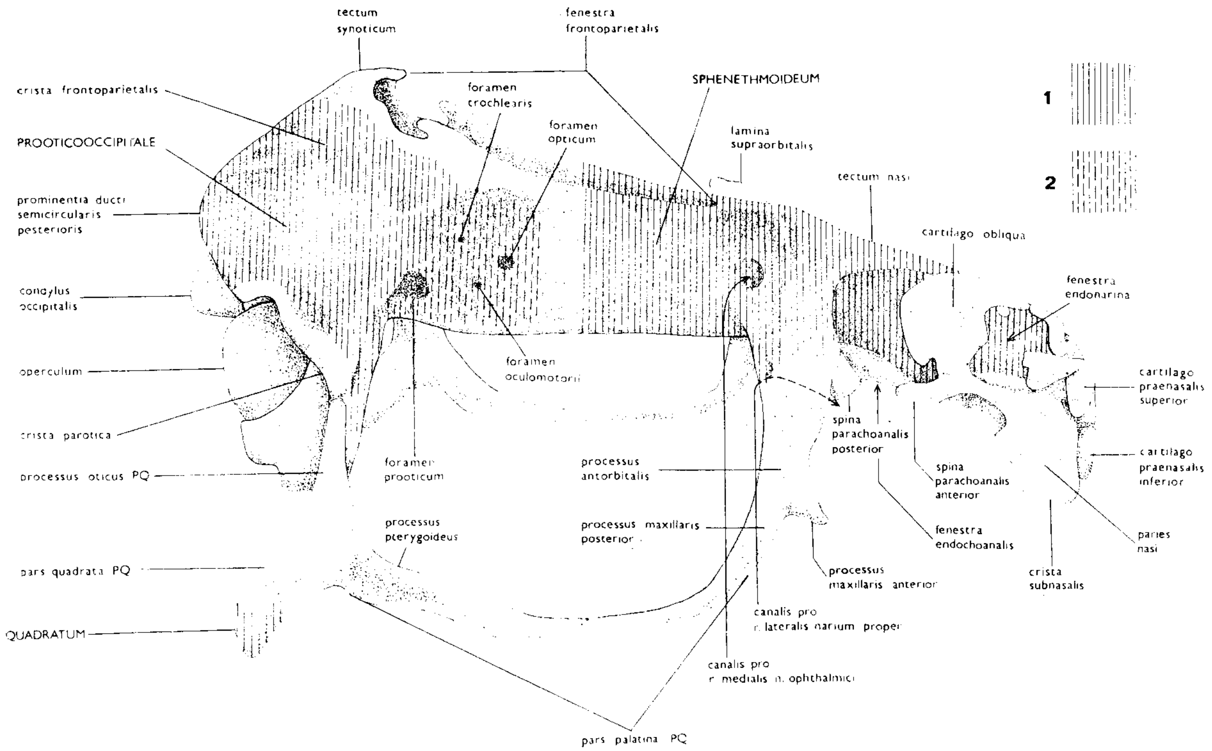


Fig. 2. Endocranium of an adult *Pelobates fuscus* in lateral aspect. 1 - ossified parts; 2 - membranous parts (fontanelles). Free elements are omitted.

lis anterior which is directed against a similar *spina parachoanalis posterior* running out in the anterior direction from the postnasal wall, medially to the opening for *canalis pro ramus lateralis narium proper* (see below). Both processes form a part of the lateral incomplete margin of the *fenestra endochoanalis*.

Among the elements of the lateral wall of the nasal capsule one may include also the *cartilago alaris* (seu *processus alaris* sensu JARVIK, 1942; 311) which is a thin, dorsomedially concave and ventrolaterally convex structure attached to the lateral margin of the praenasal wall by a tiny flat bridge directed medially, and to the anterior margin of the *lamina superior cristae intermediae* ventrally. Moreover, it is connected dorsomedially with the *tectum nasi* by another tiny bridge (see fig. 5). All three connections are very weak and do not attain a diameter of more than 0.1 mm.

The divisio praenasalis communis (figs 4, 7, 8) forms anterior walls of both nasal capsules, and it runs out anteriorly in the mid-line as a considerably large *processus praenasalis medius*. This process represents the most anterior part of the endocranium (cf. BORN, 1876: 589). Its interior consists of an osseous tissue, while only its relatively thin superficial layer is cartilaginous. Those parts of the *divisio praenasalis communis* which are situated laterally to both *fenestrae nasobasales* are completely cartilaginous.

The anterior walls of the nasal cavities are in their upper parts conspicuously thin (approx. 0.05 mm). They pass dorsally into the *tectum nasi*; laterally, the anterior wall produces flat and tiny bridge serving as connection with *cartilago alaris*, and *lamina inferior cristae intermediae* and *paries nasi* rather more ventrally. The praenasal wall meets the *solum nasi* approximately at a right angle.

The *processus praenasalis medius* gradually narrows in the posterior direction and passes into the *septum nasi*. There are considerably large *fenestrae nasobasales* in the solum, which are adjacent to the processus (figs 6, 8). The dorsal surface of the *processus praenasalis medius* is pierced by narrow *foramina frontalia*. In the specimen investigated there were two on both sides, and their position was asymmetrical (fig. 4). They represent the dorsal orifices of vertical canals which run through the ossified interior of *processus praenasalis medius*, joining each other and opening on the ventral surface of the above mentioned process by a single orifice on both sides, situated approximately at the level of the anterior margin of the *fenestra nasobasalis*. It is difficult to decide on the basis of only one specimen whether or not the branching of these canals and the number of their dorsal orifices (2 on both sides) are characteristic features of *Pelobates*. GAUPP (1896: 46) and STADTMÜLLER (1936: 552) found in *Rana* and in ranids generally merely one opening on both sides. The mentioned canals contain the *ramus externus narium* (sensu GAUPP, 1896: 137) which splits from the *ramus medialis narium* during its course through *fenestra nasobasalis*. The surface of the *processus praenasalis medius* is pierced at the level of the posterior part of the *fenestra nasobasalis* by a tiny opening (*foramen caecum*) which continues by a blind canal. It contains a branch of the *ramus medialis narium*.

The postnasal wall is formed by a vertical and rather thin partition between the nasal cavity and the orbit. It is completely ossified, and if viewed from the nasal cavity it is pierced by two openings: the *canalis olfactorius* is situated medially, the *canalis pro ramus medialis n. ophthalmici* (see below) which is the communication with the orbit, is situated laterally. Besides, the postnasal wall is pierced by another canal running anteroventrally from the orbit but which opens beyond the nasal capsule (figs 2, 3, 7). The highly confused terminology concerning the latter two canals will be discussed later.

The openings to the nasal cavity may be distinguished into those which connect the cavities of the nasal sac either with the mouth cavity or with the external environment, further into those which contain vessels and nerves, and finally into those which can be interpreted as lacking parts of the nasal capsule walls.

Fenestra endonarina (seu *apertura nasalis externa* sensu Born 1876) is an opening which contains the external nostril (figs 2, 4, 8). However, this nostril fills only the anterior part of this opening, while its posterior part is closed by septomaxilla. The margins of *fenestra endonarina* consist of the *cartilago obliqua, tectum nasi,* and in a short section also of the praenasal wall and the bridge for the attachment

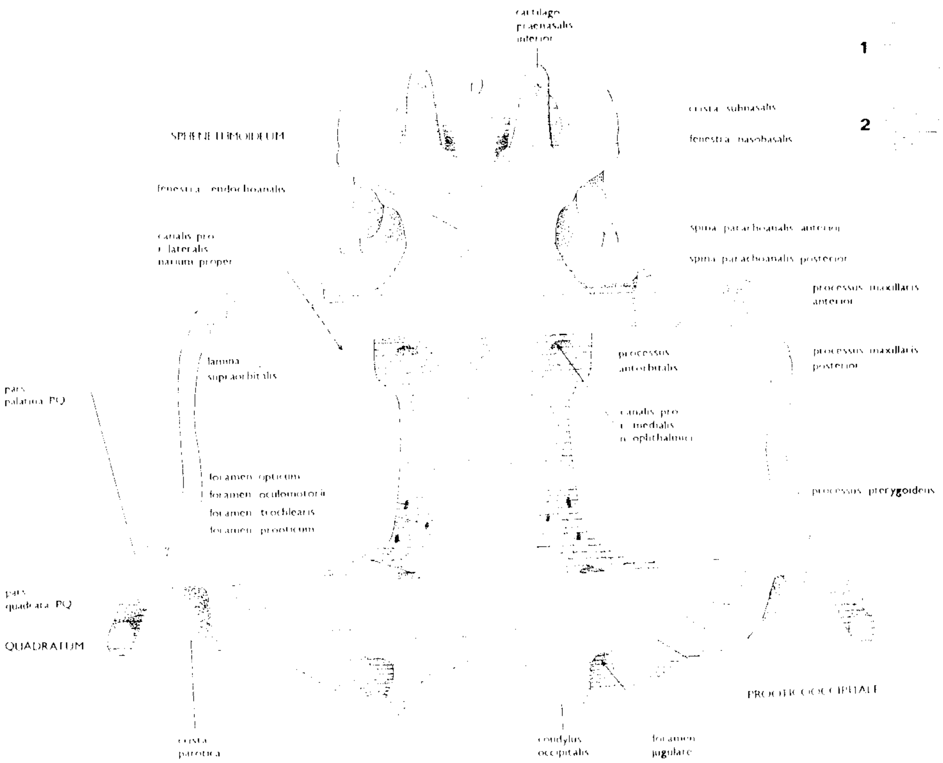


Fig. 3. Endocranium of an adult *Pelobates fuscus* in ventral aspect. 1 - ossified parts; 2 - membrabous parts (fontanelles). Free elements are omitted.

of the *cartilago alaris,* the *cartilago alaris* itself, the *lamina inferior cristae intermediae,* and the *planum terminale.*

The *fenestra endochoanalis* is a considerably large opening in the posterolateral part of the nasal capsule floor. It contains the choana, which continues by the lateral fold of the mouth cavity mucous membrane in the posterior direction up to the level of the anterior orbital margin (*sulcus maxillopalatinus* sensu JURGENS, 1971, fig. 9 C, D). Anterior to the choana, the *fenestra endochoanalis* is filled by the fold of the nasal sac (*sinus lateralis*). This sinus is an anterior continuation of the *sulcus maxillopalatinus,* but its walls are already formed by olfactory epithelium and it is completely separated from the mouth cavity, though only by soft tissue. Both the *sinus lateralis* and the *sulcus maxillopalatinus* extend lateroventrally up to the *lamina horizontalis maxillae.* They are structures situated laterally to the choana. The margins of *fenestra endochoanalis* are formed above all by the thickened ossified lateral margin of *solum nasi,* by the thin cartilaginous part of *solum nasi,* by the medial margin of *lamina inferior cristae intermediae,* and by the *spina parachoanalis anterior et posterior.* Laterally, the *fenestra endochoanalis* is closed only incompletely (figs 2, 3).

Nasal and cranial cavities are connected with each other by the *canalis olfactorius* which opens in the posteromedial corner of the nasal cavity; it is comparatively short, as the partition between both mentioned cavities is thin. Only one of the remaining canals in the postnasal wall opens into the nasal cavity; the medial branch of *n. ophthalmicus* (seu *ramus ophthalmicus profundus* sensu JURGENS, 1971, fig. 7, seu *n. profundus* sensu Jarvik 1942) enters the nasal capsule through this way, splitting here into the *ramus medialis narium* (running along with the *arteria orbitonasalis* farther in the anterior direction parallel with the medial margin of the olfactory sac, on the surface of the nervous plexus arisen by a branching of the *n. olfactorius*), and the *ramus lateralis narium* (running anterolaterally along the dorsal surface of the olfactory sac together with an accompanying vessel which is a branch of the *arteria orbitonasalis*; at a certain point they are both sharply bent dorsally, and run through the opening between the *tectum nasi* and *cartilago obliqua* (*fenestra nasolateralis*), close to the lateral margin of nasal bone which is the only dermal bone in this area, into the subcutaneous space. Besides the medial branch of *n. opthalmicus* just described, there is also a lateral one called the *ramus lateralis narium proper* (seu *ramus lateralis nasi proper* sensu JURGENS, 1971). Both split from each other still in the orbit. The latter enters obliquely into the postnasal wall, then it runs anterolaterally within this structure, and opens beyond the nasal cavity lateral to the *spina parachoanalis posterior* (figs 2, 3, 7). However, this canal was so thin-walled in the specimen investigated that the wall separating it from the nasal cavity was perforated.

These two canals are called by JARVIK (1942, fig. 1) the *canalis profundus medialis* and *lateralis* (he designates by the term *ramus ophthalmicus* only the distal section of the medial branch of the *nervus profundus*); the use of the term *foramen orbitonasale* is avoided by him (op. cit.: 243). JURGENS (1971, fig. 7) used the term *foramen orbito-*

nasale mediale for the medial opening; however, it is impossible to use an analogous term for the lateral canal, as it is not a connection between the orbit and the nasal cavity. The most convenient from the point of view of the terminology used in the present paper is to use the terms *canalis pro ramus medialis n. ophthalmici* and *canalis pro ramus lateralis narium proper*, respectively.

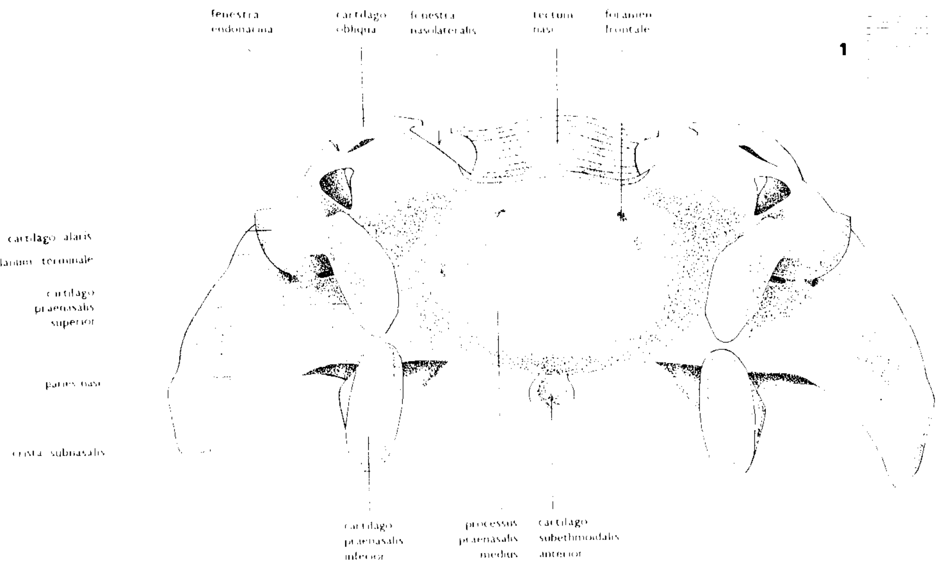


Fig. 4. Ethmoidal region of the endocranium of an adult *Pelobates fuscus* in anterior aspect. 1 - ossified part.

In the anteromedial corner of the floor of the nasal capsule there is an opening called the *fenestra nasobasalis* (figs 3, 6, 8). Jarvik (1942: 244) considers this term more suitable than *foramen apicale* and *foramen epiphaniale* used alternatively by Gaupp (1896). Born (1876: 587, tab. XXXIX/2) described two openings instead of one in this area. As mentioned above in connection with the description of the *divisio praenasalis communis*, the *ramus medialis narium* runs together with the accompanying *arteria orbitonasalis* through the mentioned opening into the *cavum praenasale*, and it gives out the *ramus externus narium* in this area (in the anterior part of *fenestra nasobasalis*), as well as the tiny branch entering through the *foramen caecum* into the *processus praenasalis medius* (close to the posterior margin of *fenestra nasobasalis*). The positions of these openings were described in connection with the description of *divisio praenasalis communis*.

In the roof of the nasal capsule and in the posterior part of its lateral wall there is a large opening called the *fenestra nasolateralis* (figs 4, 7, 8) which is situated between the *cartilago obliqua* and the *tectum nasi*. In *Pelobates*, this opening is not separated from the *fenestra endochoanalis* by a complete bridge, and only the *spina parachoanalis* *anterior et posterior* are present instead. This part of the endocranium in *Pelobates* may probably vary, as the occurrence of the cartilaginous bridge (designated, however, as a connection between the *planum terminale* and the posterior part of the nasal capsule roof) was reported by STADTMÜLLER (1936: 557). There is no mention, in the literature, of the connection between the *cartilago obliqua* and the *tectum nasi* in adults of *Pelobates,* although in some other frogs this connection similar to that found in urodels (*planum conchale*) occurs (see STADTMÜLLER op. cit.: 557; JARVIK, 1942: 316).

The cavitas nasalis (fig. 8) is considerably wide and low in its posterior part close to the postnasal wall, and maintains this width also in its anterior part (although the elements of the *crista intermedia* convey the impression that the space here is narrower). It contains the olfactory sac which, however, runs out of it ventrolaterally through the anterior part of the *fenestra endochoanalis.*

The posterior part of the cavity, whose main aperture is the *fenestra endochoanalis,* is very simple in its arrangement. A sign of partition here is the thickened ossified margin of the *solum nasi,* called the skeletal support of the *eminentia olfactoria* by some authors. However, this ridge is much higher in scaphiopodids for instance (JURGENS, 1971, fig. 9 B, C, D; RAMASWAMI, 1936, fig. 4). It forms the base for *eminentia olfactoria* projecting into the *cavum principale* of the nasal sac.

The anterior part of the cavity is more complicated in comparison with the posterior one. On the surface of the praenasal wall the *crista intermedia* arises as a low and indistinct lateroventrally running ridge, and without projecting expressively into the nasal cavity it splits into the *lamina superior* and *lamina inferior.* The *lamina superior* is flattened cartilage, slightly S-shaped in the horizontal plane (see fig. 5), which reaches up to the level of the centre of the *planum terminale.* With the exception of its anterior attachment to the praenasal wall it is entirely free. The *lamina inferior,* whose lateral part is called by JARVIK (1942: 312) the *lamina nariochoanalis* (see also p. 8), runs out from the *crista intermedia* at a rather more ventral level. The anterior part of its lateral margin slants down lateroventrally to the *crista subnasalis,* while its medial, lateral and posterior margins are free. The *planum terminale* attaches the *cartilago obliqua* to the upper surface of *crista intermedia.*

The above mentioned laminae divide the anterior part of nasal cavity into the *recessus superior, medius* and *inferior.* The *recessus superior* is that part of the *cavitas nasalis* which is situated above the level of the *crista intermedia,* and above its *lamina superior.* It is filled by the anterior part of the *diverticulum principale,* whose aperture is the *naris externa,* and by the *diverticulum sacciformis.* The *recessus medius* is that part of the nasal cavity which is situated between the *lamina superior* and *inferior*; it contains the *diverticulum medium.* Between the *solum nasi* and the *lamina inferior* is situated the *diverticulum inferius,* which runs out lateroventrally from the nasal cavity through the anterior part of the *fenestra endochoanalis.*

Topographical and functional relations of the ethmoidal region to the exocranial elements (figs 9—11). The ethmoidal region is only incomple-

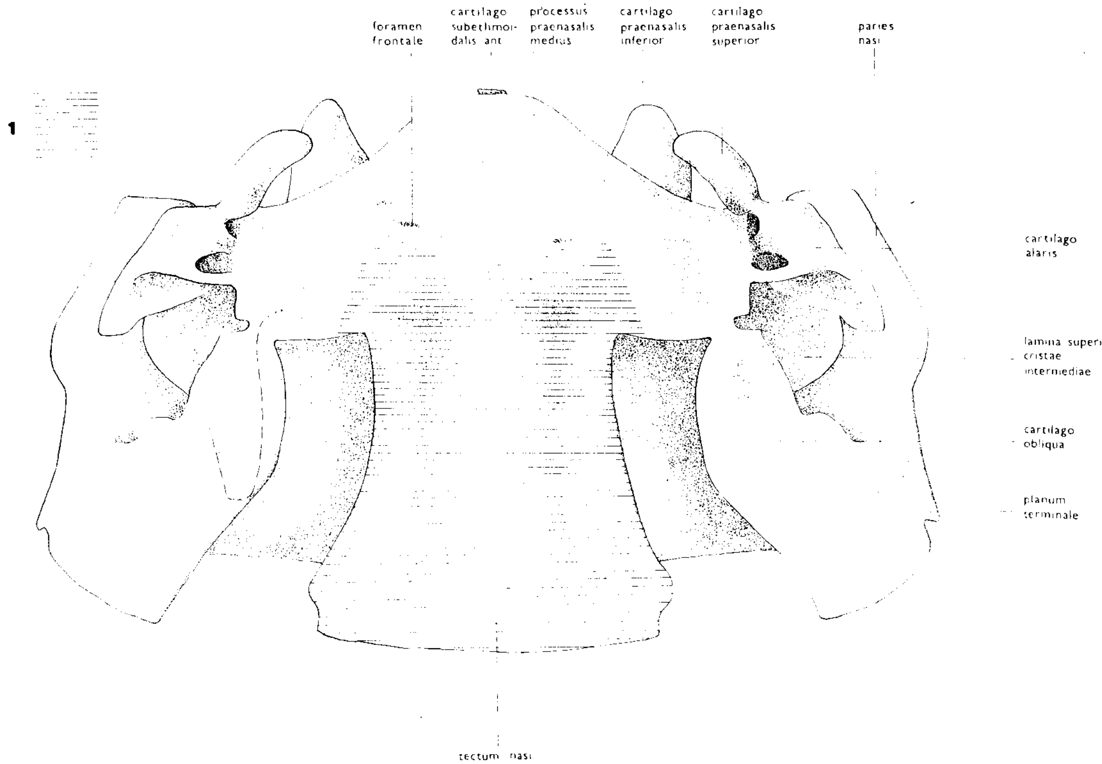


Fig. 5. Anterior part of the ethmoidal region of the endocranium of an adult *Pelobates fuscus* in dorsal aspect. 1 - ossified part. The shape of the left *lamina superior cristae intermediae* is indicated by a broken line.

tely covered by exocranial bones. The largest elements adjoining its dorsal side are the nasal bones which cover the *tectum nasi*. However, they considerably overlap its margins anterolaterally, so that they cover also the *fenestra nasolateralis*, and even a considerable part of *cartilago obliqua*. As the *cartilago obliqua* rather protrudes above the level of the dorsal surface of the *tectum nasi*, in transversal sections through the skull the dorsal outlines of the nasals form together with the uncovered part of the *cartilago obliqua* a continuous line, modelling the dorsal head profile in this region. The layer of tissue by which the nasal bone is fixed to the *cartilago obliqua* is pierced by the *ramus lateralis narium* which passes through it to the subcutaneous space (see p. 12). If one is to decide which elements take part in the bordering of the *fenestra exonarina*, it is necessary to start with the statement that in the area among the *nasale*, *maxilla* and *praemaxilla* the exocranium is interrupted by a rather large opening which causes the underlaying cartilaginous endocranial elements to be uncovered (*cartilago obliqua*, cartilaginous part of *tectum nasi*, and *cartilago alaris*). In this exocranial opening is situated the *septomaxilla* which is an otherwise typical exocranial element exclusively attached, however, to the endocranial structures and entirely separated from other exocranial structures. The *septomaxilla* considerably restricts the communication of the nasal sac with the external environment, as it projects posteriorly and partly also dorsally and ventrally into the *fenestra endonarina* (see also BORN, 1876: 591). Thus the *fenestra exonarina* refers to the opening rounded by the nasal, maxilla and praemaxilla. Within this opening is situated the septomaxilla which separates its anterior part containing the *naris externa*, the cartilaginous part of the *tectum nasi* and the *cartilago alaris* from its posterior part which is entirely filled by the *cartilago obliqua*. The support of the margins of the external nostril is formed by both the exocranium (*septomaxilla*) and endocranium (cartilaginous part of *tectum nasi* and *cartilago alaris*). Hence there is no such opening in the exocranium which would be of the same size as the corresponding opening in the endocranium and which would be a direct continuation of the latter, as is the case with most fishes and stegocephalians. In *Pelobates*, the *fenestra exonarina* is considerably larger than the *fenestra endonarina*.

Both nasals meet together in the mid-line, so that *tectum nasi* here is completely covered. However, in some specimens it may also be uncovered to an extent within the angle between the posteromedial margins of both nasals. Thus, a distinct triangular field is discernible (*glabella* sensu BOLKAY, 1919: 293, fig. 6) which may be relatively small so that it does not extend across the boundary of the ethmoidal region, or it may be larger and extend across this boundary into the orbitotemporal region (fig. 12). Its surface is sculptured similarly to the surface of the adjacent nasals and frontoparietal. JARVIK (1968: 508) erroneously considered this uncovered part of the sphenethmoid as the dermal bone, which according to him should be interpreted as the postrostral. BASOĞLU and ZALOĞLU (1964: 236, fig. 13—16) expressed the view that in *Pelobates syriacus* an uncovered sphenethmoid occurs only

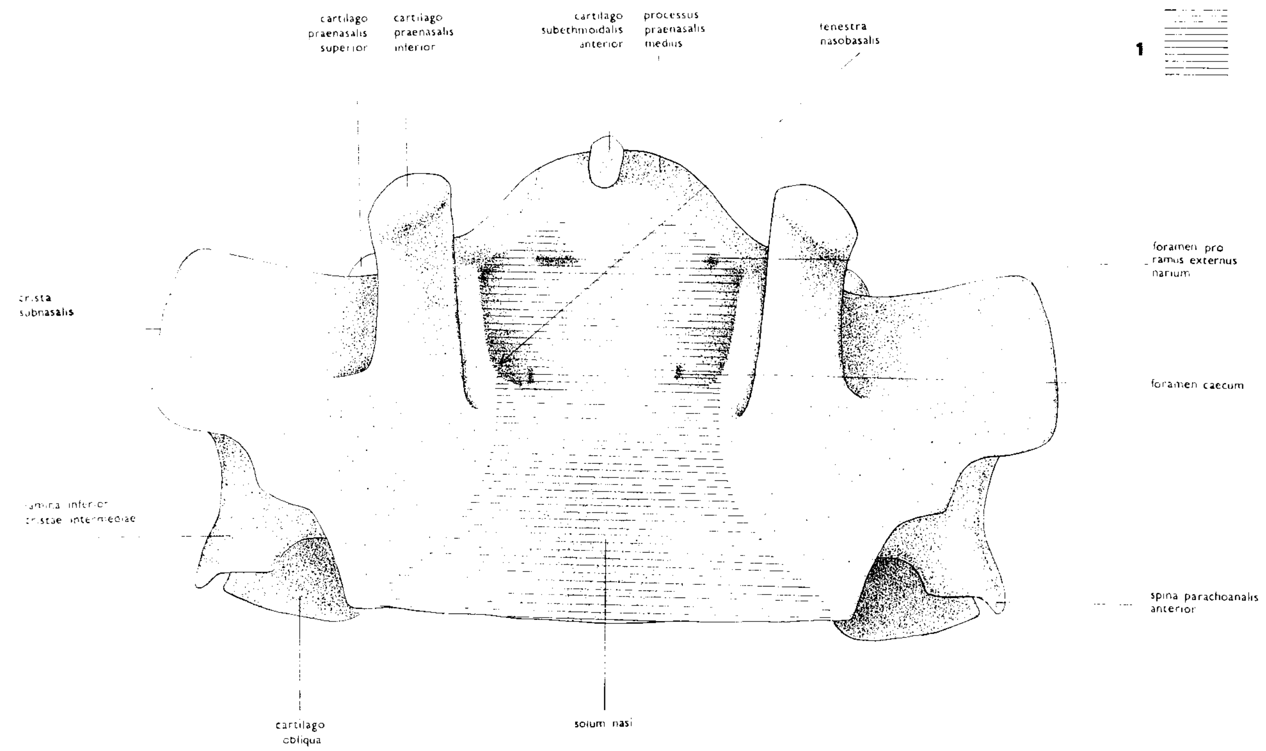


Fig. 6. Anterior part of the ethmoidal region of the endocranium of an adult *Pelobates fuscus* in ventral aspect. 1 - ossified part.

in young specimens, while in older ones it is covered by the nasals and frontoparietal which enlarge with age.

Anteriorly, both nasals reach the level of the praenasal walls; further anteriorwards their *processus anteriores* are embedded in the superficial cartilage of the *processus praenasalis medius,* so that the dorsal surface of the nasals and the surface of this cartilage form a continuous profile, similarly as is the case with the nasal bone and *cartilago obliqua* (see p. 16).

The anterior part of the ethmoidal region is covered by the paired praemaxilla. The *cartilago praenasalis superior et inferior* are fixed by tissue into the concavity on the inner surface of the *pars facialis praemaxillae.* The medial part of *pars dentalis praemaxillae* adjoins the corresponding part of the opposite praemaxilla ventrally to the tip of the *processus praenasalis medius,* but it has no contact with this process. The posterolateral process of the *pars dentalis praemaxillae* adjoins the *crista subnasalis* ventromedially, so that this part of the endocranium serves as a supporting structure against the forces pressing the praemaxilla from below, but not from the lateral side. The *pars palatina praemaxillae* runs out posteriorly into the space below the ventral surface of *processus praenasalis medius* and the anterior part of *solum nasi,* yet it is not attached to them. The space between both structures is filled by *glandulae intermaxillares.* The tip of the *processus palatinus* reaches posteriorly to the level of the base of *cartilago praenasalis inferior.* The rather subtle

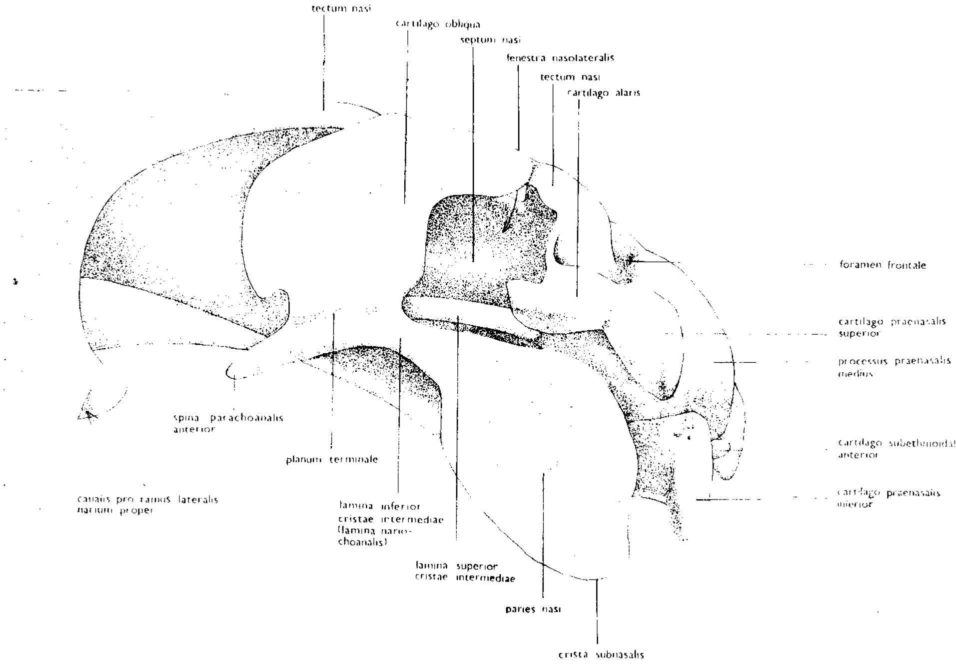


Fig. 7. Ethmoidal region of the endocranium of an adult *Pelobates fuscus* in lateral aspect.

cartilago praenasalis superior et inferior serve as »bumpers« against frontal shocks (cf. STADTMÜLLER, 1936: 552).

The maxilla is attached to the ethmoidal region in the areas of the *paries nasi* and ventral surface of the postnasal wall. The *lamina anterior maxillae* is very thin and fits into the concavity on the surface of the *paries nasi*. The *crista subnasalis* is fixed into the groove formed along the attachment of the *lamina horizontalis maxillae* to the *lamina anterior maxillae*. The *processus palatinus maxillae* is a flattened structure ventrally adjoined to the postnasal wall. In fact it is the palatine ankylosed to the maxilla and hence it also takes over its function. Besides, the part of the dorsomedial margin of the maxilla close anterior to the *processus palatinus* adjoins the lateral surface of the *spina parachoanalis posterior*. The hollow which arises between the maxilla and the spina serves as a continuation of the *canalis pro ramus lateralis narium proper*. The nerve just mentioned splits in this hollow into two branches, one of them running into the subcutaneous space, the second one into the space between the inner surface of the maxilla and the *saccus olfactorius*. The above mentioned dorsomedial margin of the maxilla serves farther in the anterior direction as a support for the lateral margin of the choana where the margin of the *fenestra endochoanalis* is incompleted. Thus, this part of the maxilla forms the lateral limits of the *fenestra exochoanalis*. Besides this, the *fenestra exochoanalis* is bordered posteriorly by the *processus palatinus maxillae*, and anteriorly and medially by the vomer. The vomer is attached by its *margo medialis* to the thickened lateral margin of the *solum nasi*, and its thin lamina between the *processus choanalis anterior et posterior vomeri* partly closes the *fenestra endochoanalis* medially. That part of

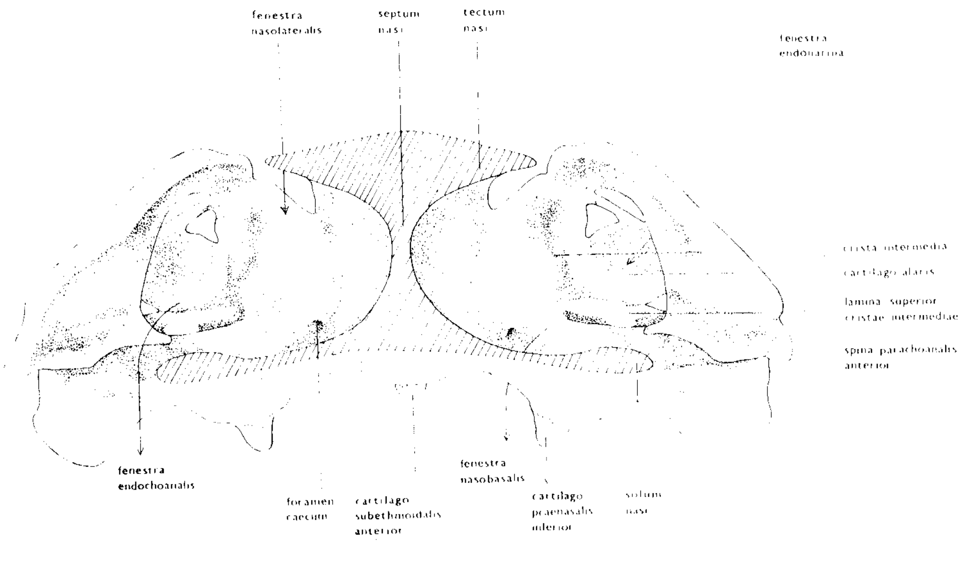


Fig. 8. Inner arrangement of the nasal cavities in an adult *Pelobates fuscus*.

the vomer which bears the *torus dentigerus* is attached firmly to the ventral surface of the sphenethmoid.

The last dermal bone having some relation to the ethmoidal region of the endocranium is the already mentioned septomaxilla (fig. 11). In its anterior part situated ventrally to the *cartilago alaris,* it is fixed by its *crista contacta* (see the description of septomaxilla) to the lateral margin of the *lamina superior cristae intermediae,* and by its lower part to the ridge arisen along the contact between the *lamina inferior cristae intermediae* and *paries nasi* (in this area the septomaxilla is also in contact with the dorsal margin of the *lamina anterior maxillae*). On the transversal section, the septomaxilla forms a horseshoe structure filled by the lateral part of the *diverticulum medium* of the nasal sac. Besides, septomaxilla forms a rather wide osseous border along the anterolateral margin of the *cartilago obliqua,* and thus conspicuously restricts the *fenestra endochoanalis.* The posterior part of the septomaxilla is pierced by a canal through which the *ductus nasolacrimalis* runs out from the nasal cavity, and then continues in the posterior direction along the outer surface of that part of the septomaxilla which is fixed to the *planum terminale.* Farther posteriorly, the *ductus nasolacrimalis* runs through the subcutaneous tissue in the groove formed by the dorsal margin of the maxilla and the lateral margin of nasal.

Ventrally to the anterior tip of the *processus praenasalis medius* is situated an elongated cartilaginous structure which is fixed to the endocranium only by soft tissue. As the dorsal margin of the symphysis of both praemaxillae has no contact with the endocranium, so that the *cavum praenasale* is in direct communication with the subcutaneous space of the anterior part of the head, this cartilaginous structure is not covered by exoskeleton, similarly to the *processus praenasalis medius.* JURGENS (1971: 25) found a similar cartilage in *Scaphiopus intermontanus,* and homologized it with the subethmoidal cartilage found in tadpoles of *Megophrys parva.* It follows from comparison with Jurgens's data that in *Pelobates fuscus* is it an element of the same nature. However, with regard to the different position it must be termed *cartilago subethmoidalis anterior.*

One can summarize that the ethmoidal region is only incompletely covered by exocranium. This fact is most conspicuous if the skull is viewed ventrally, as with the exception of the *processus palatinus maxillae* and the vomer there are no other dermal bones. Both ossified and cartilaginous parts of endocranium are uncovered. Cartilaginous parts are uncovered in the area of the *fenestra exonarina* and between the *partes faciales* of both praemaxillae. In a considerable number of specimens (perhaps of younger age? - see p. 16-18) the exocranium is opened above the dorsal part of ethmoidal region in the area between the posteromedial margins of nasals and the anterior margin of the frontoparietal.

The orbitotemporal region (figs 1—3)

The ground plan of the orbitotemporal region is much more simple than the ethmoidal one. It is formed by an incompletely closed case containing the anterior part of the brain. Besides its main function which is the protection of the brain, the braincase in its orbitotemporal section forms the medial wall of the orbit. The isolated lateral part of the orbitotemporal region which belongs to the palatoquadrate forms a support for that part of the exocranium which borders orbit laterally.

This region is constructed from all fundamental types of tissue. The large sphenethmoid coming from the ethmoidal region consists of bone tissue. Posterior to this ossification the braincase is constructed from cartilage tissue (which is also the material of the palatoquadrate), and its lateral walls further posteriorly are membranous, thus forming a large fontanelle, through which important cranial nerves run out from the braincase. Dorsally, the braincase is entirely open (there is no fontanelle, as between the ventral surface of frontoparietal and outer covering layers of the brain (*dura mater*) there is no other tissue layer.

The braincase in the orbitotemporal region consists of the floor and lateral walls, which incompletely close the cranial cavity (*cavum cranii*). The braincase roof is complete only in its most anterior part which can be considered a continuation of the *tectum nasi* from the ethmoidal region. The *cavum cranii* here overreaches the level of the foramen by which the *canalis pro ramus medialis n. ophthalmici* opens into the orbit, so that according to the basic division of the endocranium into four regions (see p. 5) this part of the braincase should already be included into the ethmoidal region; however, for practical reasons it is included in the orbitotemporal region. The roof of the braincase in this area, if viewed from the inner side, forms a vault, while if viewed dorsally, it uncorrespondingly slants down to the median line. Consequently, the braincase roof is thinnest along the mid-line, while laterally it increases in thickness. However, further posteriorly this roof is incomplete, as it is interrupted by the opening *fenestra frontoparietalis*. It consists only of overhanging sharp margins anteriorly bordering the above mentioned opening, while posteriorly this overhanging border is gradually reduced, so that posterior to the boundary between the anterior and middle thirds of the length of the *fenestra frontoparietalis* it is completely absent. The dorsal surface of the reduced part of the braincase roof is more or less flat. Only an indistinct groove is present running parallel to the sharp crista by which the braincase roof sharply passes onto the outer surface of the lateral walls. Such a formation of the braincase roof, even considerably reduced in this area, permits a firm attachment of the frontoparietal bone to the endocranium. The sharp ridge mentioned above between the dorsal and lateral surfaces of the braincase extends in the dorsolateral direction in the area of the anteromedial corner of the orbit, forming the *lamina supraorbitalis*, which is moreover bordered by a strip of cartilage. This lamina overlies the above mentioned part of the orbit so that it forms a roof above the opening of the *canalis pro ramus medialis n. ophthalmici*. However, it occupies a relatively short section of the orbital circumference (figs 1, 3).

The distance between the lateral walls of the braincase is the longest along their upper margins, becoming gradually shorter ventrally. Consequently, the walls run down ventromedially, and pass without any distinct boundary into the floor of the braincase. Both their outer and inner surfaces are smooth. The dorsal termination of their outer surface passes through a distinct ridge in the dorsolateral elongated plane, bordering the *fenestra frontoparietalis*. This ridge represents a continuation of the sharp crista which anteriorly forms the lateral borders of the reduced braincase roof, and posteriorly it passes onto the surface of prooticooccipital. Thus it is possible to consider it a part of the *crista frontoparietalis* (see the description of otic region).

On the ventral surface of the braincase floor in the area of sphenethmoid there are two distinct ridges bordering the area of attachment of the most anterior part of the parasphenoid.

Both the floor and the lateral walls of the braincase are comparatively thick anteriorly, and are formed by the osseous tissue (sphenethmoid). The thinnest parts of the walls are formed by membranous tissue (thus forming a large fontanelle), while the floor is thinnest in the area of cartilaginous stripe between both fontanelles. The remaining parts of the braincase walls in the orbitotemporal region are formed by the most anterior processes of the prooticooccipitals, and although they are formed by bone tissue, they are very thin.

As it has already been stated, the braincase walls are mostly ossified anteriorly (here they are parts of the sphenethmoid). The boundary between ossified and carti-

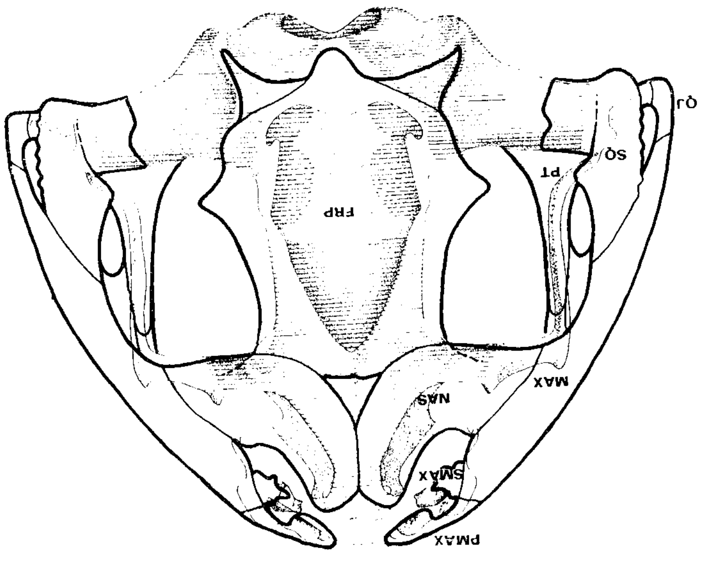


Fig. 9. Skull of an adult *Pelobates fuscus* in dorsal aspect. Dermal bones drawn as if transparent to show topographical relations of the exocranium to the endocranium. Lower jaw and hyoid omitted. MAX - maxilla; NAS - nasal; FRP - frontoparietal; PMAX - praemaxilla; PT - pterygoid; QJ - quadratojugal; SMAX - septomaxilla; SQ - squamosal.

laginous parts runs along the transversal vertical plane, and is remarkably straight. This boundary is situated approximately in the middle of the anterior-posterior diameter of the orbit (if viewed on the endocranium without its exocranial cover), which corresponds approximately to the level situated rather anterior to the middle of the anterior-posterior diameter of the *fenestra frontoparietalis*. This section of the braincase, of which both walls and floor are formed exclusively by cartilage tissue, is considerably short, and farther posteriorly it passes into a section where cartilage forms only the floor and narrow stripes along the margins of *fenestra frontoparietalis*, thus bordering the large lateral fontanelle. Hence this fontanelle is bordered by cartilage anteriorly, dorsally and ventrally, while posteriorly by the prooticooccipital bone.

Braincase openings. The largest one is the *fenestra frontoparietalis* which is situated within the braincase roof. The course of the lateral margins of this opening corresponds approximately to the general shape of the braincase in this region of the endocranium, although anteriorly these margins meet forming a point. No irregularities occur on the margins, with the exception of small processes directed to the posterior which are formed at the level of the anterior processes of the prooticooccipitals.

The cranial cavity communicates anteriorly with both nasal cavities by two *canales olfactorii*.

The fontanelle in the posterior part of the lateral wall of the braincase in the orbitotemporal region (orbitotemporal fontanelle) is pierced by important cranial nerves. The posterior part of this fontanelle is occupied by the *ganglion trigeminofaciale* which is partly situated inside the braincase (in the lower part of the *recessus prooticus*), partly in the orbit. The opening in the fontanelle through which the mentioned ganglion runs out is called the *foramen prooticum*, and is the largest foramen in the fontanelle. The *nervus trochlearis* runs out through the tiny opening called *foramen trochlearis* which is situated within the fontanelle close to the ventral margin of the anterior part of the prooticooccipital. Ventral to this opening is situated the *foramen oculomotorii* which is of similar size, but which can also pierce the cartilaginous part of the braincase in some specimens, i. e. beyond the fontanelle (in the specimen investigated this nerve pierced on one side the tissue of the fontanelle, while on the opposite side it pierced the cartilaginous wall close to the margin of fontanelle).

In the anterior part of the fontanelle is situated the *foramen opticum*. The *nervus opticus* is covered after its passage through the membrane of the fontanelle by a considerably thick tissue sheath which is the derivative of the mentioned membrane.

The palatoquadrate. The lateral part of the endocranium in the orbitotemporal region is formed by a subtle rod-like structure which already belongs to the viscerocranium. Anteriorly it is attached to the postnasal wall (lateral to the opening of the *canalis pro r. lateralis narium proper*), posteriorly (already in the otic region) to the lateral part of the prooticooccipital. This structure is called the palatoquadrate (termed also the *suspensorium* by earlier authors). It is cartilaginous throughout its extent in the orbitotemporal region, and both anteriorly and posteriorly it is possible clearly to distinguish its boundaries, as it is attached to the ossified sphenethmoid and prooticooccipital. Only in the area of its attachment to the postnasal wall is the cartilaginous *spina parachoanalis posterior* present, this being considered a part of the ethmoidal region, not of the palatoquadrate or related structures.

For descriptional purposes it is possible to distinguish on the palatoquadrate (not quite correctly, see chap. Ontogenetical development of the endocranium) the *pars palatina,* which is situated laterally to the orbit, and is an essential part of the palatoquadrate, and the *pars quadrata,* which is situated lateral to the prooticooccipital (already in the otic region), serving for articulation with Meckel's element. For naming individual sections of the *pars palatina* different terms have been introduced, which are more important in those forms whose palatoquadrate is considerably reduced (e.g. *Urodela*). The posterior part of the *pars palatina* running out from the *pars quadrata* anteriorwards is called the *processus pterygoideus.* That part of the *pars palatina* which forms a lateral extension of the postnasal walls is usually designated the *processus antorbitalis* (see e.g. DE JONGH, 1968, tab. 26). From the lateral end of the antorbital process the *processus maxillaris posterior* is directed posteriorly passing without any distinct boundary into the *processus pterygoideus,* while the tiny *processus maxillaris anterior* is directed anteriorly. However, the descriptional terminology of frog palatoquadrate is considerably confused,

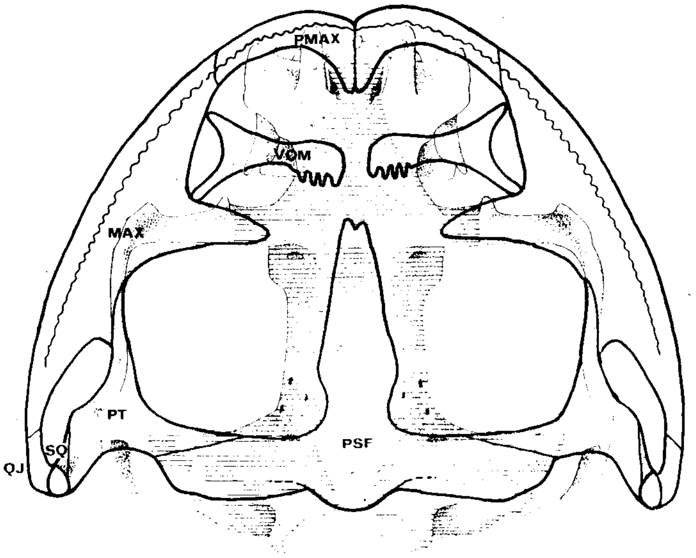


Fig. 10. Skull of an adult *Pelobates fuscus* in ventral aspect. Dermal bones drawn as if transparent to show topographical relations of the exocranium to the endocranium. Lower jaw and hyoid omitted. MAX - maxilla; PMAX - praemaxilla; PSF - parasphenoid; PT - pterygoid; QJ - quadratojugal; SQ - squamosal; VOM - vomer.

so that e.g. STADTMÜLLER (1936: 566, 569) used the terms *pars paltina* and *processus pterygoideus* as synonyms.

Topographical and functional relations of the orbitotemporal region to the exocranial elements (figs 9, 10), The frontoparietal is the only element covering the braincase dorsally. As the endocranium opens dorsally by a large *fenestra frontoparietalis,* the braincase is completed here only by the exocranial element. As it was already mentioned, only the *dura mater* lines that part of its ventral surface which fills the mentioned fenestra and hence there is no other tissue layer between the exocranium and the outer layer of the brain cover.

The frontoparietal rests firmly on the plane bordering the *fenestra frontoparietalis* and its *incrassatio frontoparietalis* (»dorsal endocranial pattern« sensu ŠPINAR, 1976) fills this opening. This incrassation, if viewed ventrally, forms a distinct figure (see fig. 27, ifp) which thus provides information on the configuration of the braincase roof even if the endocranium is lacking (e.g. in fossil material).

In the area where both margins of *fenestra frontoparietalis* meet together forming a point anteriorly, a tiny ossified element was found in the tissue layer between the braincase roof and the frontoparietal bone (fig. 29). It is not excluded that it could be a vestige of some exocranial element which was reduced during the course of evolution (for detailed discussion see chap. 4. 2. 3 Homologization of the exocranium).

The *pars medialis parasphenoidei* is attached to the ventral surface of the braincase in the orbitotemporal region. This part of the parasphenoid is fixed between two parallel ridges which thus ensure a firmer attachment.

The essential partof the palatoquadrate is enclosed within the pterygoid posteriorly, and stored between pterygoid and maxilla anteriorly, and thus an inner rod-like support of the lateral margin of orbit is formed. Part of the dorsal surface of *processus antorbitalis* is covered by the nasal bone, which reaches this area from the dorsal surface of the postnasal wall. The remaining anterior part of the palatoquadrate is covered by the maxilla. The *processus antorbitalis* is covered ventrally by the *processus palatinus maxillae,* dorsally by the *processus frontalis maxillae.* However, the *processus antorbitalis* is uncovered from the orbit, similarly to the surface of the postnasal wall directed in the same way. The *processus maxillaris posterior* is stored in the groove running along the base of *lamina horizontalis maxillae* (see fig. 31: spq). Its anterior part directed to the orbit is also uncovered, similarly to the *processus antorbitalis.* Further posteriorly a short section of the palatoquadrate (corresponding to the length of the *margo orbitalis pterygoidei*) is covered by the maxilla laterally, while in the direction to orbit it is covered by the pterygoid. Farther posteriorly it plunges into the groove, which gradually deepens in the posterior direction (*sulcus pterygoideus*) and which at the level of the posterior border of the sphenethmoid becomes the canal. However, this canal is open throughout its course by a narrow slot into the space between pterygoid and maxilla in younger specimens, while in older ones this slot is lacking. The dorsolateral wall of the *canalis pterygoideus* disappears closely anterior to the branching of pterygoid into its *ramus interior* and *ramus posterior,* and the palatoquadrate is stored in the groove again, and faces the space called by BOLKAY (1919, fig. 6) the *spatium zygomaticum inferius.*

The otic region (figs 1—3)*)

This endocranial region is relatively short in the antero-posterior direction, although it represents the widest part of the skull. Along the mid-line is the posterior section of the braincase, containing the posterior part of the brain. Both otic capsules containing statoacoustic organs are attached laterally to the braincase. Besides, each otic capsule serves as a posterior wall of the orbit. Cartilage tissue is restricted only to limited parts of the roof and floor of the braincase, and to the lateral peripheral parts of the otic capsules. The walls of the capsules proper are ossified with the exception of the limited area ventral to the *fenestra ovalis,* and of the *operculum.*

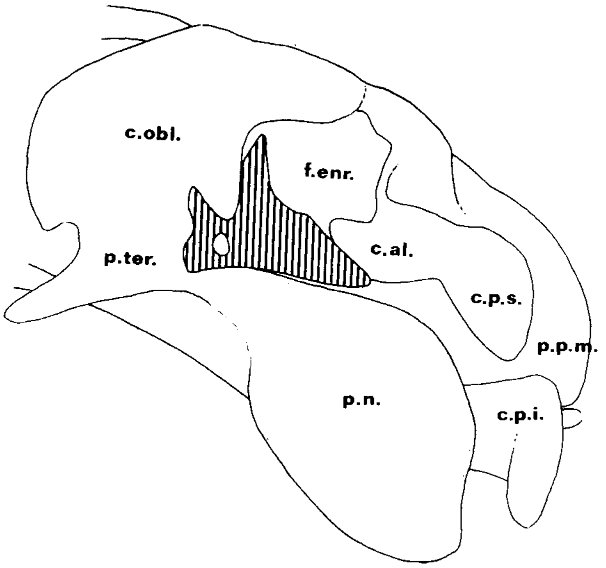


Fig. 11. Ethmoidal region of the endocranium of an adult *Pelobates fuscus* showing the position of the septomaxilla. c. al. - *cartilago alaris*; c. obl. - *cartilago obliqua*; c.p.i. - *cartilago praenasalis inferior*; c.p.s. - *cartilago praenasalis superior*; f.enr. - *fenestra endonarina*; p.n. - *paries nasi*; p.p.m. - *processus praenasalis medius*; p.ter. - *planum terminale.*

The braincase. Its floor is almost flat, situated horizontally. Laterally, it passes in the right angle into the lateral walls. The stripe of the floor along the mid-line is formed by cartilage (»*solum synoticum*« sensu GAUPP, 1896: 40). This carti-

---

*) In frogs, the posteroventral part of the otic capsules consists of lateral occipitals, i.e. of elements belonging already to the occipital region. For practical reasons, however, otic capsules are described as a whole.

laginous stripe is widest in the anterior part of the otic region, while it considerably narrows in the posterior direction. On histological sections an obliterated notochordal canal is well discernible in this area. The lateral parts of the floor are ossified.

The longest distance of the lateral walls is in the area of the *recessus prootici* (see p. 46). Posterior to these recesses the walls of the braincase are convex into the *cavum cranii*. They pass without any distinct boundary into the vaulted roof. The highest point of this roof is in the mid-line on the margin of the *fenestra frontoparietalis*. Posteriorly, the roof lowers steeply. As the *fenestra frontoparietalis* reaches up to the otic region, part of the braincase roof is lacking here too. The margin of this fenestra in the mid-line runs out anteriorly by a more or less distinct point which is a vestige of the *taenia tecti medialis*. Similarly to the floor, in the roof too there is median stripe of cartilage which is widest anteriorly, while it considerably narrows posteriorly. According to GAUPP (1896: 40) this part of the braincase roof is called the *tectum synoticum* (seu *tectum posterius*; cf. STADTMÜLLER, 1936: 519). It is connected anterolaterally with cartilaginous stripes which form continuations of the margins of *fenestra frontoparietalis* anteriorwards; they are called *taeniae tecti laterales*. However, the term »*tectum synoticum*« is meant to denote mostly the whole braincase roof in the otic region, without distinguishing it into osseous and cartilaginous parts.

The otic capsule (*capsula otica*) is formed in adult *Pelobates fuscus* by a hollow monolithic bone. Its medial wall separates it from the *cavum cranii* and is distinctly convex into this braincase cavity. The anterior wall separates the cavity of the otic capsule from the orbit. On its outer surface is a horizontal shallow groove containing the *vena jugularis*; it runs laterally, forming the notch on the anterolateral surface of the capsule. This notch takes part in forming the pterooccipital fissure (sensu BOAS, 1914). The lateral wall of the otic capsule in its ventral part gives off an anterolaterally directed process, which forms the lower margin of the mentioned fissure. This process is covered by cartilage, similarly to the ventral margin of the *fenestra ovalis* (seu *foramen ovale*) which is completed by a cartilaginous ledge directed dorsolaterally. The lateral wall of the otic capsule is terminated dorsally by the large horizontal *crista parotica* (seu *tegmen tympani*), which in fact is part of the capsule roof running out laterally. Hence the *fenestra ovalis* is situated in a space covered by mentioned crista anterodorsally. This space is called by GAUPP (1896: 39) the *fossa fenestrae ovalis*. The roof of the otic capsule, in connection with the capsule's general position, slants ventrolaterally, and is terminated by the mentioned *crista parotica*. A distinct low ridge called the *crista frontoparietalis* runs across the dorsal surface of the otic capsule as an anterior-posterior directed arch rather convex medially. It represents a continuation of the ridge which is the upper termination of the outer surface of the lateral braincase wall in the orbitotemporal region. This affords the frontoparietal attachment to the endocranium. It is joined to the similar short posterolateral crista coming from the medial side (*crista frontoparietalis poste-*

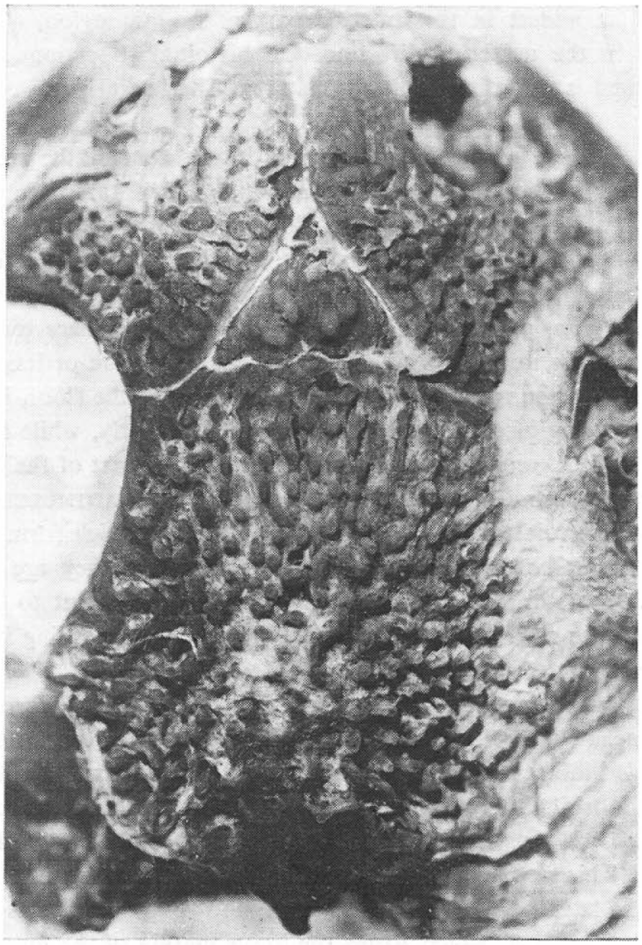


Fig. 12. Dorsal view of the skull of an adult *Pelobates syriacus syriacus*. The uncovered triangular part of the sphenethmoid is clearly visible (Photograph by courtesy of the Swedish Museum of Natural History, Stockholm).

rior) which has the same function. Both cristae join each other to form one distinct ridge which passes onto the posterior surface of the otic capsule. It becomes less acute there but increases in size, thus forming a distinct convexity called the *prominentia ducti semicircularis posterioris,* which is situated posteromedially to the *fenestra ovalis*. The floor of the otic capsule is similarly to its roof slanted lateroventrally. There is a cartilaginous ledge parallel with its lateral margin which enables a firmer attachment of the lateral processes of the parasphenoid.

The cavity of otic capsule (*cavum capsulae oticae*). Its long axis slants lateroventrally in accordance with the general position of the capsule. It is possible to distinguish there the main cavity called the *vestibulum* (seu *cavum vestibulare commune* sensu STADTMÜLLER 1936: 529), which is situated between the medial wall of the capsule and the fenestra ovalis. Two semicircular canals run out from the medial part of the *vestibulum* - the *canalis semicircularis anterior et lateralis* (seu *cavum semicirculare anterior et lateralis* sensu STADTMÜLLER 1936: 529) which contain the membranous *ductus semicircularis anterior et lateralis*. Both ends of these canals open into the *vestibulum*. The *canalis semicircularis anterior* does not manifest itself on the surface of the otic capsule, in contrast to the *canalis semicircularis lateralis* which underlies the *crista parotica*. In *Pelobates* the *canalis semicircularis posterior* is absent, though the course of the *ductus semicircularis posterior* which fills the *recessus posterior vestibuli* is manifested on the sufrace of the endocranium by the *prominentia ducti semicircularis posterioris*.

The openings to the otic capsule. The largest one is the *fenestra ovalis* directed posterolaterally. It is covered by the cup-like *operculum**) which is an ellipsoid-shaped cartilaginous structure concave from its inner side and convex from the outer side. Dorsally, the *operculum* is hung on the osseous border of the *fenestra ovalis*, and ventrally it is attached to the bone ridge running parallel to the ventral margin of this opening; this ridge forms an inconspicuous prominence into the cavity of the otic capsule and is in fact the ventral osseous margin of *fenestra ovalis*. The elastic hanging of the *operculum* is ensured by a stripe of tissue encircling it, which is a derivative of its perichondrium.

The most important opening in the medial wall of the capsule is the *foramen acusticum*. In most specimens of *Pelobates fuscus* only one *foramen acusticum* occurs. In some specimens, however, *n. acusticus* splits already in the braincase cavity, and its branches may pass through separate openings, the *foramen acusticum anterior et posterior* (cf. STADTMÜLLER 1936: 528). Some specimens also exist in which the mentioned nerve splits during its course through the wall. In the latter cases, the partition between *foramen acusticum anterior et posterior* is very subtle and convex to the cavity of the otic capsule. Dorsal to the *foramen acusticum* there is the tiny *foramen endolymphaticum*, through which the *ductus endolymphaticus* passes. The posterior wall of the otic capsule is pierced by the considerably large *foramen perilymphaticum inferius* which is situated within the *foramen jugulare* (which is in fact a canal, not an opening). The posteromedial wall of the otic capsule is pierced by the *foramen perilymphaticum superius* which is separated from the *foramen perilymphaticum inferius* only by a subtle partition. This is situated in the area where the *foramen jugulare* opens into the braincase cavity.

The palatoquadrate is situated laterally to the otic capsule, and is divided into three processes: the *processus oticus* (seu *processus oticus adulti* sensu PLASOTA, 1974: 125) is attached ventrally to the anterior end of *crista parotica* (see fig. 2), and is connected with it only by soft tissue (cf. STADTMÜLLER 1936: 585). The *processus pseudobasalis* is firmly attached to the anteroventral surface of the otic capsule.

---

*) KLUGE (1966: 10), however, stated that the *operculum* is lacking in *Pelobates fuscus* and *P. cultripes*.

Posterolaterally, the palatoquadrate runs out by a process called the *pars quadrata* whose distal part articulates with Meckel's element. This distal section ossifies, and is called the *os quadratum*.

Topographical and functional relations of the otic region to the exocranial elements (figs 9, 10). The most of the braincase roof in the otic region is covered by frontoparietal bone, whose incrassation corresponds with the shape of the *fenestra frontoparietalis,* as is the case with the orbitotemporal region. The frontoparietal fits by its *processus paraoccipitales* into the areas which are bordered by convergent ridges, the *crista frontoparietalis* and the *crista frontoparietalis posterior*. The posterior part of the frontoparietal covers the *tectum synoticum* almost up to the *foramen magnum*. Laterally, the margin of the frontoparietal is parallel with the course of the *crista frontoparietalis*.

The *ramus paroticus squamosi* is attached to the cartilaginous margin of the *crista parotica*. The *processus oticus palatoquadrati* adjoins ventrally the anterior end of the *crista parotica*. This process, together with the *processus pseudobasalis palatoquadrati* completes the pterooccipital fissure into the *foramen pterooccipitale* through which the *vena jugularis* passes. Anteroventral to *fenestra ovalis,* the distal end of *cornu hyale* of hyoid adjoins the lateral wall of otic capsule. The base of both braincase and otic capsule is covered by the parasphenoid.

The *processus pseudobasalis palatoquadrati* is covered by the *ramus interior pterygoidei,* the *processus oticus palatoquadrati* by the *ramus paroticus squamosi*. The *pars quadrata palatoquadrati* is stored in the groove running parallel to the long axis on the medial surface of the *processus posterolateralis squamosi*. This groove is in most of its extent covered by the *ramus posterior pterygoidei,* which results in the formation of a canal. The *pars quadrata* is uncovered only in its distal ossified section (*os quadratum*) which articulates with Meckel's element.

The occipital region (figs 1—3).

Despite the fact that the occipital region represents only a very limited part of the frog endocranium, it is very important, as it takes a part in the formation of the craniovertebral junction. The exoskeletal cover of this region is poorly developed. As we have already mentioned, the level of the *foramen jugulare* does not correspond to the actual boundary between the otic and occipital regions (see footnote on page 26). As certain parts of the *occipitalia lateralia* have already been described above in connection with the otic capsule the following description will be restricted only to the area of the *foramen magnum* and the *condyli occipitales*.

The *foramen jugulare* opens onto the skull surface lateral to the *condylus occipitalis* in the considerably deep *fossa condyloidea*. Through this foramen the *n. glossopharyngeus* and *n. vagus* run out from the braincase. However, SEWERTZOW (1891: 148) described a specimen in which both mentioned nerves run through separate openings similarly to some pipids (SOKOL, 1977: 361). The *condyli occipitales* in posterior view are oval-shaped, with longitudinal axis directed dorsolaterally. Their dorsomedial surface forms a part of the margin of the *foramen magnum.* Both condyli extend ventrally below the level of the braincase base. This base between the condyls is formed by cartilage (hypochordal seu basal plate; see STADTMÜLLER 1936: 523), which is a part of the median cartilage stripe coming from the otic region; it passes into the cartilaginous cover of both condyls. The dorsolateral sections of the margin of the *foramen magnum* are formed by a thin osseous lamina which is connected by a flat ligament with the neural arches of the first vertebra. The space between the mentioned cranial and vertebral structures covered only by elastic tissue enables dorsoventral nods of the head. The comparatively short section of the dorsal margin of the *foramen magnum* in the mid-line is formed by cartilage, which is a part of the cartilaginous stripe coming from the otic region. The plane of the *foramen magnum* is not perpendicular, as its upper part declines rather in the anterior direction.

Endocranial ossifications

Three ossifications occur in the neural endocranium of *Pelobates fuscus*: an unpaired sphenethmoid, and paired prooticooccipital. Some earlier authors described them as isolated bones, overlooking their relations to the cartilaginous endocranial parts (e.g. BOLKAY, 1919), which caused some errors in terminology. It is always necessary (also in the case of paleontological findings where cartilaginous parts are lacking) to consider them only fragments of endocranium.

No problems are connected with the definition of sphenethmoid in *Pelobates.* The situation is more complicated as regards the paired ossification in the otic and occipital regions which is termed by various authors the *occipitopetrosum,* the *petrooccipitale,* or *otooccipitale.* As it is an element arising by the fusion of the *prooticum* and *occipitale laterale,* the more convenient name is prooticooccipital. STADTMÜLLER (1936: 616) defined the *prooticum* as an element arising by enchondral ossification in the most anterior part of the otic capsule, which either takes part in the formation of the margins of the *fenestra ovalis,* or entirely surrounds this foramen. The lateral occipital ossifies in the posterior part of the otic capsule, dorsomedially it enters into contact with the *tectum synoticum,* and ventromedially with the cartilaginous *solum synoticum.* These definitions are in accordance with the position of ossified elements found in *Pelobates* tadpoles and in adults of e.g. *Rana esculenta* (cf. STADTMÜLLER, 1936, fig. 394; GAUPP, 1896, figs 15, 16). Already SEWERTZOW (1891: 152) found in *Pelobates fuscus* that the prooticooccipital arises in the course of ontogeny from two originally separated ossifications. In adults, landmarks between co-ossified elements are the *foramen endolymphyticum,* the anterior margin of the *foramen acusticum commune* (or *foramen acusticum anterius* in the case where both acoustic openings are developed), and stripes of cartilage on the ventral surface of otic capsule, running anteromedially from the posterior margin of *fenestra ovalis* (see fig. 3). In those frogs which have *prooticum* and *occipitale laterale* separated from each other in adults, the *synchondrosis prooticooccipitalis* occurs in this area. Briefly summarized, the otic capsule in *Pelobates* consists of two originally independent and later fused ossifications, belonging to different endocranial regions.

Another endocranial ossification is the distal section of the *pars quadrata palatoquadrati*. It is fused synostotically with the quadratojugal (fig. 35), and is called the *os quadratum*. The only ossification of the enchondral origin in the lower jaw is the mentomandibular (see chapter Free elements of visceral endocranium), which is the strongly reduced larval jaw called the *cartilago labialis inferior* (see chap. 4.1.3. a Homologization of endocranium of a tadpole with that of an adult frog). Also this ossification is synostotically fused with the dermal bone (dentary).

Other ossifications in the endocranium of *Pelobates fuscus* are lacking. SEWERTZOW's statement (1891: 156) that the supraoccipital bone occurs in this species is misleading, as some earlier authors used this term for designation of the *extrascapulare mediale* (seu *postparietale*).

Free elements of the visceral endocranium

Meckel's element is a slightly bent arch-like structure, serving as endocranial support of lower jaw. For descriptive purposes it is usually distinguished into two parts: the *pars articularis,* which articulates with the *os quadratum,* and the *pars fibularis* which is a support of the dermal bones of lower jaw. The *pars articularis* remains cartilaginous also in adults. It is stored in a wide groove on the dorsal surface of the proximal section of the praearticular (fig. 40a). Anteriorly, this groove runs onto the lateral surface of this dermal bone, and anterior to the level of the boundary between the first and second thirds of the distance between the posterior end of the praearticular and the median symphysis it is covered laterally by dentary. Thus, Meckel's element is stored in the canal between the praearticular and dentary in this section. It becomes uncovered in a short section between the anterior end of the praearticular and the mentomandibular.

The mentomandibular is an ossification situated anteromedially to the anterior end of Meckel's element, making contact with the corresponding opposite element in the median symphysis. It is fused with dentary in the ossified complex of both enchondral and endesmal origins (cf. STADTMÜLLER, 1936: 651).

The hyoid completes its remodellation still in adults (see also KOTHE, 1910: 43), and hence it is the endocranial element in which metamorphosis of the skull is completed. This statement is based on the fact that the hyoid occurs in mature specimens of *Pelobates fuscus* in two morphological types. In the first one (fig. 13 a), from central flat cartilaginous plate (*corpus*) one big process (*manubrium*) runs out on both sides, which have a flat peel-like termination. It is possible to homologize the anteromedial margin of this termination with the *processus anterior,* well developed e. g. in the hyoid of *Rana esculenta* (GAUPP, 1896, fig. 28) or in *Rana temporaria* (STADTMÜLLER, 1936, fig. 517). Much less prominent is the posterolateral margin of this termination, which is possible to homologize with the *cornu hyale* (seu *cornu principale* sensu Gaupp, 1896: 58). However, the *processus anterior* is generally considered also a part of the *cornu hyale* (e. g. Trewavas, 1933: 407). The distal section of the *cornu hyale* in specimens with metamorphosis completed is connected with its proximal section only by tissue (fig. 13 b). Another process which runs from the lateral margin of the manubrium is called the *processus anterolateralis* (seu *processus alaris* sensu Gaupp, 1896: 57; seu *processus lateralis anterior* sensu Fuchs, 1929, fig. 19). The *cornu hyale* and the *processus anterolateralis* enclose between them the *sinus nervi hypoglossi*. Both *manubria*, together with the *processus anteriores* border a deep *sinus hyoglossus*, which according to the degree of development of the *processus anteriores* may be almost completely closed. Another two subtle processes called the *processus posterolaterales* (seu *processus laterales posteriores* sensu Fuchs, 1929, fig. 19) run out from the *corpus* in the posterolateral direction, and two *processus posteromediales* (seu *processus thyreoidei*, seu *ossa thyreoidea*) run out similarly directed from its posterior margin. Their proximal ossified ends are deeply embedded in the *corpus*, almost contacting each other. The distal ends are completed by cartilage. It is unknown whether and to what degree this distal end of the *processus posteromedialis* ossifies in the course of the life of adults, similarly to the terminal growing cartilage covering the surface of the epiphysis of long bones. The space between both these processes is called the *sinus laryngeus*.

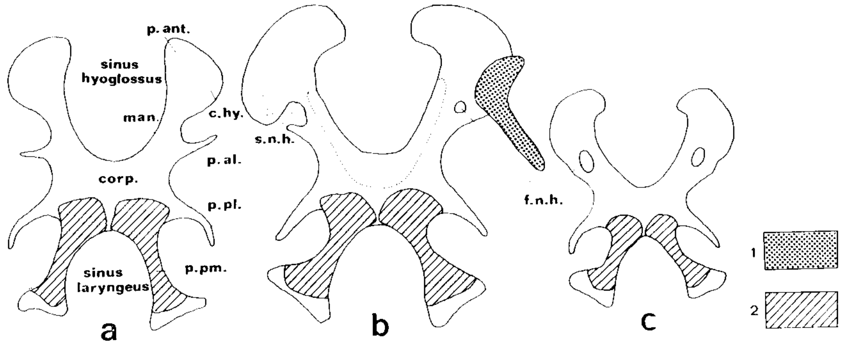


Fig. 13. Hyoid morphology of *Pelobates fuscus*. a - stage with the *processus anterolateralis* (DP FNSP 6424); b - transitional stage during the enclosing of the *sinus nervi hypoglossi* (DP FNSP 6468); that part which is probably adjoined by the *os parahyoideum* is indicated by a dotted line; also the topographical relation of an independent part of the *cornu hyale* to the main part of hyoid is schematically shown on one side; c - final stage with well developed *foramina nervi hypoglossi* (DP FNSP 6466). 1 - independent part of *cornu hyale*; 2 - ossified part of *processus posteromedialis* (*os thyreoideum*); c.hy. - *cornu hyale*; corp. - *corpus hyoidei*; f.n.h. - *foramen nervi hypoglossi*; man. - *manubrium hyoidei*; p.al. - *processus anterolateralis*; p.ant. - *processus anterior*; p.pl. - *processus posteromedialis*; s.n.h. - *sinus nervi hypoglossi*.

The second type of hyoid (fig. 13 c) is similar, but the *sinus nervi hypoglossi* is completely enclosed by the stripe of cartilage called the *processus confluens* (sensu Kothe, 1910: 40, 43), so that an opening arises here (*foramen nervi hypoglossi*, seu *foramen laterale* sensu STADTMÜLLER, 1936: 682). Both these two types of hyoid represent ontogenetical stages by which metamorphosis is completed (see KOTHE, 1910: 43—44).

With the exception of the posteromedial processes no other ossification of the hyoid was found macroscopically in the specimens investigated, which confirms the statement of TREWAVAS (1933: 510) that »*Pelodytes* possesses a parahyoid bone, similar to that of *Alytes,* but this is not represented in other *Pelobatidae*«. Also RIDEWOOD (1897: 581) did not find any parahyoid ossification in *Pelobates.* Contrary to this, FUCHS (1929: 428—429) found parahyoid ossification by means of histological methods in *Pelobates,* although he admited that the presence or absence of this ossification may be dependent on individual variation, and is probably lacking in most individuals. Fuchs also stated that in most cases it is impossible to study this ossification macroscopically, despite the fact that it has typical features of dermal bone. Material from the osteological collections of the Department of Palaeontology of Charles University, Prague, has not been studied histologically, so that only the whitish colouring of rather thickened margins of *sinus hypoglossus* in some specimens (fig. 13 b) could correspond with Fuchs' description.

4.1.2. Ontogenetic development of endocranium in the last stages before metamorphosis and during metamorphosis (figs 14—19)

See also BORN, 1876, tab. XL/7-14, 19, XLI/23, 24, 30, 32; SCHULTZE, 1892, fig. on the page 5; KOTHE, 1910, tab. I, II, LUTHER, 1914, figs 15—20, 65—70, 71, 73).

The neural endocranium of tadpole close before metamorphosis displays a surprisingly advanced development of the otic and occipital regions in comparison with other parts of the skull. The fundamental morphological features of both mentioned regions are almost identical with those in adults, while other parts still preserve their typical larval characters.

On the surface of the otic capsule there is a well developed *crista parotica* which is sharply bent anteroventrally in its anterior part where the *processus oticus* is attached. Below its posterior part is hidden the *fenestra ovalis* which opens laterally. Also the *operculum* is developed in the form of an ellipsoidal cup with its long axis situated horizontally. The special structure interpretable as the *pars interna plectri* (see PLASOTA, 1974: 119; KOTHE, 1910: 59—60) has not yet been found in this developmental stage. The inner arrangement of the otic capsule is also completed to a form practically identical with that in adults. On the surface there is a well developed *prominentia ducti semicircularis posterioris,* and also *prominentia canalis semicircularis anterioris* which protrudes well due to the fact that the otic capsule is still separated by a fissure from the lateral wall of the braincase in the orbitotemporal region. Only one *foramen acusticum* occurs. The *foramen perilymphaticum superius* and *inferius* are comparatively larger than those in adults, while the *foramen endolymphaticum* maintains a constant proportional size during the course of ontogeny. Neither the

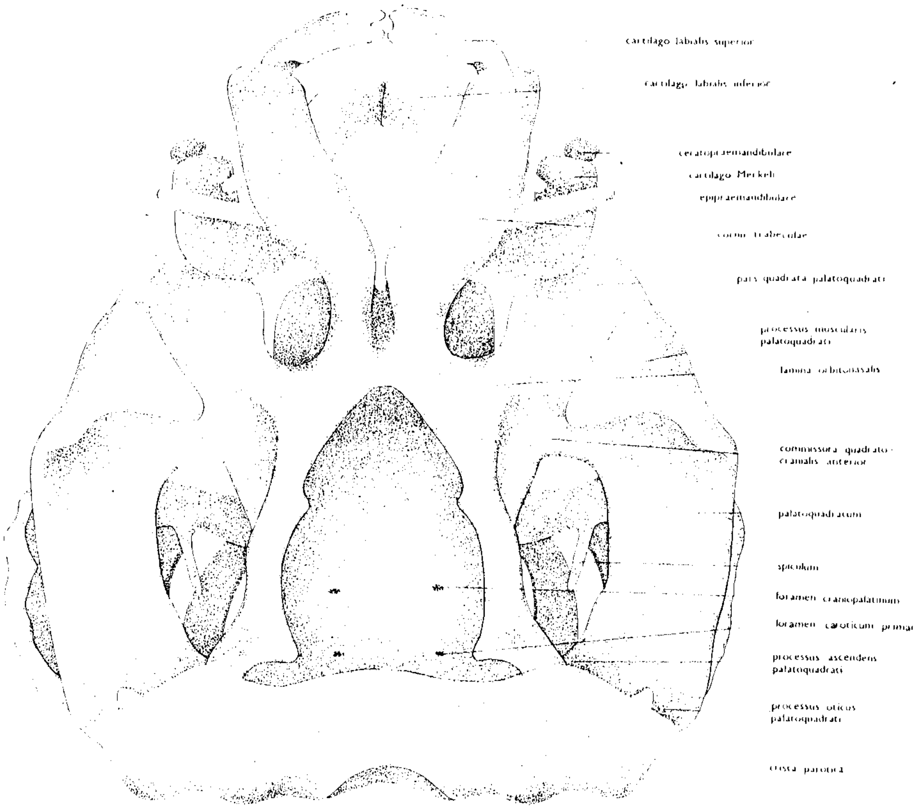


Fig. 14. Endocranium of a *Pelobates fuscus* tadpole before metamorphosis (stage 55—57) in dorsal aspect.

crista frontoparietalis nor *crista frontoparietalis posterior* are formed yet, because the process of dermal ossification in the area of the future frontoparietal is not started yet. For the same reason also ridges for the attachment of parasphenoid on the ventral surface of the braincase are not formed yet.

The floor of the braincase in the otic region is slightly convex dorsally; this convexity manifests the course of notochordal canal within the floor. However, this canal considerably narrows in the anterior direction, and in the investigated ontogenetic stage it reaches approximately the level of the posterior margins of the *foramen acusticum.*

The *foramen jugulare, condyli occipitales* and *foramen magnum* are developed in their definite shape, but the *foramen magnum* is comparatively larger than that in adults. The junction of the skull with the first vertebra by means of the so far incompletely developed *condyli occipitales* is syndesmotic, and hence in this developmental stage is only of restrained mobility.

Also the braincase in the orbitotemporal region is already finished in its basic features, although some typical larval characters are still retained which are remodelled in the next stages of ontogeny. The following features conform with those in adults: complete formation of the floor and lateral walls of the braincase, and the formation of the roof in the most anterior section of the braincase. However, larval characters still prevail: the lateral walls of the braincase are separated from the otic capsule by a narrow fissure which for descriptive purposes is interpretable in two ways. Either the whole fissure is considered the *foramen prooticum* where the dorsal cartilaginous partition against *fenestra frontoparietalis* called the *taenia tecti marginalis* is lacking (remarkably, this partition is present e. g. in *Rana*; DE JONGH, 1968, tab. V, VII). Or it is possible to designate as the *foramen prooticum* only the distinct extension of this fissure through which the *ganglion trigeminofaciale* runs. The second interpretation is more convenient, because it takes into account the final situation in adults. In this case, the whole slot may be designated as the *fissura prootica*. It should be mentioned that in the specimen investigated, the *ganglion trigeminofaciale* ran out above the *processus ascendens palatoquadrati* on one side of the skull, while below it on the opposite side. Thus the oticooccipital and orbitotemporal divisions of the skull are connected with each other only by the braincase floor and the *processus oticus*. Regarding the fact that dermal bones are not developed yet in this ontogenetic stage, it is possible to suppose a limited flexibility of the skull owing to the mentioned elastic cartilaginous connections.

The floor of the braincase is rather thin along the mid-line, while it is rather thickened along its attachment to the lateral walls. Hence the outer surface of the braincase lateroventrally bears rounded but distinct ridges which represent remnants of *trabeculae cranii*. Anteriorly, each trabecula is attached to the *lamina orbitonasalis* and *commissura quadrato-cranialis anterior*.

There are several openings in the floor and lateral walls. In the lateral wall there is the *foramen opticum*, situated below the anterior end of *processus ascendens palatoquadrati*. Similarly but rather more posteriorly situated is the *foramen oculomotorii*. Two paires of tiny openings which are lacking in adults occur in the braincase floor. The anterior one situated at the level of anterior margins of the *foramina optica* are called the *foramina craniopalatina*. The second pair situated rather posterior to the level of *foramina oculomotorii* are called the *foramina carotica primaria*. The general shape of the *fenestra frontoparietalis* is almost identical to that found in adult.

While the proportional relations of otic and orbitotemporal regions are identical in the tadpoles before metamorphosis and in adults, and also their fundamental morphological arrangement is identical or similar, the porportionality and the structure of the ethmoidal region is quite different in both ontogenetic stages mentioned. Two strong, rod-like structures called the *cornua trabeculae* (see also BORN, 1876: 600) run anteriorly from the anterior part of the braincase. In their sections adjacent to this attachment they are mediolaterally flattened, directed anterodorsally, and they slightly converge. Besides, their lower edges are connected by a horizontal stripe of cartilage, so that the whole is U-shaped in cross-section. In the area of attachment

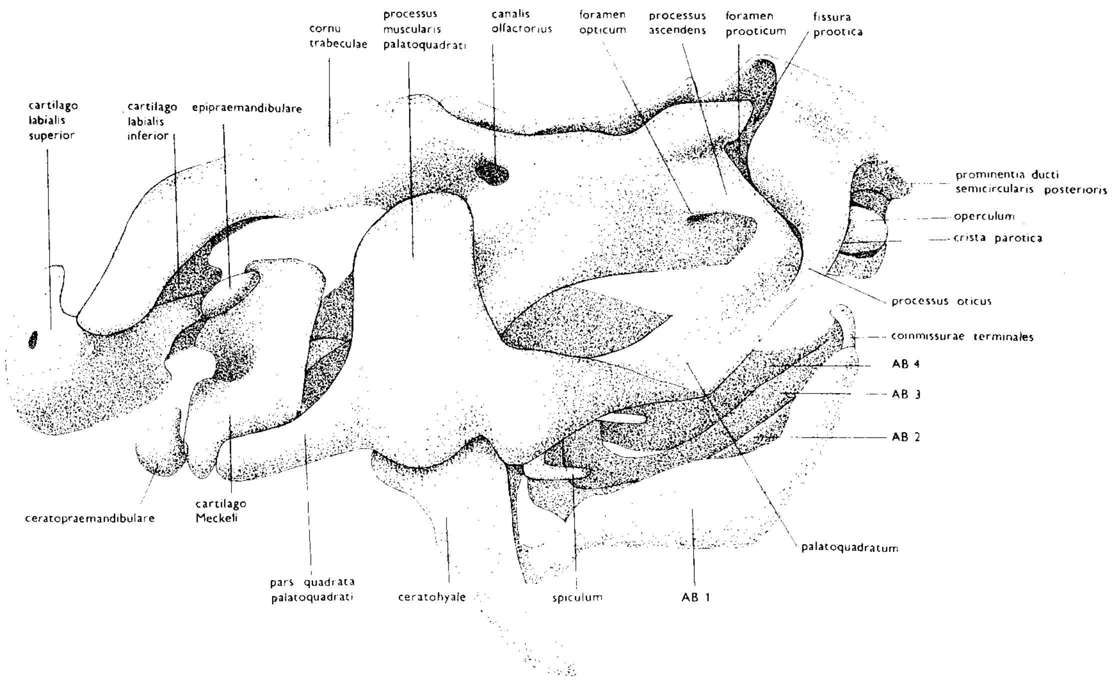


Fig. 15. Endocranium of a *Pelobates fuscus* tadpole before metamorphosis (stage 55—57) in lateral view. AB - *arcus branchialis.*

]

of *cornua trabeculae* to the braincase, the braincase wall is pierced by the *canales olfactorii* closely lateral to the cornua*). Between both bases of the *cornua trabeculae* in the mid-line there is another opening which is larger, unpaired and anteriorly directed. The anterodorsal and slightly convergent course of both cornua close to their base is suddenly changed, so that their next course is slightly divergent in dorsal aspect, and horizontal in lateral aspect. Also the medio-lateral flattening converts into a dorso-ventral one. In their distal, i. e. anterior-most sections, the morphology of both cornua is influenced by quasi torsion along their long axis, resulting in that their dorsal surface is slanted laterodorsally and the ventral surface medioventrally. *Cartilagines labiales superiores* are adjoined ventrally to their anterolateral margins, this representing an articulation of the upper part of the larval jaw apparatus. The whole length of both *cornua trabeculae* approximately in this stage of ontogenetic development equals the lengths of the orbitotemporal, otic and occipital regions altogether.

The visceral endocranium of the tadpole before metamorphosis (figs 15, 16) is composed of hyobranchial apparatus, palatoquadrate, and several cartilaginous elements representing larval jaws or taking part in their function. Of the mentioned elements only the palatoquadrate is firmly attached to the neural endocranium; the other ones are connected with the neurocranium through the palatoquadrate. *Cartilagines labiales superiores* and *inferiores***)have the fuction of larval jaws. The *cartilago labialis superior* forms together with the opposite element an arch-like structure which is sharply edged ventrally, while dorsally it is thickened and rounded; this arch is interrupted in the mid-line. According to De Jongh (1968: 9) the *cartilago labialis superior* is an unpaired element in early stages of ontogeny in *Rana temporaria,* and it desintegrates in the further course of ontogeny into the right and left halves. However, in the case of *Pelobates fuscus* Plasota (1974: 113, 120) always mentions this cartilage as a paired structure. The posterior end of this cartilage gives out two processes: the bigger and in its distal section rather laterally directed *processus superior,* and the small *processus inferior*. Both these processes do not articulate with any other viscerocranial element; they serve as attaching areas for the *adductor mandibulae posterior* muscle complex (Luther, 1914, fig. 69). The only articulation exists with the *cornu trabeculae*. According to Plasota (1974: 120) the *cartilago labialis superior* arises embryonally from the most anterior part of the *cornu trabeculae*. The ventral edge of this labial cartilage is completed by a similarly acute horny sheath which serves for biting.

Also the *cartilago labialis inferior* is a paired structure in this developmental stage, and serves together with both Meckel's elements as lower jaws. It is more robust in comparison with the upper labial cartilage. The horny layer covers the entire

---

*) The different position of these openings in *Ascaphus* and *Rana* led Van Eeden (1951: 115) to express certain doubts concerning the homology of these openings in different frog groups.

**) It is more convenient to prefer these terms to the terms »*suprarostralia*« and »*infrarostralia*« because the bases of the latter names have already been used for designation of dermal bones.

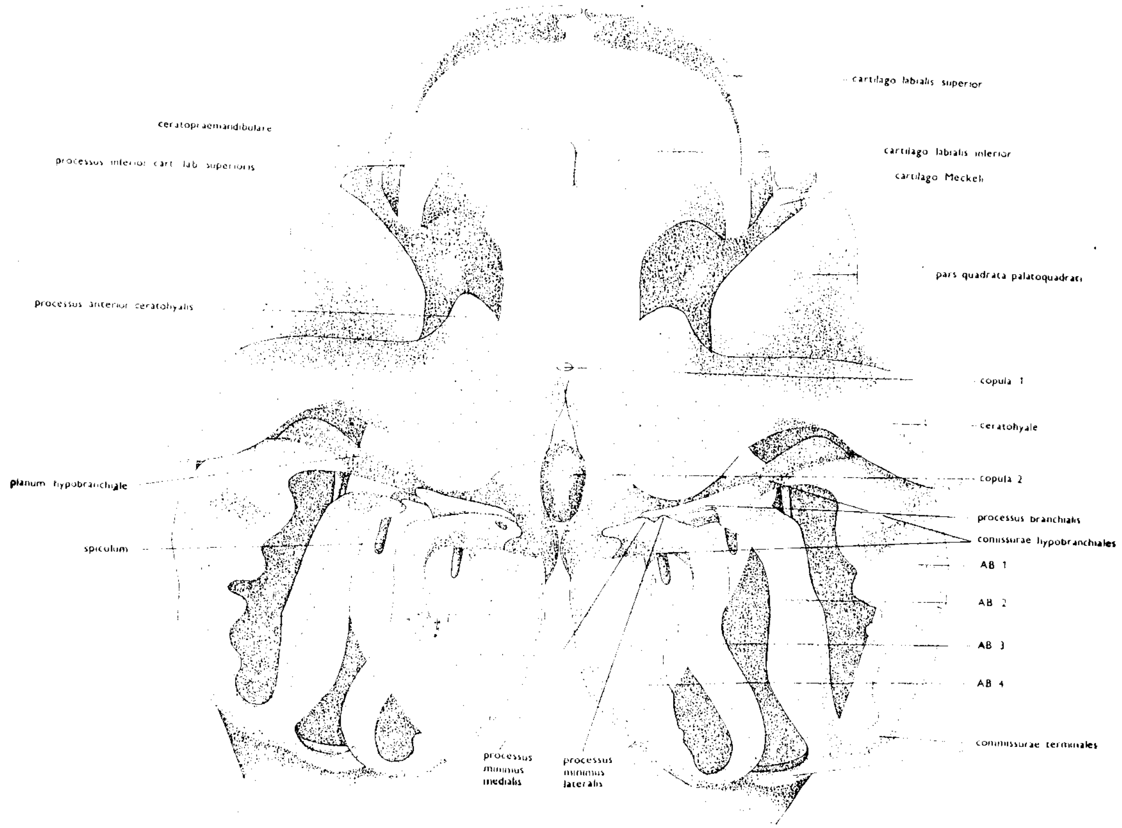


Fig. 16. Endocranium of a *Pelobates fuscus* tadpole before metamorphosis (stage 55—57) in ventral aspect. AB - *arcus branchialis*.

surface of the cartilage and dorsally it is sharply edged. This horny sheath crosses the median suture without any interruption. The *cartilago labialis inferior* gives out posteriorly three processes: the dorsolateral margin of the cartilage is terminated by a posteriorly directed *processus dorsolateralis*; rather ventrally is situated the *processus medius*, and in the lowest position there is a process which continuously passes into the cartilage of Meckel's element. This connection would be homologized with the *commissura intramandibularis* (sensu SEDRA, 1950). The *processus medius* is directed against the anterior termination of the dorsal edge of Meckel's element, and it is either in contact with it or is separated from it. The *processus dorsolateralis* is directed entirely beyond Meckel's element. DE JONGH (1968: 10) described a similar connection between the *cartilago labialis inferior* and Meckel's element in *Rana temporaria* where, however, an immovable commissura is situated dorsally, while the ventral process only fits into the pit in the Meckel's element, a situation which theoretically allows a movement. However, concerning the present stage of knowledge on individual and ontogenetic variation in this respect it is better not to emphasize the differences described.

According to PLASOTA (1974: 120) the *cartilago labialis inferior* arises in the course of embryogeny from the most anterior tips of Meckel's element.

Two small paired cartilages situated approximately at the level of the anterior margin of Meckel's element are of some interest. The dorsal one of them is a rod-like element either situated in the position of a posterolateral continuation of the *processus superior cartilaginis labialis superioris*, or adjoining this process perpendicularly, approximately in the middle of its length. The latter case confirms the presupposition that it is an element which is quite independent from *cartilago labialis superior*. If it is mentioned in literature, it is called adrostral (BORN, 1876: 599; SCHULTZE, 1892: 7). This element is lacking in *Rana esculenta* (BORN, op. cit.: 604); it seems that its presence is an archaic character. The second of these cartilages is ovoid-shaped and closely adjoins Meckel's element. It corresponds by its position to the cartilage which is designated by PLASOTA (1974: 113, fig. 18—23) as »x«. According to that autthor (op. cit.: 113) it seems that it arises from the posterior section of *cartilago labialis superior*.

Meckel's element is a rather robust structure, situated transversally. Part of its posterior surface is convex and this convexity makes contact with the anterodorsal surface of the palatoquadrate. This articulation represents the future jaw joint. The lateral part of the element is terminated by the *processus lateralis dorsalis* directed dorsally, and by the similar *processus lateralis ventralis* directed ventrally. The medial half of the element gives out anteriorly the rather large *processus anterior* which is a continuation of the *commissura intramandibularis*. As the lateral part of the element also rather protrudes anteriorly, the anterior surface of Meckel's element is distinctly concave, if viewed dorsally or ventrally.

Ceratohyal is in its general features of the similar shape as Meckel's element. Also its lateral half runs out both dorsally and ventrally giving out two processes.

The *processus lateralis dorsalis* fits into the concavity on the ventral surface of the palatoquadrate at the level of its *processus muscularis*. The *processus lateralis ventralis* (seu *processus lateralis* sensu KOTHE, 1910: 35) is directed in its distal section lateroventrally. The medial half of the ceratohyal gives out the large *processus anterior* which is in contact with Meckel's element, while the *processus posterior* fits into the short but deep groove on the dorsal surface of the anterior part of the hypobranchial plate. Medially, the convex margins of both opposite ceratohyals approach each other, but they do not fuse. The long axis of each ceratohyal is directed lateroventrally, thus similarly as in the case of Meckel's element.

Also the hypobranchial plate (»Hypobranchialplatte« sensu STADTMÜLLER, 1936: 678; seu *planum hypobranchiale* sensu GAUPP, 1905) is reminiscent of both ceratohyal and Meckel's element by its transversal position and long axis directed lateroventrally. Also in this case the lateral part of this structure gives out the *processus lateralis ventralis* to which the first posthyoid arch is firmly attached. In contrast to this, the *processus lateralis dorsalis* is only poorly developed. The *processus anterior* is represented by a convexity situated medially to the groove, for affixing of the *processus posterior ceratohyalis. Processus posterior* is fairly well developed and is terminated by a *spiculum* directed posteriorwards. Ventrally, thus approximately at a right angle, the fourth posthyoid arch is attached to the *processus posterior* by the weak cartilaginous bridge. Medially, both hypobranchial plates are in contact, although they are not fused as it is the case with *Rana* (cf. e. g. DE JONGH, 1968: 11).

In contrary to the preceding structures the posthyoid branchial arches (see also SCHULTZE, 1892: 9—13) are directed posterolaterally*). They have the forms of cartilaginous arches which are convex ventrally along their long axis. The second and third of them are rather narrow, thin and flat posteriorly, while thick and triangular in cross-section anteriorly. In contrary, both medial and lateral-most arches are wide, convex ventrally and concave dorsally in cross-section. All the four arches are attached anteriorly to the hypobranchial plate by thin bridges called the *commissurae hypobranchiales*. Hypobranchial commissures come to the hypobranchial plate ventrally, thus perpendicularly to the main plane of this plate. Both second and third posthyoid arches bear in their anterior section one small process called the *processus branchialis* (sensu SCHULTZE, 1892: 11), directed medially. Moreover, on the anterior edge of the *processus branchialis* of *arcus branchialis III* there are two tiny but ever-present processes - the *processus minimus lateralis* and *medialis* (fig. 16). The *processus branchialis* of branchial arch II adjoins these *processus minimi* of branchial arch III, thus perclosing a space between them in a short canal. On the opposite side of the skull the *processus minimi* also occur, but their tips are connected with each other by a thin cartilaginous bridge, which results in the formation of a similar canal. The *processus branchialis* of *arcus branchialis II* did not adjoin the *processus*

---

*) It should be mentioned that the position and the mode of attachment of posthyoid arches are given erroneously in PLASOTA's paper (1974, figs 20, 23).

minimi of *arcus branchialis III* in this case. In *Rana,* the *processus branchialis* of *arcus branchialis II* forms a firm cartilaginous bridge with *arcus branchialis III,* which is called by GAUPP the *processus interbranchialis* (cf. situation in the tadpole in the last stages of metamorphosis). Posteriorly, all four branchial arches are connected with each other by flat *commissurae terminales* which considerably vary in shape. From the commissure between the third and fourth arch, one more or less distinct outgrowth can run out dorsally or dorsolaterally into the space below *crista prootica.* Relatively long and thin processes called the *spicula* run out posteromedially from the area where the hypobranchial plate is connected with the *commissurae hypobranchiales.*

The only unpaired elements of the viscerocranium are the *copulae. Copula* 2 (sensu GAUPP, basihyoid sensu SCHULTZE 1892: 9) is an oval-shaped structure with a longitudinally situated ridge on its ventral surface, while flattened dorsally. It is situated in the mid-line in the space between the *processus posteriores* of both ceratohyals. By its anterior part it makes contact with the medial margins of both ceratohyals, however, it does not fuse either with them or with hypobranchial plates (cf. situation in *Rana temporaria*; DE JONGH, 1968: 11). *Copula* 1 is a tiny cartilage, owing to its size perceptible only on histological cross-sections. It is situated within the soft tissue between the bases of the *processus anteriores* of both ceratohyals.

The last element belonging to the visceral endocranium is the palatoquadrate. This is a big, dorsoventrally flattened stripe of cartilage, which is situated at the level of the braincase floor, extended from the otic capsule posteriorly, up to Meckel's element anteriorly. At the boundary between the anterior and middle thirds of its length its lateral margin gives out the conspicuous *processus muscularis.* This big and flat outgrowth is directed dorsally, and in its distal section also rather medially. It is terminated by a rounded tip. The palatoquadrate is the only element of the visceral endocranium which is firmly fixed to the neural endocranium. Anteriorly, at the level of the *processus muscularis* it is connected with the neurocranium by the *commissura quadrato-cranialis anterior.* This commissure is attached not only to the braincase, but also to the horizontal and antero-posteriorly flattened stripe of cartilage called the *lamina orbitonasalis,* which is also attached to the braincase below the *canalis olfactorius.* In its posterior part, the *commissura quadrato-cranialis anterior* is attached to the rudiment of *trabecula cranii. Lamina orbitonasalis,* adjacent parts of the braincase, and the rudimentary *trabecula cranii* border a distinct triangular depression.

The posterior part of the palatoquadrate is firmly connected with the lateral walls of the braincase, as well as with the otic capsule. Its posteromedial end gives out the *processus ascendens* which is flat close to its base, while oval in cross-section in its distal section. It runs medially to the braincase wall where it turns anteriorly. Thus it forms an arch lying along the dorsomedially slanting plane whose outer surface closely approaches the anterior surface of otic capsule, but it is not attached to it. It is attached to the lateral wall of the braincase above the level of the *foramen opticum,* *minimi* of *arcus branchialis III* in this case. In *Rana,* the *processus branchialis* of *arcus branchialis II* forms a firm cartilaginous bridge with *arcus branchialis III,* which is called by GAUPP the *processus interbranchialis* (cf. situation in the tadpole in the last stages of metamorphosis). Posteriorly, all four branchial arches are connected with each other by flat *commissurae terminales* which considerably vary in shape. From the commissure between the third and fourth arch, one more or less distinct outgrowth can run out dorsally or dorsolaterally into the space below *crista prootica.* Relatively long and thin processes called the *spicula* run out posteromedially from the area where the hypobranchial plate is connected with the *commissurae hypobranchiales.*

The only unpaired elements of the viscerocranium are the *copulae. Copula* 2 (sensu GAUPP, basihyoid sensu SCHULTZE 1892: 9) is an oval-shaped structure with a longitudinally situated ridge on its ventral surface, while flattened dorsally. It is situated in the mid-line in the space between the *processus posteriores* of both ceratohyals. By its anterior part it makes contact with the medial margins of both ceratohyals, however, it does not fuse either with them or with hypobranchial plates (cf. situation in *Rana temporaria*; DE JONGH, 1968: 11). *Copula* 1 is a tiny cartilage, owing to its size perceptible only on histological cross-sections. It is situated within the soft tissue between the bases of the *processus anteriores* of both ceratohyals.

The last element belonging to the visceral endocranium is the palatoquadrate. This is a big, dorsoventrally flattened stripe of cartilage, which is situated at the level of the braincase floor, extended from the otic capsule posteriorly, up to Meckel's element anteriorly. At the boundary between the anterior and middle thirds of its length its lateral margin gives out the conspicuous *processus muscularis.* This big and flat outgrowth is directed dorsally, and in its distal section also rather medially. It is terminated by a rounded tip. The palatoquadrate is the only element of the visceral endocranium which is firmly fixed to the neural endocranium. Anteriorly, at the level of the *processus muscularis* it is connected with the neurocranium by the *commissura quadrato-cranialis anterior.* This commissure is attached not only to the braincase, but also to the horizontal and antero-posteriorly flattened stripe of cartilage called the *lamina orbitonasalis,* which is also attached to the braincase below the *canalis olfactorius.* In its posterior part, the *commissura quadrato-cranialis anterior* is attached to the rudiment of *trabecula cranii. Lamina orbitonasalis,* adjacent parts of the braincase, and the rudimentary *trabecula cranii* border a distinct triangular depression.

The posterior part of the palatoquadrate is firmly connected with the lateral walls of the braincase, as well as with the otic capsule. Its posteromedial end gives out the *processus ascendens* which is flat close to its base, while oval in cross-section in its distal section. It runs medially to the braincase wall where it turns anteriorly. Thus it forms an arch lying along the dorsomedially slanting plane whose outer surface closely approaches the anterior surface of otic capsule, but it is not attached to it. It is attached to the lateral wall of the braincase above the level of the *foramen opticum,* not to the rudimentary *trabecula cranii* (i. e. at the level of braincase floor) as it is the case with e. g. *Rana temporaria* (DE JONGH, 1968: 9).

The posterior section of the palatoquadrate in its lateral part gives out the *processus oticus* directed posterodorsally, which is attached to the anterior end of the *crista parotica*. According to PLASOTA (1974: 129) this process disappears during metamorphosis and a quite new outgrowth of the same function arises in this place. To emphasize that the two structures are not homologues the mentioned author used the terms *processus oticus larvalis* and *processus oticus adulti*.

The deep notch between the *processus ascendens* and the *processus oticus* is called the *incisura posterior palatoquadrati*.

With the palatoquadrate, both Meckel's element and the ceratohyal articulate. Meckel's element adjoins by its posterior convex surface the anteromedially slanting part of the palatoquadrate, called the *pars quadrata*. The articulation between palatoquadrate and ceratohyal is more complicated in structure. On the ventral surface of palatoquadrate at the level of the *processus muscularis* there is a distinct, transversally situated groove in which the *processus lateralis dorsalis* of the ceratohyal, correspondingly elongated medio-laterally, fits as an articular head.

Thus, the visceral endocranium is fixed to the neurocranium at four points, three of them being synchondroses - the *processus oticus palatoquadrati*, the *processus ascendens palatoquadrati*, and the *commissura quadrato-cranialis anterior*. The only movable connection is the articulation of *cartilago labialis superior* with *cornu trabeculae*.

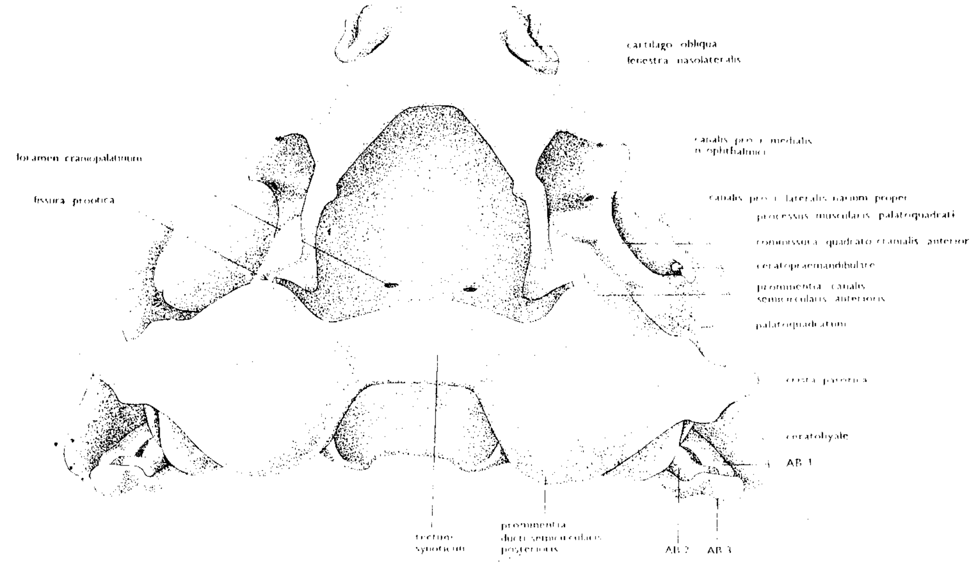


Fig. 17. Endocranium of a *Pelobates fuscus* tadpole in final stages of metamorphosis (stage 64) in dorsal aspect. AB - *arcus branchialis*.

During the metamorphosis (figs 17—19), the endocranium is fundamentally changed. These changes are characterized by a reduction or complete disappearance of some structures, the appearence of quite new structures, and by topographical modifications.

Both otic and occipital regions are changed only very slightly, as in their general features they were already earlier identical with those in adults. A persisting larval feature is e. g. considerably short *tectum synoticum*. In contrast to this both otic capsules are more elongated antero-posteriorly in comparison with earlier ontogenetic stages. The *fenestra ovalis* moved from its originally lateral to the posterolateral position, and also increased in its relative size. In connection with this, the *operculum* also increased in size. On the anterior margin of the *operculum* the *pars interna plectri* is perceptible, which probably arises during this stage of ontogeny (cf. Plasota, 1974: 119). Some parts of the otic and occipital regions start to ossify and in fact they represent the first ossification centres appeared on the whole endocranium. These are especially the anteroventral walls of the otic capsules (ossification centre of *prooticum)*, and small areas of their bases closely anterior to the occipital condyls (ossification centre of lateral occipital). All other parts of the

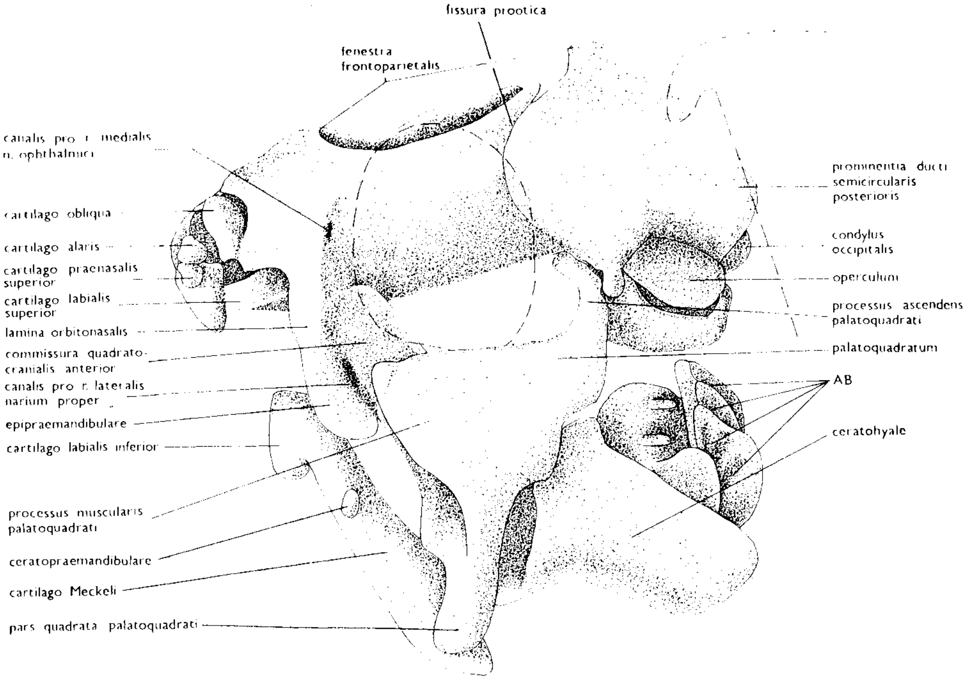


Fig. 18. Endocranium of a *Pelobates fuscus* tadpole in final stages of metamorphosis (stage 64) in lateral aspect. AB - *arcus branchialis*. The scleral capsule and the anterior part of scapula are indicated by a broken line.

endocranium still remain cartilaginous and/or membranous, despite the advanced ossification of vertebrae. At this stage, the dermal bones start to ossify in the tissue resting on the surface of endocranium, but this fact does not yet influence its morphological details. Both *crista frontoparietalis* and *crista frontoparietalis posterior* arise later in connection with the more advanced developmental stages of dermal bones.

The *foramen acusticum* may already be divided at this stage by the thin, membranous partition into the anterior and posterior parts, as it is the case with the specimen investigated. Other openings in the otic capsule are formed in the same way as in adults. The only difference is that the *foramen magnum* is still considerably large as to its proportional relations to various parts of the otic region. In contrary to earlier stages, the occipital condyls are well developed so that the craniovertebral junction becomes movable.

In comparison with the adult, the braincase in the orbitotemporal region is still comparatively short and wide. The essential part of its lateral walls is membranous, thus forming large prootic fontanelle which is pierced by the *nervus opticus* and by other nerves (see description of adult specimen, p. 23). In earlier stages these lateral walls were completely cartilaginous and considerably thick, and the *processus ascendens palatoquadrati* was attached to them. During the metamorphosis the distal part of this process is gradually moved dorsally up to the upper margin of this wall,

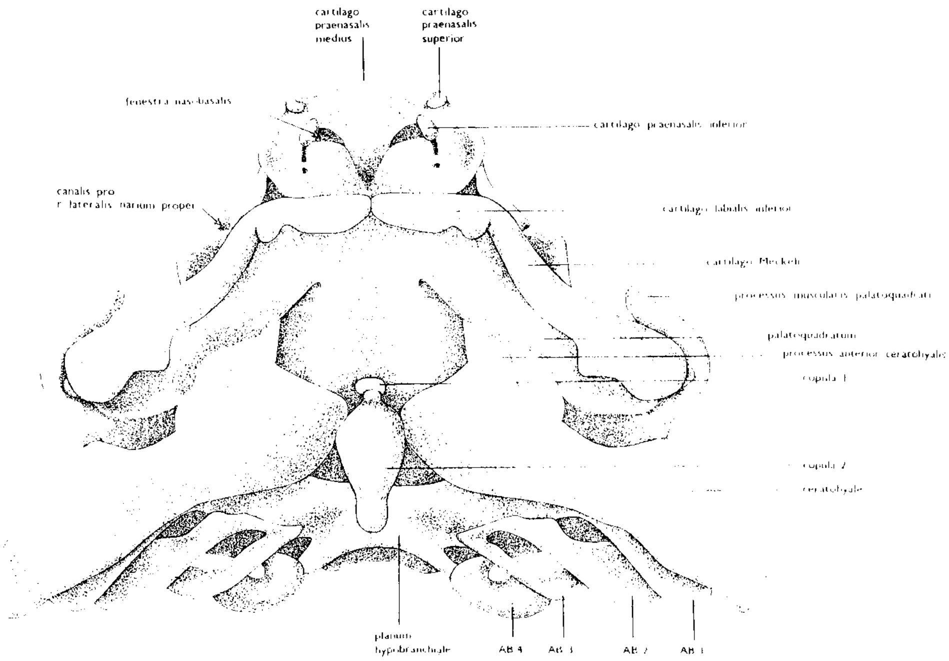


Fig. 19. Endocranium of a *Pelobates fuscus* tadpole in final stages of metamorphosis (stage 64) in ventral aspect. AB - *arcus branchialis*.

it becomes slender, and finally its remnant is represented by a ridge serving for fixation of the frontoparietal bone. Regarding these topographical changes, the origin of the prootic fontanelle is not due to the reduction of the originally cartilaginous walls into membranous ones, but due to the movement of the *processus ascendens* dorsally and the subsequent extension of the originally small area for passing of *n. opticus*.

Remarkably, the *fissura prootica* is very distinct also in the last stages of metamorphosis. In the middle of its length it is extended into the *foramen prooticum*. Anteriorly, this extension is covered by tissue thus forming the prootic fontanelle described above. Anterior to the *fissura prootica,* the margin of *fenestra frontoparietalis* gives out a small, posteriorly directed outgrowth which is preserved also in adults (figs 1, 17). It is possible to ascertain after it the original position of *fissura prootica,* even though it is closed in adults. Another landmark which can serve for ascertainment of the original position of the *fissura prootica* is the *recessus prooticus* which is probably its remnant on the inner surface of the braincase in the adult.

The floor of the braincase is only membranous at the level of both prootic fissures. Consequently, this tissue serves as the only connection between anterior part of the neural endocranium and its oticooccipital part in the metamorphosing tadpole. In earlier stages, this part is rather thicker (similarly to the lateral braincase walls), because the notochordal canal reaches up to this level. The flexibility of the neural endocranium is prevented by the palatoquadrate, as well as the arising frontoparietal and parasphenoid. Anterior to the mentioned membranous area the braincase floor is formed by a thin cartilaginous plate which laterally is bent dorsally, thus serving as the lower margins of the prootic fontanelle. This cartilaginous area of the braincase floor is pierced by a pair of openings which according to their relations to the *foramina optica* are to be considered the *foramina carotica primaria. Foramina craniopalatina* disappeared, similarly as is the case with *Rana.* However, in *Ascaphus truei* these openings, as well as *foramina carotica primaria,* persist also in adults (VAN EEDEN, 1951: 112—113). Further in the anterior direction, the braincase floor is formed by gradually thickening cartilage.

The general shape of the *fenestra frontoparietalis* corresponds by its proportions to the shape of the braincase. This means that this opening is comparatively short and wide, with its anterior termination rounded or pointed. It gradually becomes longer in adults.

Fundamental changes occur in the ethmoidal region. First of all, this part of the endocranium is gradually shortened owing to the resorption of *cornua trabeculae.* PLASOTA (1974: 115) followed this process histologically and found a degeneration of chondrocytes in the structures mentioned. He spoke about a general structural disintegration of cartilage which begins within the anterior ends of both cornua (similarly BORN, 1876: 619—620). Between both *cornua trabeculae* new cartilaginous material starts to be formed, which plays a role in the formation of the *septum nasi.* The formation of the *septum nasi* begins posteriorly in those sections of the cornua which are adjacent to their bases*), then progressing in the anterior direction. This results in the obliteration of median opening which was earlier between both cornua. The statement that both cornua do not fuse directly, and that new material arises between them is confirmed by the study of cross-sections (fig. 20; cf. also BORN, 1876: 607) where boundaries between the cartilage of the *cornua trabeculae* and this new material are very distinct. These boundaries disappear during subsequent developmental stages, first posteriorly and later anteriorly. Both *cornua trabeculae* manifest themselves by rounded ridges on the ventral surface of the *solum nasi* which gradually become lower and the indistinct during the later stages of ontogeny. The newly arisen cartilage between both *cornua trabeculae* expands anteriorly, finally reaching over their reduced ends, thus forming the *processus praenasalis medius*. In their anterior-most sections the *cornua trabeculae* form only part of the *solum*

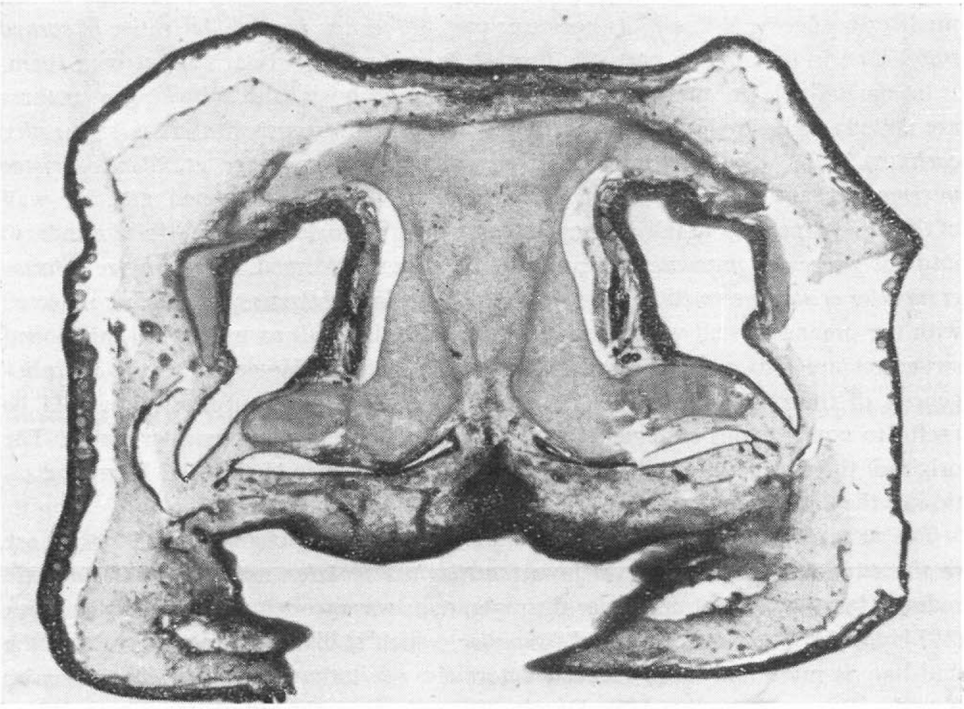


Fig. 20. Cross section through the ethmoidal region of a *Pelobates fuscus* tadpole in final stages of metamorphosis (stage 64). Both *cornua trabeculae* forming ventrolateral parts of *septum nasi* are still distinguishable. The newly formed cartilaginous tissue is enclosed between the mentioned structures.

---

*) VAN EEDEN (1951: 112) found in *Ascaphus truei* that cells released during the disintegration of other parts of the larval ethmoidal region take a part in the formation of the posterior section of the septum.

nasi. Remarkably, the ossification in the area of the future *septum nasi* starts already in the period when both cornua are still detached.

Canales olfactorii maintain a constant position during metamorphosis, i. e. they have an anterolateral course both in tadpoles and adults. Their outer openings to the space of future nasal cavity gradually become covered dorsally by *tectum nasi* which arises by the laterally directed expansion of the dorsolateral margins of the *cornua trabeculae.* Thus the *tectum nasi* is a derivative of the neural endocranium, and starts to appear posteriorly above the *foramen canalis olfactorii,* growing anteriorly during the later ontogeny. While in its posterior part the *tectum nasi* is a derivative of *cornua trabeculae,* in its anterior part it is formed by material newly arisen between them.

In the tadpole in the final stages of metamorphosis, the following structures are already well developed: the *cartilago obliqua, paries nasi* with *crista subnasalis, cartilago alaris, cartilago praenasalis superior, lamina superior et inferior cristae intermediae,* and *divisio praenasalis communis.* The last mentioned anterior wall of the nasal capsule gradually passes (without any histologically perceptible boundary) into the *processus praenasalis medius* which is newly formed. The *laminae inferior et superior cristae intermediae, paries nasi,* and *cartilago obliqua* are similarly connected with the praenasal wall which suggests that both this wall as well as all mentioned structures are also newly formed (cf. BORN, 1876: 632). However, as the morphogenesis of the ethmoidal region is rather fast during metamorphosis it would be useful to confirm this statement by the study of more numerous inter-stages. The origin of these structures will be discussed in detail later in chap. 4.1.3 Homologization of the endocranium.

The visceral endocranium also undergoes fundamental changes similar to those in the ethmoidal region. Larval jaws (*cartilagines labiales superior et inferior*) are reduced but they do not disappear throughout, as was erroneously stated by PLASOTA (1974: 115)*). The *cartilago labialis superior,* which is divided into two parts in the mid-line, is more and more reduced anteriorly, similarly to both *cornua trabeculae* (see also PLASOTA op. cit.: 115). Despite this reduction, the remnants of both halves maintain a constant position in relation to both anterior ends of the *cornua trabeculae* (these too being reduced). It is possible to see a distinct boundary between the remnants of *cartilago labialis superior* and *cornu trabeculae* still during the last stages of metamorphosis. Both structures fuse together in the course of subsequent development, thus giving origin to the *cartilago praenasalis inferior* (fig. 21; see also STADTMÜLLER, 1936: 551, fig. 410/III, IV). The hook-like termination of the cartilage becomes more distinct during metamorphosis, when this cartilage achieves the typical shape of the *cartilago praenasalis inferior.* The shape of the termination is caused by a posteriorly directed process which represents without any doubts a homologue of the *processus inferior cartilaginis labialis superioris.* It is possible to follow the course

---

*) Also VAN EEDEN (1951: 112) believed that *cartilago labialis superior* completely disappears during the metamorphosis in *Ascaphus truei.*

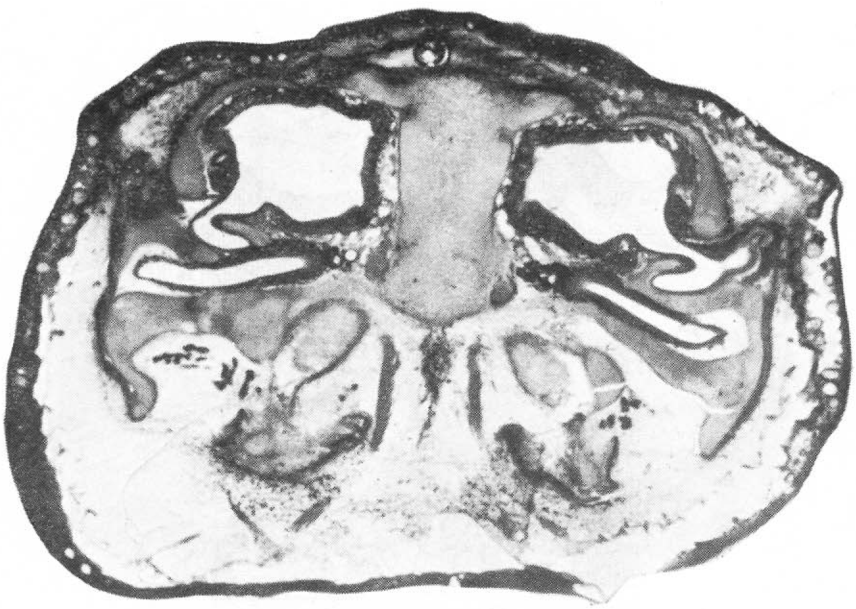


Fig. 21. Cross section through the ethmoidal region of a *Pelobates fuscus* tadpole in final stages of metamorphosis (stage 64), at the level of the bases of future *cartilagines praenasales inferiores*. Structures which are original to them (*cartilagines labiales superiores*) are still separated from the future *solum nasi*.

of these morphological changes also in figures 21, 22 and 24 given in the paper by PLASOTA (1974). Initially, the *cartilago praenasalis inferior* is situated far posterior to the level of the *processus praenasalis medius,* and only in the course of further development does it move to the level of the anterior tip of the *processus praenasalis medius,* owing to the disproportional growth of different parts of the ethmoidal region, thus becoming the main support of the arising *pars facialis praemaxillae.*

The *cartilago labialis inferior* is also preserved and its resorption is even retarded in comparison with the upper labial cartilage. This means that if e.g. the *cartilago labialis superior* is completely converted into *cartilago praenasalis inferior,* the *cartilago labialis inferior* still maintains its typical shape found in the tadpole. If viewed anteriorly, both lower labial cartilages are widely U-shaped, connected by a distinct syndesmosis in the mid-line. This structure as a whole is connected syndesmotically or synchondrotically by its lateral ends with anterior ends of Meckel's element. Besides this, there is an outgrowth protruding from the surface of this labial cartilage posteriorly below the connection of the *cartilago labialis inferior* with Meckel's element. It is difficult to decide which of the originally three processes occurring on this cartilage in tadpoles before metamorphosis (see p. 40) this may concern. It is possible to state only that the whole labial cartilage has been moved ventrally so that its upper margin approaches the level of the upper margin of Meckel's element. The *cartilago labialis inferior* is further reduced during the course of subsequent

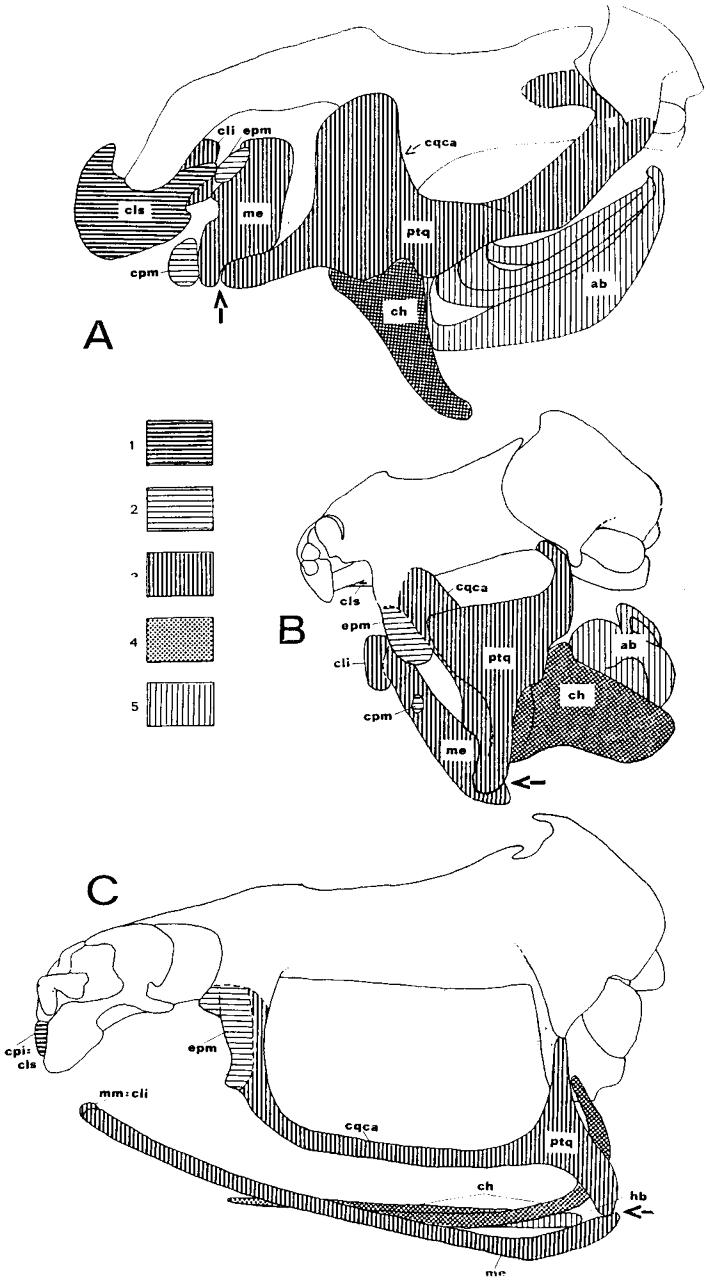


Fig. 22. Sketch showing size and proportional changes of visceral endocranium elements of ***Pelobates fuscus***, lateral aspect. A - tadpole before metamorphosis; B - tadpole in final stages of metamorphosis; C - adult. 1 - pharyngopraemandibular (?); 2 - praemandibular branchial arch; 3 - mandibular arch; 4 - hyoid arch; 5 - posthyoid arches; cls - *cartilago labialis superior*; cli - *cartilago labialis inferior*; epm - epipraemandibular; cpm - ceratopraemandibular; me - Meckel's element; ch - ceratohyal; ptq - palatoquadrate; cqca - *commissura quadrato-cranialis anterior*; ab - posthyoid branchial arches. Positions of jaw joint are indicated by arrows.

development, and finally its remnant is preserved as the mentomandibular, which ossifies in adults.

The cartilage adjoining Meckel's element anterolaterally is reduced during the metamorphosis, and finally it entirely disappears. However, it maintains a constant position lateral to Meckel's element during the whole course of its existence. The dorsal element which was in close topographical relation with the *cartilago labialis superior* becomes attached to *lamina orbitonasalis,* owing to changes caused by a shortening and moving of the palatoquadrate. In the tadpole undergoing the final stages of metamorphosis this element is still morphologically well distinguishable, as it forms a lateral extension of the postnasal wall, lateral to the *canalis pro ramus lateralis narium proper*. This canal arises by a closing of the mentioned nerve between the cartilaginous element in question and the *lamina orbitonasalis*. The part arisen in such a way is called the *processus antorbitalis* in the endocranium of an adult.

Meckel's element which gradually becomes the main endocranial support of the lower jaw, maintains its articulation with the *pars quadrata palatoquadrati*. Owing to the positional changes of the whole palatoquadrate (see below), however, this mandibular joint gradually moves posteriorly up to the level of the otic region (fig. 22). In connection with this, Meckel's element is transformed from an originally robust and transversally situated structure into a slender, rod-like one, to whose anterior end the *cartilago labialis inferior* remains attached (figs 22, 24). Initially, Meckel's element is straight, not bent arch-like, directed anteromedially from the mandibular joint, and even anterodorsally, if the mouth opening is closed. Only later, due to a further gradual reduction of the *cartilago labialis inferior,* does Meckel's element become bent into its typical arch-like shape. The traces of its original shape are preserved only in its section close to the mandibular joint. However, these features too disappear in the adult.

Ceratohyals remain a dominant part of the hyobranchial skeleton also in the course of metamorphosis. However, they are moved below the otic capsules due to the positional changes of palatoquadrate with which each ceratohyal articulates. Both become reduced later, and finally they are converted into a part of the hyoid. In *Pelobates* this process was sufficiently known already at the beginning of this century (see e.g. KOTHE, 1910). Therefore, it is rather surprising that PLASOTA (1974: 119, figs 23, 25) considers the ceratohyal a completely disappearing structure, which is substituted by newly arisen *cartilago hyoidea.*

It follows from KOTHE's description (1910: 39) that the lateral part of ceratohyal has been bent dorsally in the course of metamorphosis and becomes attached to the otic capsule. This part is transformed into a thin cartilaginous stripe called the *cornu hyale*. The original articulation of the ceratohyal with palatoquadrate is preserved till the final stages of metamorphosis, but in adults it has disappeared. However, attachment between the arising *cornu hyale* and the *pars articularis* of Meckel's element exists transitionally for a short time. On the surface of the *cornu hyale* the place of attachment is emphasized by a small and also temporarily existing outgrowth (KOTHE, 1910, tab. 1/8). That part of the *cornu hyale* which is arisen from the lateral part of the ceratohyal is detached from the hyoid at the conclusion of metamorphosis, and remains merely adjoined to it (see KOTHE, 1910: 43, tab. 1/11-12, 17-18). The mentioned separation of the *cornu hyale,* along with the formation of the *formen nervi hypoglossi,* are the last changes in the endocranium which occur in an otherwise fully metamorphosed individual.

The *processus anterior* and whole medial part of ceratohyal remain preserved as the *processus anterior hyoidei,* which together with the corresponding opposite element border the orifice of the *sinus hyoglossus.*

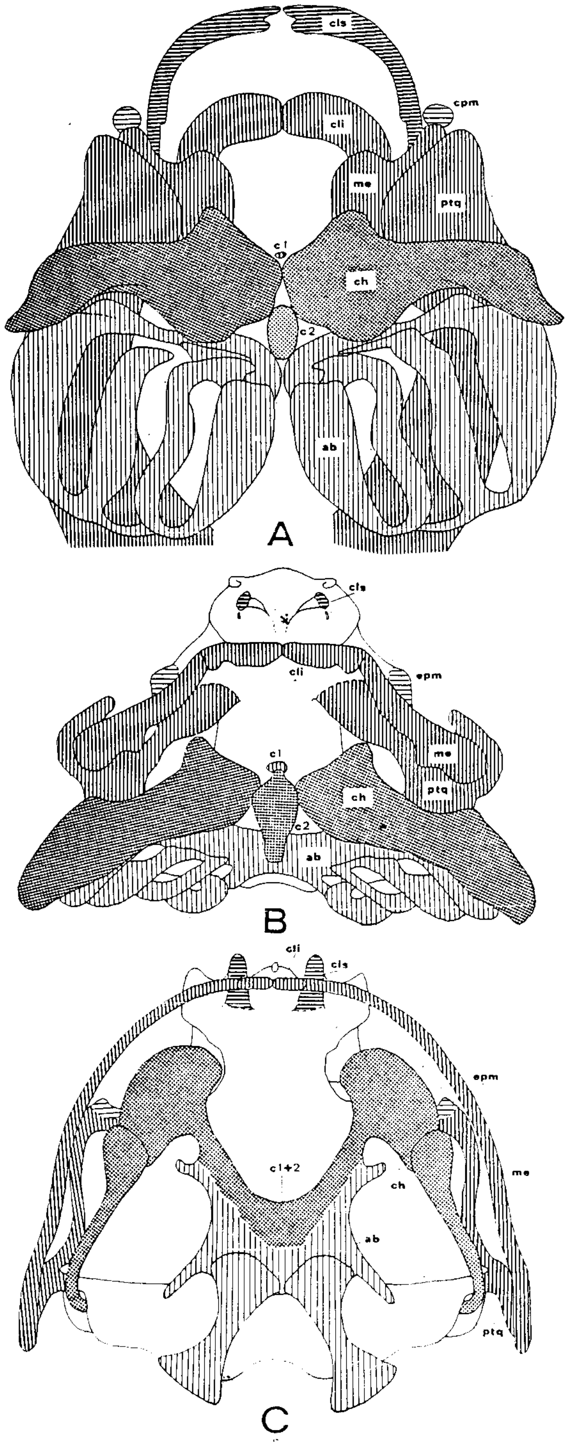
When describing the hyobranchial skeleton earlier authors attach importance to the so-called *pars reuniens* which is a tissue connection of both ceratohyals. Posteriorly, this tissue connection is in contact with the *copula* 2 in the mid-line, anteriorly with *copula* 1. Both copulae move close to each other during the further development, so that *copula* 1 becomes adjoined to the dorsal surface of the anterior outgrowth of *copula* 2. KOTHE (1910, tab. 1/2, 4) did not mention this movement apparently due to the fact that he investigated specimens dissecting them, which necessarily led to the positional changes. Owing to the gradual approach and final fusion of both copulae, the tissue connection called the *pars reuniens* is also gradually reduced and finally disappears. Thus, this tissue does not take part in the origin of *corpus hyoidei.* However, with definite *copula* arisen by fusion of *copula 1* and *2,* the posteromedial margin of the *processus posterior ceratohyalis* fuses and hence this adjacent part of the ceratohyal takes part in the construction of the *corpus hyoidei.*

The ceratohyal originally articulates by its *processus posterior* with the hypobranchial plate situated posteriorly. The course of ontogenetic changes occurring in the area of the hypobranchial plates is as follows: initially, both hypobranchial plates fuse together (at the time when both copulae are adjoined but not yet fused). Then, probably simultaneously, the articulation between the *processus posterior ceratohyalis* and hypobranchial plate becomes immobile and later these elements fuse together, the dorsal margin of the posterior part of the *copula* fuses with the anterior margins of both hypobranchial plates, and the anterior part of *copula* fuses with the posteromedial margin of the ceratohyal. The opening which remains among these elements gradually narrows and finally closes. This results in the formation of the *corpus hyoidei.*

Hypobranchial plates of both sides form after their fusion an unpaired element to which the vestiges of four branchial arches are attached. With the exception of the first of them, the *commissurae hypobranchiales* of all the arches, though much reduced, maintain their dorsoventral course. The anterior margin of the hypobranchial plate gives out anteriorly an indistinct *processus anterior* (which fuses in this area with ceratohyal); lateral to this outgrowth, the mentioned margin is directed

→

Fig. 23. Sketch showing size and proportional changes of visceral endocranium elements of *Pelobates fuscus,* ventral aspect. c 1 - *copula* 1; c 2 - *copula* 2. For other abbreviations see fig. 22.


cls
cpm
cli
me
ptq
c1
ch
c2
ab
A
cls
cli
epm
c1
me
ptq
ch
c2
ab
B
cli
cls
epm
c1+2
me
ch
ab
ptq
C

laterally. The slender lateral part of the hypobranchial plate is completely overlain by ceratohyal ventrolaterally, and the first posthyoid arch is attached to it. There is a distinct posterolaterally directed mound along the posterior margin of the hypobranchial plate. A free, dorsally directed outgrowth is given out from the hypobranchial plate in this area. The *commissura hypobranchialis* of the vestigial *arcus branchialis IV* is attached to it; however, it bends immediately and similarly to commissures of the second and third posthyoid arches it is directed ventrally. From the mentioned thickened posterior margin of the hypobranchial plate arises initially a cartilaginous *processus posteromedialis,* which later ossifies (inclusive of a certain area embedded into the *corpus hyoidei*) into the *os thyreoideum.*

The *commissurae hypobranchiales* of the second and third posthyoid arches run out from the posterolateral margin of hypobranchial plate, which would suggest that the *processus anterolateralis* and the *processus posterolateralis hyoidei* are their remnants. However, both mentioned outgrowths of hyoid apparently form secondarily, as according to KOTHE (1910, tab. 1/5, 6), the margins of hypobranchial plate lack any irregularities at the stage of development when the branchial arches are already preserved as isolated elements.

The vestiges of the posthyoid arches gradually move up to the level of the posterior margin of the otic capsules. It should be mentioned that in the investigated specimen in the final stages of the metamorphosis there was a bridge connecting the second and third posthyoid arches, formed in the area of the attachment of their hypobranchial commissures (cf. the situation in the tadpole before metamorphosis, p. 41-42). Later, the posthyoid arches lose their contact with the hypobranchial plate and also among themselves. They are converted into isolated cartilaginous rods directed posterolaterally, which are gradually resorbed, and finally they entirely disappear.

The palatoquadrate undergoes some modifications during the course of metamorphosis which concern the positional and proportional changes, as well as the mode of its attachment to the otic region of the endocranium (fig. 24). In tadpoles before metamorphosis, the palatoquadrate was formed in its essential part by a dorsoventrally flattened and comparatively wide stripe of cartilage, attached posteriorly to the otic capsule, while having its anterior section attached medially to the braincase. The whole of this structure moves from its originally horizontal position into a vertical position during metamorphosis, which results in a considerable prolongation and slendering of the *commissura quadrato-cranialis anterior*. As that part of the palatoquadrate which gives out the mentioned commissure is moved to below the level of anterior margin of the otic capsule, the cartilaginous stripe which represents the original *commissura quadrato-cranialis anterior* initially has an anterodorsal and rather medial course. The *lamina orbitonasalis* meanwhile increases in size. The essential part of the postnasal wall arises in this way, but moreover also the originally isolated cartilaginous element (*epipraemandibulare,* fig. 22) adjoins laterally, and this later converts into the *processus antorbitalis*. Hence, the *commissura quadrato-*

-*cranialis anterior* which converts into the gradually slendered and prolonged cartilaginous rod is situated approximately in the antero-posterior direction. In the adult it forms a thin support of the lateral wall of the orbit which is called the *pars palatina palatoquadrati* (or, more precisely, the *processus pterygoideus palatoquadrati* and the *processus maxillaris posterior palatoquadrati*). Thus, PLASOTA'S statement (1974: 119) that the *commissura quadrato-cranialis anterior* completely disappears is erroneous. It should be mentioned that in *Ascaphus truei* (VAN EEDEN, 1951: 120, 122) this commissure becomes completely detached from the remnants of *trabeculae cranii* during the metamorphosis, and its anteriorly directed free part is called the *processus pterygoideus*.

Owing to the positional changes of the palatoquadrate the position of its *processus muscularis* is also changed, so that it becomes directed anteriorwards, and partially takes part in the formation of the lateral border of the orbit in metamorphosing tadpole. However, later it gradually resorbs, and finally it completely disappears. Another important modification which is caused by the positional change of the palatoquadrate is the movement of the mandibular joint to below the level of the anterior margins of the otic capsules, which is its definite position. It only moves closer to the otic capsule during the final stages of metamorphosis, which results from the shortening of the vertical part of the palatoquadrate (fig. 22).

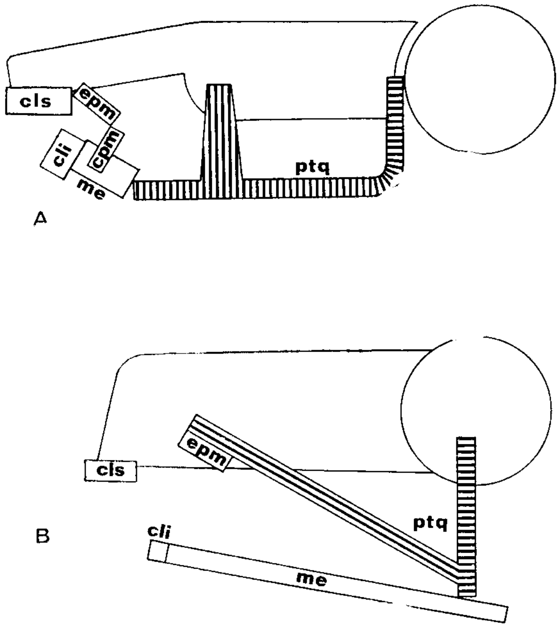


Fig. 24. Diagram to show proportional and positional changes of palatoquadrate during metamorphosis. A - tadpole before metamorphosis; B - adult. For abbreviations see fig. 22.

The original articulation between the palatoquadrate and the ceratohyal, which initially was situated at the level of the *commissura quadrato-cranialis anterior* in such a way that the ceratohyal adjoined the palatoquadrate ventrally, due to the positional changes of the palatoquadrate also moved to the level of the otic capsules. Consequently the ceratohyal adjoins the palatoquadrate posteriorly. However, the two elements lose contact with each other with the gradual decrease in size of the ceratohyal, become separated, and their further development is entirely independent.

Important changes occur in the area of attachment of the palatoquadrate to the otic capsule and adjacent parts of the braincase. The distal part of the *processus ascendens palatoquadrati* which is attached to the braincase separates from the base of this process. PLASOTA (1974: 119, 124) interpreted this change as a complete disappearance of the *processus ascendens.* In adults, synchondrosis arises between the palatoquadrate and the otic capsule in this area, but not between the palatoquadrate and the braincase*). In contrast to the condition in the *processus ascendens,* the originally synchondrotical connection of the palatoquadrate with the otic capsule which is described as the *processus oticus* (seu *processus oticus larvalis*) and which occurs in tadpoles before the metamorphosis is interrupted so that this outgrowth adjoins only syndesmotically the ventral surface of the anterior part of *crista parotica.* Hence it is impossible to agree with PLASOTA (1974: 118, 124, 129) who stated that the *processus oticus* of tadpoles is not homologous with the *processus oticus* of adults. Such an interpretation would be correct only if the mentioned outgrowth completely disappeared, and were substituted by an entirely new structure (cf. the statement of VAN EEDEN, 1951: 121, that there is no discontinuity between the palatoquadrate and the otic capsule in the whole course of metamorphosis in *Ascaphus truei*).

The *pars quadrata palatoquadrati* which at its end point articulates with Meckel's element is moved during further development into the posteroventral and slightly lateral position, and its distal section ossifies into the *os quadratum.*

4.1.3 Homologization of the endocranium

The skeleton of an adult frog is fairly specialized due to adaptation to a specific mode of life, and considerably deviates in its structure from that of its fish ancestor (in this context it is not important whether there was a long or short sequence of intermediate stages manifested by the forms corresponding anatomically and morphologically to some type of stegocephalian). This is also true of the skull. It is quite natural that the extent of the evolutionary changes was more pronounced on the viscerocranium than on the neurocranium, which was associated with the transition

---

*) In *Ascaphus truei* the *processus ascendens* ossifies and its base fuses synostotically with the *prooticum* (VAN EEDEN, 1951: 118, 120).

onto dry land. But homologization of the individual elements of the endocranium, based on a comparison of conditions in adult frogs with those of their osteolepiform ancestors represented by the anatomy of *Eusthenopteron* would not necessarily lead to unequivocal results. For instance, although the ethmoidal region in *Eusthenopteron* and that of an adult frog display numerous homologies (JARVIK, 1942), it is not possible to homologize in the same way the postmandibular division of the viscerocranium, as in adult frogs this underwent radical changes. The homologization of this part of the skull would however be natural and simple if we used a tadpole instead of an adult frog for this purpose, as in the former the viscerocranium is comparatively well developed in its original appearance although having already been modified due to various specializations (SEVERTZOV, 1970: 5). The homologization of the cranial structures of a tadpole with those of an adult frog does not then cause any difficulties. From what has been said above it follows that some parts of the skull which due to specialization considerably deviate structurally from those of archaic osteolepiform ancestors, may be interpreted only with regard to tadpoles. For this reason, in this paper considerable attention is paid to homologization of the skull of a tadpole with that of an adult frog, as well as of the skull of *Eusthenopteron* with that of a tadpole, and of *Eusthenopteron* with that of an adult frog.

The question may be raised why e.g. the ethmoidal region may be homologized by means of a direct comparison between *Eusthenopteron* and an adult frog, but why the homologization of this region cannot be carried out by a direct comparison of *Eusthenopteron* and a tadpole. And inversely, why the major part of the viscerocranium may be interpreted only by a direct comparison between *Eusthenopteron* and a tadpole, but not by directly comparing *Eusthenopteron* with an adult frog. This may be explained by the fact that whereas the tadpole before its metamorphosis represents a relatively early stage of ontogeny, our anatomical knowledge of *Eusthenopteron* concerns only adult invividuals. Thus, in the case of comparison of the ethmoidal region of *Eusthenopteron* and a tadpole, we are incorrectly comparing different ontogenetic stages, in which both structures must necessarily differ. But as tadpoles as well as *Eusthenopteron* are water-dwellers, it is quite natural that, in contrast, their viscerocrania should display consistent features. In some cases it is therefore necessary to compare the corresponding stages of ontogenetic development; in the cases concerning other parts of the skull, this approach is not possible. In this context we have to assume that a larva of *Eusthenopteron* undoubtedly existed which had closer anatomical relations to a frog tadpole than an adult *Eusthenopteron* (in this way we may explain the differences between the structure of the ethmoidal region of a tadpole and that of an adult *Eusthenopteron*) and that this larva, similarly as a tadpole, underwent some anatomical and morphological changes in developing into an adult individual.

However, the homologization of structures is not the definitive aim for the sake of which this comparative study is undertaken. In addition, by comparing homologous structures we may determine the extent and intensity of the changes during phylogeny, and also we may assess the evolutionary distance which frogs covered during their development from their osteolepiform ancestors as well as the trend followed by this evolution.

The criteria of homology were discussed in detail by SZARSKI (1962: 189—191). He regards the following criteria to be principal and fully sufficient for the determination of homology: (1) mutual location; (2) particularities of structure and morphology; (3) connection by intermediate stages. In homologizing the structure of a tadpole with that of an adult frog, only the above-mentioned first and third criteria may mostly be applied, as in these cases the morphologies of the compared elements strongly differ. By investigating the course of the changes during the metamorphosis, i. e. by applying the third criterion, the homologies between these elements may be proved with certainty. The first criterion serves here mostly only for checking the results obtained.

In contrast, in homologizing the structures of frogs with their tadpoles on the one hand, and with *Eusthenopteron* on the other hand, it is not possible to apply the criterion of intermediate stages, as the fossil material which is interpreted by some palaeozoologists as inter-stages of the phylogenetic development of frogs (e. g. *Doleserpeton* and *Triadobatrachus*) is still the object of critical discussion and, in addition, many of their structures necessary for study (especially those of endocranium) have not been preserved. Nevertheless the structural specialization, sometimes attaining astonishing details (e. g. the structure of the ethmoidal region; see JARVIK, 1942) enables the determination of homologues even on the basis of the two above-mentioned criteria only.

Serial homologization is important particularly for the introductory analysis of the conditions of the viscerocranium, as by this means it may be revealed to what extent the branchial arches have been re-shaped in connection with their taking over different functions. But this is complicated by the fact that as early as in *Eusthenopteron* part of the viscerocranium was modified for other purposes, so that the criterion of intermediate stages may be applied only to a limited extent.

4.1.3.a Homologization of the endocranium of a tadpole with that of an adult frog

It has already been stated that the orbitotemporal, otic and occipital regions of the neural endocranium in tadpoles before metamorphosis are in fundamental features developed in the same way as those in adults. The essential differences consist here only in the *fissura prootica* which persists up to very late stages of the metamorphosis and in the proportional relations among mentioned regions. Some of this proportional relations temporarily become even more pronounced during metamorphosis (e. g. the antero-posterior length of the *tectum synoticum* and thus also the size of the *foramen magnum*). In this way the homologization of these regions of the neural endocranium is facilitated. The *fissura prootica* on the endocranium of an adult individual closed and its traces appear as the *recessus prooticus* and *foramen prooticum*. Likewise, the posterior margin of the prootic fontanelle, through which the *nervus opticus* passes together with further important cranial nerves, indicates the course of the previous *fissura prootica*. The position of this previous slot on the margin of the *fenestra frontoparietalis* is indicated by a subtle process directed posteriorly, which was developed as early as in the tadpole. The *fissura prootica* ran closely behind this processus. It is clear that the boundary between the orbitotemporal region and the otic region in frogs may be drawn quite naturally according to the previous *fissura prootica*.

In the ethmoidal region, where the differences between a tadpole and an adult frog are pronounced, things are different. However, on the basis of an analysis of the changes taking place during the metamorphosis, the following conclusions may be drawn: the *septum nasi* is formed in its posterior section partly from the remnants of the *cornua trabeculae*, and partly also from a newly arising cartilaginous mass appearing between both *cornua trabeculae*. But the anterior part of the septum consists exclusively of this newly arisen mass, therefore representing a new developmental formation originating as late as during metamorphosis. This is also true of the *processus praenasalis medius* which is an anterior continuation of the *septum nasi*. In its medial part adjoining the septum the *solum nasi* is also formed of the remainders of the *cornua trabeculae*, and reaches the level of the *fenestra nasobasalis*. The lateral part of the *solum nasi* which participates in forming part of the margins of the *fenestra endochoanalis* also represents a new formation which laterally adjoined the *cornua trabeculae* relatively late during ontogeny. The *cartilago praenasalis inferior* represents a remnant of the considerably reduced *cartilago labialis superior* which however retains its original position in relation to the *cornua trabeculae*. The *tectum nasi* is formed in its posterior part by lateral expansion of the dorsal surface of *cornua trabeculae*; thus in this posterior part it is its derivative. But anteriorly, it arises by the lateral expansion of the newly formed cartilage which constitutes here a septum (see also Born, 1876: 618). At the level of the *processus praenasalis medius*, the *divisio praenasalis communis* developed in the same way; the latter therefore also represents a new developmental formation arising as late as during metamorphosis. It is also in the course of metamorphosis that the *laminae inferior et superior cristae intermediae* come into existence as well as the *paries nasi, cartilago obliqua, cartilago alaris* and *cartilago praenasalis superior*. These results rather differ from the conclusions of Bjerring (1977: 179) who interprets the *lamina nariochoanalis* (which in the present paper is considered to be part of the *lamina inferior cristae intermediae* - see p. 8), the *septum nasi* and the whole medial wall of the nasal capsule as derivatives of the terminal branchial arch. The *cartilago subethmoidalis* originates only after metamorphosis and has no homologue in tadpoles.

The base of the postnasal wall arises from the *lamina orbitonasalis* and partly also from the *commissura quadrato-cranialis anterior* which is adjoined laterally by a cartilage representing a vestige of the dorsal part of the praemandibular arch (*epipraemandibulare*). This formation then give rise to the *processus antorbitalis* (figs 22, 23). The boundary between the part of the postnasal wall originating from the *lamina orbitonasalis* and the part developing from the *epipraemandibulare* is drawn in an adult individual by the cartilage/bone boundary (the *processus antorbitalis* remains cartilaginous) and by the position of the *canalis pro ramus lateralis narium proper*.

The positions of the palatoquadrate of a tadpole and an adult frog seemingly resemble one another. This is due to the fact that in both cases the support of the orbit is the main function of the horizontal part of the palatoquadrate. But these horizontal parts are not homologous. The whole *pars palatina palatoquadrati* of an adult individual represents only a fairly slendered part of the *commissura quadrato-cranialis anterior*. The *pars quadrata palatoquadrati* represents the originally most anterior protruding part of the palatoquadrate. PLASOTA (1974: 125) dealt with the homologization of the *processus oticus*; he maintains that it is only in *Liopelma archei* that the *processus oticus* of a tadpole is homologous with that of an adult individual. According to him, in all the other forms studied inclusive of *Pelobates,* the *processus oticus* in adults appears as late as in the final phase of metamorphosis, whereas the process which was developed in its place in the tadpole disappears throughout (cf. STADTMÜLLER, 1936: 585—586). In order to emphasize that he does not consider these two processes to be homologous, Plasota introduced for them the terms *processus oticus larvalis* and *processus oticus adulti*. But it seems that the *processus oticus* does not disappear during metamorphosis, merely becoming separated from the otic capsule (similarly as is the case in urodeles - see STADTMÜLLER, 1936: 586). According to SHISHKIN (1973: 184) the larval and adult otic processes represent strict homologues. The vertical part of the palatoquadrate in adults from which the *pars quadrata* projects posterolaterally and ventrally, the *processus oticus* dorsally and *processus pseudobasalis* medially, represents a vestige of the originally well developed horizontal part of the palatoquadrate in the orbitotemporal region of the tadpole. The *os quadratum* is that part of the palatoquadrate which originally was most projecting forward.

PLASOTA (1974: 128) calls attention to the remarkable fact that adults display a lower degree of autostyly as their *processus oticus* is separated from the otic capsule, and their *processus ascendens* is reduced. This is probably in connection with the fact that the originally functionally important element to which massive muscles are attached and with which a fairly large part of the viscerocranium is joined is reduced in adult individuals partly due to the development of dermal bones which take over part of the functions of the palatoquadrate and partly in consequence of the resorption of a substantial part of the hyobranchial skeleton.

There are no particular difficulties in homologization of the endocranial support of the lower jaw, as its transformation during metamorphosis can be followed relatively easily. It consists of Meckel's element which although not reaching anteriorly up to the symphysis is completed here by the mentomandibular which in adults ossifies and fuses with the dentary. The mentomandibular is a remnant of the larval *cartilago labialis inferior*.

The homologization of the hyoid is also unequivocal, as its origin from the hyobranchial skeleton has been studied on numerous frog species inclusive of *Pelobates* (e.g. KOTHE, 1910). The *cornu hyale* arises by the transformation of the ceratohyal. Its contact with the otic capsule is secondary, appearing as late as after metamorphosis, in consequence of the changed position of the palatoquadrate. The *processus anterior hyoidei* arises from the medial part of the ceratohyal. The *corpus hyoidei* consists in its central part of two fused copulae and hyobranchial plates. The *manubrium hyoidei* arises by the transformation of the *processus anterior* of the hypobranchial plate. The *processus posteromedialis* (*os thyreoideum*) is formed from the thickened posterior margin of the hypobranchial plate. The *processus anterolateralis et posterolateralis* represent developmentally new formations.

4.1.3.b Homologization of the endocranium of *Eusthenopteron* with that of the tadpole

It has been said in the introduction to this chapter (p. 57) that in homologizing the cranial structures of a tadpole with those of an adult *Eusthenopteron,* two different ontogenetic stages are compared. Fundamental structural differences in the ethmoidal region follow from the fact that in a tadpole before metamorphosis the olfactory organ is not yet developed. The postnasal wall appears only in connection with the formation of the nasal sac (so that it is justifiable to attribute this wall to the ethmoidal region - see the discussion of this term on p. 6-7).

However, pronounced structural agreements may be revealed in the orbitotemporal region. In *Eusthenopteron* (JARVIK, 1942: 428—429, fig. 47 A and B; 1954: 7—12, fig. 1) the suborbital ledge is a striking formation projecting from the outer surface of the braincase along the passage of its lateral walls into the braincase floor. The same position and a similar morphology may be observed in the *trabeculae cranii* of a tadpole. After the metamorphosis into an adult frog, the *trabeculae cranii* cease to exist as a morphologically independent formation, but in an adult *Eusthenopteron,* this structure is well developed, particularly its anterior and posterior ends.

In *Eusthenopteron,* the opening for the passage of the *nervus opticus* is situated below the level of the *processus ascendens palatoquadrati* (JARVIK, 1954: fig. 23 B); the opening for the *nervus oculomotorius* is at the same level posterior to it, and the *nervus trochlearis* passes closely anteriorly to the point of the *processus ascendens palatoquadrati.* In a tadpole quite equal topographical conditions may be found. The *processus basipterygoideus* and the *processus suprapterygoideus* which in *Eusthenopteron* represent points of attachment for the *pars pterygoquadrata palatoquadrati* are not developed in a tadpole because of the firm attachment of the *processus ascendens* to the neural endocranium. In a tadpole, the *pars autopalatina* and the *crista* *suspendens* do not occur, this possibly resulting from the fact that the main part of the palatoquadrate in the orbitotemporal region is not supported by the braincase.

There is a problem which would require fairly thorough study - the homologization of the intracranial juncture apparatus in *Eusthenopteron* and the *fissura prootica* in tadpoles. Evidence that the two are homologues follows from the fact that both these slits lie at the level which during the ontogeny is reached most anteriorly by the end of the notochord. But in a tadpole, the *nervus trigeminus* also passes through this slit; it is here that the *ganglion trigeminofaciale* is located, whereas in *Eusthenopteron* this nerve passes through a separate opening which lies posterior to the intracranial juncture apparatus, in the oticooccipital division of the neurocranium. This difference may consist in the large size of the *ganglion trigeminofaciale*; this could have been responsible for the fusion of the originally separated opening with the *fissura prootica*. In *Eusthenopteron,* as in most other vertebrates inclusive of two frog groups (*Leiopelmatidae* and *Discoglossidae*), both nerves ran separately, independent of each other, not forming the above-mentioned ganglion. The *nervus trigeminus* could therefore pass from the braincase through a much smaller opening isolated from the intracranial juncture apparatus. Another possible explanation has been indirectly suggested by SHISHKIN (1973: 166) who points out the considerable shortening of the anterior part of the otic region. Even this could cause the fusion of the opening for the *nervus trigeminus* with the original intracranial juncture apparaturs. The assumption that the intracranial juncture apparatus and prootic fissure are homologous is also supported by the topographical relations of the palatoquadrate to the neural endocranium.

In a comparison of the orbitotemporal regions of *Eusthenopteron* and the tadpole, only one difference appears — the large opening of the *fenestra frontoparietalis* in the tadpole, whereas in *Eusthenopteron* the roof of the braincase is almost completely closed.

The otic region of *Eusthenopteron* (JARVIK, 1954: 12—19, fig. 1; 1975, figs 8, 9) has a more complicated structure and also other proportions than is the case in a tadpole. Whereas in *Eusthenopteron* the antero-posterior length of the otic region corresponds approximately to that of the orbitotemporal region, in a tadpole this dimension is much shorter. However, the otic capsules proper of a tadpole retain proportions similar to those of *Eusthenopteron*; the impression of a greater width in a tadpole is caused by the *crista parotica* which considerably expands laterally. On the surface of the otic capsules of *Eusthenopteron* the *canalis jugularis* is conspicuous; the *vena jugularis* passes through it. This canal is bridged by the *commissura lateralis* whose lower margin joins the otic ledge. From an analysis of the topographic conditions of both these forms compared it follows that the *canalis jugularis* is a homologue of that part of the surface of the otic capsule of a tadpole which is bordered laterally by the *incisura posterior palatoquadrati* situated between the *processus oticus* and *processus ascendens*. In an adult this space is called the prooccipital fissure. In *Eusthenopteron* the horizontal ledge dorsally covering the *canalis jugularis* undoubtedly represents a homologue of the *crista parotica* of a tadpole (cf. JARVIK, 1975, figs 8 A and C). The otic ledge does not exist in tadpoles but JARVIK (1954, fig. 13) considers the so-called auditory ledge — present in *Ascaphus truei* — to be its homologue.

The *fenestra ovalis* (vestibular fontanella according to JARVIK, 1954: 7) is well developed both in *Eusthenopteron* as well as in tadpole. In both cases it is exposed posterolaterally, and has constant topographical relations to the other formations of the otic capsule, so that the homologization is unequivocal (see also JARVIK, 1972: 210). In this context the problem of the homologization of the *operculum* should be mentioned. There are some doubts whether the *fenestra ovalis* of *Eusthenopteron* was completely or partly closed with cartilage (see JARVIK, 1954: 7). but as in this animal the opening lies in the *fissura occipitalis lateralis* whose surface is not lined by periost, it is possible to assume that this conspicuous groove inclusive of the above-mentioned opening was filled with cartilage. Thus, the cartilage closing the *fenestra ovalis* is part of the otic capsule and therefore also of the neural endocranium. This has also been confirmed by the results of some embryological studies (KINGSBURY and REED, 1909; VAN EEDEN, 1951: 117; MARCUS, 1955; SEDRA and MICHAEL, 1959; see also PLASOTA, 1974) according to which the *operculum* originates by chondrification in the membranous tissue closing the *fenestra ovalis*; it is therefore part of the neural and not visceral endocranium. In *Eusthenopteron,* the dorsal surface of the otic capsule medial to the *crista parotica* is considerably depressed and is called the *fossa bridgei.* In a tadpole this is represented by part of the surface of the otic capsule between the margin of the *crista parotica* and the *prominentia ducti semicircularis posterioris,* though at first glance it is clear that no fossa is formed here, but only a slight depression. In *Eusthenopteron, nervus glossopharyngeus* and *nervus vagus* enter the surface of the neural endocranium by separate openings in the *fissura occipitalis lateralis.* This groove also forms the boundary between the otic and the occipital regions. In a tadpole as well as in an adult frog, both these nerves mostly pass through common *foramen jugulare.* However, SEWERTZOW (1891: 141) reports on a case in *Pelobates* where both these nerves passed through separate openings. The *fossa condyloidea* is without doubt a homologue of the *fissura occipitalis lateralis.* The postotic process which in *Eusthenopteron* is a prominent outgrowth on the posterior wall of the otic capsule, is evidently represented in frogs and tadpoles by a marked *prominentia ducti semicircularis posterioris.* In tadpoles too, a clearly visible depression lies medially to this prominence which is a homologue of the dorsal end of the *fissura occipitalis lateralis.*

The most significant formations distinguishing the otic region of *Eusthenopteron* from the corresponding region in a tadpole are the following: the spiracular canal, the supraotic cavity, and a peculiar subtle process which is termed the anterolateral rod of the oticooccipital. In addition, as in the orbitotemporal region, the dorsal part of the braincase is completely closed except for a small *fenestra supraoticalis* which however represents a communication to the supraotic cavity. In a tadpole, as in *Eusthenopteron,* the *arteria occipitalis* runs on the dorsal side of the neural endocranium, but does not form here any groove. In an adult, it is closed within the frontoparietal. The occiput, well developed in *Eusthenopteron* on the neural endocranium, is present also in *Pelobates* but in an adult only, in the shape of a slanting ridge terminating on the *processus posterior inferior* of the *facies posterior frontoparietalis.* Although these structures have the same function (the site of the attachment of the ligament comming from the spinal processes of vertebrae) they cannot be regarded as homologues but as analogues because of their origin. In the tadpole no homologue or analogue of the occiput exists.

The occipital region in *Eusthenopteron* is limited by the *fissura occipitalis lateralis* which on the ventral side joins the *fissura oticalis ventralis.* In a tadpole the analogous part of the neural endocranium is bounded by the depression among the dorsolateral part of the *foramen magnum,* the *prominentia ducti semicircularis posterioris,* the *foramen jugulare* and the *fenestra ovalis*; this suggests that the occipital region defined in this way also comprises the posteroventral part of the otic capsule.

The occipital region does not display a conspicuous structure on its surface, which would serve for homologization. The differences concern especially the proportions. Neither in *Eusthenopteron**) nor in a tadpole before metamorphosis are the *condyli occipitales* developed.

The essential clue for homologization of the viscerocranium of a tadpole with that of *Eusthenopteron* may be seen in the palatoquadrate. In *Eusthenopteron* (Jarvik, 1942: 451—453, figs 54 and 55; 1954: 27—32, figs 23 B, 24; Bjerring, 1977, fig. 26) palatoquadrate consists of two main parts, i.g. *pars autopalatina* and *pars pterygoquadrata* which are connected with each other by a narrow stripe of bone called the *vinculum* or commissural lamina. It is not possible to use the shape as a main criterion for homologization of a similar element in a tadpole, as in the latter no element formed in this way exists. Thus, its relations to the neural endocranium are important. The palatoquadrate of *Eusthenopteron* adjoins the neurocranium in the following articulations: the *pars autopalatina* is attached to the postnasal wall in two places (so that anteromedial and posterolateral ethmoidal articulation develops) and adjoins also the braincase, constituting the so-called orbital articulation (Jarvik, 1954, fig. 40 A). In addition, the medial part of the *pars autopalatina* is supported by the *crista suspendens* to which it was fixed by ligaments during the animal's life. The *processus basalis* and the *processus ascendens palatoquadrati* adjoin the basipterygoid and suprapterygoid processes of the neurocranium, thus forming the basal and suprapterygoid articulations. Behind the intracranial juncture apparatus is developed the paratemporal articulation (the *processus paratemporalis palatoquadrati* adjoins the anterior end of the otic ledge). The neurocranium of a tadpole

---

*) In *Eusthenopteron,* instead of *condyli occipitales* a paired process occurs, but its function in the cranio-vertebral junction is doubtful (Jarvik, 1975: 204).

has the following connections with the element designated as the *palatoquadratum:* the *processus ascendens* and *commissura quadrato-cranialis anterior* lying in front of the *fissura prootica,* and behind it *processus oticus.* The proximal part of the *processus ascendens* adjoins the anterolateral part of the wall of the otic capsule. From the topographical relations if follows that a homology between the *processus ascendens palatoquadrati* and the suprapterygoid articulation undoubtedly exists between the tadpole and *Eusthenopteron* (see also PLASOTA, 1974: 125). The homologization of other connections is not so unequivocal, as the position of the palatoquadrate in a tadpole is different from that in *Eusthenopteron.* But there is no doubt that this position in a tadpole represents a specialization, and not the primary state: the palatoquadrate undoubtedly changed its position in connection with the fact that in a tadpole the jaw apparatus developed from other elements of the viscerocranium than is the case in an adult frog. It is probably due to this change of the position of the palatoquadrate that PUSEY (1938: 528—529) expressed the opinion that the *commissura quadrato-cranialis anterior* is a homologue of the basal articulation existing in the ancestors of amphibians, which due to the shift of the *pars quadrata palatoquadrati* also moved anteriorly. However, the idea of a shift of the *processus basalis* along the surface of the braincase appears to be mere speculation lacking any evidence. In contrast, REINBACH (1939a) is of the opinion that the *commissura quadrato-cranialis anterior* is a derivate of the ethmoidal region. JARVIK (1942: 521—523) however considers this commissure to be homologous with the anteromedial ethmoidal articulation in *Eusthenopteron.* This interpretation is undoubtedly more correct, as it is evidently supported by the fact that the *commissura quadrato--cranialis* represents a formation situated at the level of the anterior end of the braincase.

There are also difficulties in homologizing the posttemporal articulation, as in a *Pelobates* tadpole before metamorphosis a well developed *processus pseudobasalis* is still lacking. But the posteromedial margin of the palatoquadrate which also forms part of the base of the *processus ascendens* meets the anterolateral part of the otic capsule in the area anterior to the *fenestra ovalis.* It may be assumed that this contact represents a homologue of the paratemporal articulation of *Eusthenopteron.* It is in this area that during the metamorphosis a firm connection arises which is termed the *processus pseudobasalis* (according to DE BEER, 1926: 310, fig. 77). However, it is not a homologue of the *processus basalis* of *Eusthenopteron,* and for this reason it cannot be designated as the *processus basalis* as it was termed by some authors as e.g. STADTMÜLLER (1936: 576—579) and SHISHKIN (1973: 179—181). Although a discussion on whether *processus pseudobasalis* is derivative of neural endocranium or palatoquadrate is not substantial in this context, it is logical to interpret the firm connection existing in adult frogs as a derivative of the palatoquadrate. The opinion that this connection is associated with the hyoid arch (see PLASOTA 1974: 128) seems to be justified in so far as consideration is given to JARVIK'S (1954: 73, 75, fig. 39 A) interpretation of the otic ledge in *Eusthenopteron* as an infrapharyngohyal.

The *processus oticus* does not have a homologue in *Eusthenopteron* and it may therefore be regarded as a formation developed in connection with the later specialization of the viscerocranium. It is interesting that in pipids this process does not exist as an independent formation (SOKOL, 1977: 362) but fuses with the *processus ascendens* into the so-called otic plate. In a tadpole, further processes may develop on the palatoquadrate which are analogous to *processus oticus*: in some species of frogs, the development of accessory processes may be the cause why the *processus oticus* is sometimes not developed at all (see PLASOTA, 1974: 126).

From the above analysis of the topographical conditions it follows that a substantial part of the palatoquadrate (as to homology of *pars autopalatina* see below) in *Eusthenopteron* corresponds to the palatoquadrate in tadpoles; but in the latter the articular part (*pars quadrata*) is turned anteriorly, not posterolaterally.

In *Eusthenopteron,* the *hyomandibula* follows immediately behind the *pars pterygoquadrata palatoquadrati* (JARVIK, 1954: 32—34, fig. 16 A, B); it joins the otic capsule anterodorsally to the *fenestra ovalis* by two small articular facets (JARVIK, 1954, fig. 23 A, B). The stylohyal is a further element situated behind the *pars articularis palatoquadrati* (JARVIK, 1954: 22, fig. 23 B). Considering that the relations of the elements of viscerocranium to the neurocranium is the determining factor, and that the mutual position of the various elements of the viscerocranium may vary (due to this, the topographical relations of the individual elements of viscerocranium to each other cannot be used for homologization) the *hyomandibula* in *Eusthenopteron* may be unequivocally interpreted as a *plectrum,* and the dorsal part of the *hyomandibula* like the *pars interna plectri* of a *Pelobates* tadpole (cf. JARVIK, 1972: 209—210; PLASOTA, 1974: 130—137). Thus, the element which articulates ventrally with the palatoquadrate should be homologized with some of the elements of the hyoid arch situated more ventrally. In *Eusthenopteron* the stylohyal partly remains in a cartilaginous state (JARVIK, 1954: 22), just as the posterior ceratohyal. Hence it is most probable that this above-mentioned robust element of a tadpole may be homologized with the *ceratohyale anterior* of *Eusthenopteron.* However according to JOLLIE (1968, fig. 4/22) only the lateral part of this structure is a homologue of the ceratohyal, and the medial part inclusive of the *processus anterior* is considered hypohyal.

Behind the ceratohyal there lies the hypobranchial plate with which the posthyoid branchial arches link up. Although these arches have completely lost contact with the neural endocranium (in *Eusthenopteron* at least the two most anterior of them still articulate with neurocranium), and although the arches in addition to their function of a branchial slit support received a further function connected with the mode of feeding (SEVERTZOV, 1970: 5), they represent the part of the visceral endocranium which was least changed. They are commonly termed ceratobranchials, but their homologization is not unequivocal to such an extent. The following fact should be considered: (1) although their ends join each other by means of the *commissurae terminales,* they sometimes give off processes directed dorsally which always form a continuation of the respective arch; (2) the arches pass ventrolaterally into the *commissurae hypobranchiales* which can be well distinguished from them, as this passage forms a sharp break; (3) the *commissurae hypobranchiales* are attached to one sole element - the hypobranchial plate. In *Eusthenopteron* (JARVIK, 1954: 22, fig. 8) the first two arches join the neural endocranium by means of their infrapharyngobranchials, but the dorsal parts of the remaining arches have already joined each other (i. e. the epibranchial of the third arch joined the epibranchial of the second arch etc.; the pharyngobranchials have evidently disappeared). In connection with these conditions in *Eusthenopteron* we may therefore assume that at least in the area of the *commissurae terminales* the branchial arches of a tadpole represent epibranchials (cf. KOTHE, 1910: 34). The occassionally developed small processes could then be regarded as remnants of pharyngobranchials. In this case, the arch itself would really represent a homologue of that in *Eusthenopteron*. Then, the sole possible interpretation of the hypobranchial plate would be fused hypobranchials*). This interpretation is supported by the fact that in *Eusthenopteron* too, the hypobranchials are more robust elements than the subtle elongate ceratobranchials. The hypobranchial commissures — in the sense of this interpretation — should be regarded as part of the ceratobranchials. But if only these commissures were considered to be ceratobranchials then the remaining dorsal parts of the arches would necessarily represent epibranchials. With regard to the fact that in *Eusthenopteron* gills were situated mostly on ceratobranchials — which are also the most part of the arches — the first interpretation is more acceptable. For a complete view it should be added that earlier authors (e. g. KOTHE, 1910, fig. 1) designated *spicula* as ceratobranchials.

Between both opposite ceratohyals of a tadpole, *copula* 2 is situated on the mid-line. It is no doubt a homologue of the posterior basibranchial of *Eusthenopteron* (JARVIK, 1954: 23, fig. 8 B), whereas the anterior basibranchial of the latter may most probably be a homologue of *copula* 1. In *Eusthenopteron*, the anterior basibranchial is more robust than the posterior one and reaches from the hypohyal up to the hypobranchial of the second posthyoid arch. The posterior basibranchial closely links up with it. This basibranchial is adjoined by the hypobranchial of the fourth or perhaps also the fifth arch. In a *Pelobates* tadpole, the proportions are inverse — the *copula* 1 is much smaller than *copula* 2. During ontogeny the *copulae* also approach each other, and later fuse. The *basibranchialia anterior* and *posterior* undoubtedly originated through the fusion of the basibranchials of the respective arches; the *copulae* are therefore of the same nature. For this reason JOLLIE's (1968, fig. 4/22) opinion that *copula* 2 is a homologue of the basihyal cannot be confirmed.

Meckel's element does not cause any essential difficulties in homologization, as its relation to the *pars quadrata* (seu *articularis*) *palatoquadrati* is constant. Distinct morphological differences between this element in *Eusthenopteron* and that in the

---

*) SOKOL (1977: 363) maintains that in pipids this plate consists of two hypobranchials.

tadpole may be regarded as a consequence of the specialization of the tadpole's viscerocranium.

The anterior end of Meckel's element of a tadpole is joined by the *cartilago labialis inferior* which in an adult frog is transformed into an ossified mentomandibular. In *Pipa carvalhoi* tadpoles, this cartilage occupies the same position in relation to Meckel's element (Sokol, 1977: 362); in this case Meckel's element more strongly resembles the support of the lower jaw of adults (Sokol op. cit., fig. 4). A similar element has not hitherto been found in *Eusthenopteron,* but it occurs in its most closely related recent form *Amia* (Jarvik, 1980: 50, fig. 32). It may therefore be assumed that also in osteolepiform fishes or at least in some of their representatives, the mentomandibular was developed, although it could have been considerably reduced in adults.

The rod-like cartilage which is closely related to the posterodorsal end of the *cartilago labialis superior,* fused — as has been stated above — during metamorphosis with the *commissura quadrato-cranialis anterior palatoquadrati* of the tadpole. Jarvik (1954: 75—88, figs 39 B, C, 40, 43), on the basis of a thorough analysis, has drawn the conclusion that the *pars autopalatina palatoquadrati* represents the epibranchial of the praemandibular arch (*epipraemandibulare*) being secondarily fused with the palatoquadrate (which originated from the epipraemandibular and suprapharyngomandibular). It may be assumed that in *Eusthenopteron* larvae these elements were separated from each other. During the metamorphosis of a *Pelobates* tadpole into an adult frog, a similar process may be followed, so that the anterolateral part of the *commissura quadrato-cranialis anterior* (and consequently the *processus antorbitalis* of an adult frog) may be homologized with the anterolateral part of the *pars autopalatina* of an adult *Eusthenopteron.* From this it follows that the palatoquadrate of a tadpole is a homologue of only a part of the palatoquadrate of an adult frog as well as of an adult *Eusthenopteron.* The above-mentioned cartilage adjoining the palatoquadrate of a tadpole may be interpreted as the epipraemandibular.

The small cartilage situated anterolaterally to Meckel's element, and designated by Plasota (1974) as »x« becomes reduced during metamorphosis, and finally disappears. Merely according to its ventral position in relation to the above discussed epipraemandibular, it may be regarded as the lower part of the praemandibular arch. It has not been preserved in an adult *Eusthenopteron.*

The *cartilago labialis superior* is the last independent element; a similar structure is however lacking in an adult *Eusthenopteron.* In considering its homologization, we may only start from the fact that during metamorphosis it is transformed into the *cartilago praenasalis inferior,* i. e. part of the ethmoidal region of the neural endocranium. It is only on the basis of its position that Jarvik (1942: 505) homologizes this outgrowth with that part of the *divisio praenasalis communis* of *Eusthenopteron* which lies closely laterally to the anterior part of the *canalis* (*fenestra*) *nasobasalis* and to the lateral branch of this canal. It may be assumed that either one of the pharyngomandibulars is concerned (which would be suggested by a close topographical relation between the *cartilago labialis superior* and the epipraemandibular), or the upper part of the terminal arch. However, the latter alternative lack any supporting evidence, apart from the fact that Jarvik regards the *lamina nariochoanalis* (*lamina inferior cristae intermediae* of adult frogs - see p. 6-7) as a converted epiterminal, not that part of the ethmoidal region which is homologized by him with the *cartilago praenasalis inferior*.

4.1.3.c Homologization of the endocranium of *Eusthenopteron* with that of an adult frog

It has been stated above that the orbitotemporal, otic and occipital regions of the neural endocranium of a tadpole are in essential character already developed into the state which may be found in an adult frog. The homologization of this part of the skull of an adult frog with that of *Eusthenopteron* may therefore be based on the results of homologization of the endocranium of a tadpole with that of *Eusthenopteron.* The latter homologization shows that the intracranial juncture apparatus of *Eusthenopteron* may be compared with that area of the endocranium of an adult frog which lies closely behind the subtle process on the margin of the *fenestra frontoparietalis* and with the posterior margin of the prootic fontanelle. The remains of this intracranial juncture apparatus are represented by the *recessus prooticus* and *foramen prooticum.*

In *Eusthenopteron* as well as in the adult frog, the ethmoidal region of the neural endocranium is well developed due to the development of the olfactory organ. Jarvik (1942: 495—554) has carried out a homologization of this region in *Eusthenopteron* with that of an adult representative of the genus *Rana* on the basis of a very thorough analysis. There are no essential differences in the structure of the ethmoidal region except for proportions between *Rana* and *Pelobates,* and thus Jarvik's conclusions concerning homologization of this region may be accepted also for *Pelobates.* The objection that the phylogenetically advanced form (which *Rana* is regarded as) cannot be compared with a form so archaic as *Eusthenopteron* is not tenable, as the fundamental structural plan of the ethmoidal region in *Pelobates,* which is generally considered to be phylogenetically more archaic form (e. g. REIG, 1958), is the same as in *Rana.* Jarvik's conclusions may be briefly summarized as follows:

1. The basic structural plan of the ethmoidal region is identical in *Eusthenopteron* and frogs. Differences are due to a regressive development whose manifestations may be observed on all parts of the skeleton of frogs.
2. In both *Eusthenopteron* and frogs, homologues of the following structures may readily be found: the *septum nasi,* praenasal wall, *crista subnasalis, fenestra nasobasalis, lamina nariochoanalis, solum nasi, fenestra endonarina anterior et posterior, fenestra endochoanalis,* postnasal wall and *lamina superior et inferior cristae intermediae.*
3. In some of these elements not only may an undoubted homology be stated but also striking resemblances as to their structure; for instance, in both above mentioned forms the *septum nasi*

is represented only by a thin cartilaginous partition which does not contain any further continuous cavities, and is not reached into by the braincase. In the inner arrangement of the nasal cavities similarities may also be found.

4. Jarvik has also found homologies and morphological similarities on the exocranial cover of the ethmoidal region as well as in some soft organs in so far as it was possible to reconstruct them in *Eusthenopteron* on the basis of the skeletal structures (e. g. the olfactory sac and *ductus nasolacrimalis*).
5. The differences between *Eusthenopteron* and frogs - except the more subtle structures in frogs - consist only in details of the course of some nerves occurring in the ethmoidal region. According to Jarvik (1942: 510), the *cartilago subethmoidalis* represents a remnant of the ventral medial part of the ethmoidal region in *Eusthenopteron*.

It must be emphasized that the the objections to Jarvik's ideas are mostly not focused on these homologizations but concern his interpretations of them.

From the above description of the changes occurring during metamorphosis in the palatoquadrate it follows that in *Eusthenopteron* the palatoquadrate is homologous with that of an adult frog, but only partly homologous with the palatoquadrate of a tadpole. The *pars autopalatina* or its part lying laterally from the anterolateral ethmoidal articulation corresponds to the *processus antorbitalis* of a frog. The area proper of this articulation is homologous with the *commissura quadrato-cranialis anterior* of a tadpole (see JARVIK, 1942: 521); in an adult frog this commissure is transformed into the long and slender *pars palatina palatoquadrati*.

The homologization of Meckel's element does not cause difficulties. The mentomandibular in frogs and the possibility of the existence of its homologue in *Eusthenopteron* has already been mentioned above (p. 68). The postmandibular division of the visceral endocranium of an adult frog has partly been preserved as some of the organs of middle ear, partly as the hyoid. The hyomandibular or its dorsal part corresponds to *pars interna plectri* (see above p. 66; PLASOTA, 1974: 133; JARVIK, 1972: 210) which in *Pelobates* is discernible only in the larval stages, appearing as a tiny vestige (KOTHE, 1910: 59—60).

The origin of the hyoid in an adult frog is composite. The *cornua hyoidei* and *processus anteriores* are homologues of ceratohyals. The substantial part of the *corpus hyoidei* consists of *copulae* which are homologues of the basibranchials. The lateral part of the hyoid body inclusive of *manubria* are homologous with the hypobranchial plates, i. g. most probably with fused hypobranchials. The homologization of the *processus posteromediales* is most difficult. From the topographical relations to the branchial arches of a tadpole it follows that hypobranchials of the fourth posthyoid arch may be concerned, but it should not remain unnoticed that the *processus posteromedialis* arises only in the course of metamorphosis by the thickening of the margins and the hypobranchial plate becoming more massive, so that these formations may have originated secondarily (similarly as to *processus anterolateralis* and *posterolateralis*).

4.1.4 The changes in the endocranium occurring during the evolution of frogs from their ancestors, corresponding by their anatomy to *Eusthenopteron*

In spite of many congruences between the structure of the endocranium of *Eusthenopteron* and that of frogs, differences may also be found, given by the mere fact that *Eusthenopteron* was a water dweller whereas the frog lives on dry land. These differences may be interpreted as evolutionary, taking place during the evolution of frogs from their ancestor which was not necessarily *Eusthenopteron* but which certainly belonged to the circle of this form. This conclusion may be drawn with regard to the fact that up to the present time no other form of water dwellers has been found which would be anatomically closer to frogs.

But it is beyond doubt that a number of transitional forms necessarily existed between frogs and their fish ancestor, whose general appearance and basic structure corresponded to some types of stegocephalians. Today, one of the most important problems which are being discussed in paleontology is the question which group of Palaeozoic amphibians are concerned in this connection. The solution of this problem may be supported by a determination of the changes occurring during the evolution of frogs. Assuming an irreversible development of the complexes of characters to be functionally independent, it may be taken that the intermediate forms occurring in the evolution of frogs from lobe-fin fishes should display features within a variability range whose limits are represented by the characters of their fish ancestors and on the other hand by those of frogs. In other words, the forms whose characters are beyond this variability range cannot be regarded as transitional between fishes and frogs. On the basis of this assumption, anatomical and morphological properties may be determined which may be supposed to have existed in the immediate ancestors of frogs.

The knowledge of the evolutionary changes occurring during the origin of frogs is also important for the determination of the phylogenetic trends within this group itself. The origin of frogs is a result of evolution bringing about marked specializations. It may therefore be assumed that this evolution continued or reverberated even after the interval where frogs were already well constituted a group, although differently in various lines.

The first such changes are undoubtedly represented by the adaptation to the dry land mode of life, and therefore these changes are manifested in all terrestrial tetrapods, not only in frogs. In the endocranium, such changes are as follows:

(1) Reduction of the visceral skeleton resulting from the change in the mode of breathing.

(2) Origin of the hyoid by modification of the hypobranchial skeleton in connection with the origin of the tongue.

(3) Origin of the *columella* in connection with the development of the capability of receiving acustic impulses. In most ancient amphibians (e. g. the Lower Carbo-

niferous labyrinthodont *Greeerpeton*; CARROL and HOLMES, 1980: 17) the *hyomandibula* was still large. Its reduction took place later.

(4) In connection with the development of the capability of receiving acustic impulses, the *fenestra ovalis* expanded.

(5) The skull became flattened dorsoventrally. This change was very rapid, and its result was already manifested in the most ancient known terrestrial tetrapods (*Ichthyostega* and *Acanthostega*). However, the braincase proper flattened relatively more slowly.

(6) In connection with the preceding change, part of the palatoquadrate which formed the support of the ventrolateral margin of the orbit shifted laterally, and due to this, the orbit changed its position from prevailingly lateral to dominantly dorsal.

(7) Posterior parts of the neural endocranium shortened antero-posteriorly; this was most pronounced in the occipital region (see JARVIK 1967, fig. 9 A, B) and relatively less conspicuous in the otic region. However, JARVIK (1967: 188) is of the opinion that similar changes which may also be observed, but as traces only, in osteolepiform fishes, should be explained rather by an elongation of the preotic division of the skull.

(8) The cranio-vertebral junction was reconstructed; it was associated with the origin of occipital condyls, so that the head became more mobile.

(9) The intracranial juncture apparatus ceased to exist (it appears only as a trace in the larva). This change was slower than e. g. the change of skull proportions, because *Ichthyostega* had this joint apparatus still preserved (JARVIK 1980: 234).

(10) The notochord was reduced, and therefore the notochordal canal was obliterated.

These changes have also been found in Palaeozoic amphibians (e. g. SHISHKIN, 1973: 165—168). Specialization is also represented by a complex of changes which were manifested with various intensities in diverse evolutionary lines of amphibians; they may occur however only in some lineages. Many of them, e. g. the changes on the palatoquadrate, were associated with other modifications; it is therefore necessary to judge them from this point of view .These changes are as follows:

(1) The endocranium underwent a markedly regressive development which resulted in its more subtle general structure. This development is manifested not only by some elements becoming more slender (e. g. palatoquadrate) but also by the origin of new openings (e. g. the lateral wall of the nasal capsule) or also by the enlargement of those already existing (e. g. the *fenestra endonarina*).

(2) A distinct modification which may be associated with regressive development consists in the lower degree of ossification of the endocranium. In *Eusthenopteron*, the endocranium is constituted by bone (probably except for some rather minute components of the visceral skeleton and the *fenestra ventralis* of the neural endocranium - JARVIK, 1954: 16—18, fig. 7). In the frog, the endocranium is ossified only in the areas of sphenethmoid, prootics and exooccipitals. In labyrinthodonts, the endocranium was partly chondrified but the extent of ossification here was always larger than in frogs. The following wholes are ossified to various degrees: the basisphenoid, sphenethmoid, laterosphenoid, orbitosphenoid, exooccipital, prootic, opisthotic,

tectum posterior and basioccipital (see SHISHKIN, 1973: 162—164). Still in Triassic labyrinthodonts, there exists one sole (so-called orbitotemporal) ossification in the area of the basisphenoid (SÄVE-SÖDERBERGH, 1944: 1, 3); in this even the prootic fontanelle is not formed. Nerves II, III, IV, V and VI run out through separate openings from this ossification. Most ancient frogs (e. g. *Vieraella*; ESTES and REIG, 1973) possess otic capsules which are still ossified completely; no cartilaginous stripe exists here, separating the prootic from the lateral occipital.

(3) The *lamina supraorbitalis* is markedly reduced. In *Eusthenopteron*, it is developed nearly throughout length of the orbitotemporal region; in *Pelobates*, it is restricted to the anteromedial angle of the orbit. In labyrinthodonts the extent of the *lamina supraorbitalis* may be reconstructed from the impressions on the inner side of the respective exocranial elements. According to SHISHKIN (1973: 162—163, fig. 66), the tendency to shortening of this supraorbital ledge may be regarded as one of the evolutionary trends occurring in an endocranium of this group, as in various forms of labyrinthodonts different degrees of its reduction may be observed.

(4) The change of location of some openings (e. g. the opening for *nervus trigeminus*; the *fenestra ovalis* from its originally lateral position proceeded into a posterolateral position) is evidently associated with the changes in proportions in the posterior parts of the skull.

(5) In *Eusthenopteron* the surface of the otic region is considerably complicated, and became simplified in frogs. In labyrinthodonts, a transitional condition may be observed.

(6) The structure of the surface of the ethmoidal region became fairly intricate due not only to the expansion of the existing openings but also to the origin of the new ones. Some openings undoubtedly originated as a result of the changes in the adjacent parts of the exocranium (e. g. the *cartilago praenasalis superior*).

(7) Marked changes took place on the palatoquadrate, partly in its proportions, partly in the mode and quality of its attachment to the neural endocranium.

Whereas in *Eusthenopteron* the palatoquadrate is represented by a relatively robust structure bounding the orbit ventrally and laterally, in an adult frog it is reduced to the *processus antorbitalis* (a homologue of the lateral part of *pars autopalatina*), and also to a subtle posterior part of the palatoquadrate (a homologue of the *pars pterygoquadrata*). Both these parts are connected by the rod-like *pars palatina* which is partially homologous with the medial part of the *pars autopalatina*, and partly with the *vinculum*. Hence in frogs the palatoquadrate has lost the function of the ventral wall of the orbit. SHISHKIN'S (1973, figs 48—50) reconstructions show that in labyrinthodonts the palatoquadrate was not yet so strongly reduced as that of frogs; this refers particularly to the *pars palatina*. Likewise, the position of the *pars quadrata palatoquadrati* suggests rather the conditions in *Eusthenopteron*, as it is still much more expanded laterally than is the case in frogs.

In *Eusthenopteron*, the attachment of the palatoquadrate to the neurocranium was immobile, though being represented probably only by syndesmoses. In frogs, this attachment is more firm (synchondroses). Only in the *processus oticus,* which however is a new evolutionary formation, does the original larval synchondrosis change into syndesmosis in adults. A synchondrotic attachment probably existed as early as in labyrinthodonts.

The original attachment of the anterior part of the palatoquadrate, such as was developed in *Eusthenopteron,* occurs at only three sites (anteromedial and posterolateral ethmoidal articulation and attachment to the *crista suspendens*). In frogs this changed, and only one attachment exists, i. e. the attachment of the *processus antorbitalis* to the postnasal wall (from a description of the course of metamorphosis it is however clear that this attachment is of composite origin). It is interesting that various forms of labyrinthodonts display a connection between the *processus pterygoideus palatoquadrati* with the postnasal wall, which corresponds to different stages of the development of this attachment during the metamorphosis of a *Pelobates* tadpole into an adult frog. The conditions in a *Dvinosaurus primus* (SHISHKIN, 1973: 177, fig. 73 A) corresponds approximately to the stage of metamorphosis of the tadpole during which the epipraemandibular cartilage was already attached to the *commissura quadrato-cranialis anterior,* but the cartilaginous posterolateral margin is still separated from the commissura by a deep incision. Shishkin designates the part corresponding to the epipraemandibular of frogs (which in labyrinthodonts in their rather early stages of ontogeny was undoubtedly an independent element) as the *pars postchoanalis* of the postnasal wall. In contrast, the condition of *Dvinosaurus egregius* (SHISHKIN, op. cit.: 177—178, fig. 73 B, C) corresponds to a later stage of metamorphosis of frogs. It may be concluded that the palatoquadrate of *Eusthenopteron* or some more primitive types of labyrinthodonts corresponds in its structure to the palatoquadrate of a *Pelobates* tadpole in the late stages of its metamorphosis. Thus, further ontogenetic changes in the final stages of metamorphosis correspond to the phylogenetic stages taking place during the evolution of frogs from lobe-fin fishes or primitive labyrinthodonts.

The *processus ascendens* which is well developed in *Eusthenopteron* and takes part in the suprapterygoid articulation, is lacking throughout in adult frogs. It does not leave any traces on the bones of the exocranium in labyrinthodonts, and it is therefore not possible to determine the degree of its development in them. It is assumed that in the latter it became gradually reduced to the vestige synchondrotically adjoining the neurocranium (SHISHKIN, 1973: 177).

Likewise, the *processus basalis* has not been preserved, and due to this the basipterygoid articulation also disappeared. But the paratemporal articulation continues to exist, although also modified into a synchondrosis. This articulation has been erroneously homologized by many authors with the basipterygoid articulation. However, it is clearly perceptible on SHISHKIN'S (op. cit., figs 48, 50) reconstructions that the process designated here as the *processus basipterygoideus* really forms part of the otic ledge and that therefore a paratemporal articulation is concerned. From the above-mentioned reconstructions it may also be inferred that the otic ledge of labyrinthodonts was still mostly well ossified, forming a conspicuous morphological structure.

Processus oticus arises in frogs as a new formation. It already existed in labyrinthodonts (Shishkin, op. cit.: 181—184) where it adjoined the *processus postorbitalis* of the neural endocranium; in frogs, the *processus postorbitalis* is lacking as an independent formation. According to the latter author (op. cit.: 183) the postorbital process could represent a vestige of the lateral commissure of lobe-fin fishes.

(8) The openings for IX and X cranial nerves in *Eusthenopteron*, which were originally separated, became joined in the frog into a single *foramen jugulare*. The same condition may also be stated in labyrinthodonts (Shishkin, 1973: 108). In *Pipa carvalhoi* both openings are still separated (Sokol, 1977: 361), which is sometimes also the case in *Pelobates* (Sewertzow, 1891: 141).

(9) The originally narrow and high braincase of *Eusthenopteron* in the orbitotemporal region whose floor is so thick that its height exceeds that of the braincase itself (Jarvik, 1980, fig. 38 C) changed in the frog into a braincase whose width fairly exceeds the height, and whose bottom is relatively thin. Judging by the impressions on the ventral side of bones of exocranial roof, in labyrinthodonts the braincase in this region was very narrow (Säve-Söderbergh, 1944: 3; Shishkin, 1973: 111, figs 47, 49), and in contrast to frogs, was wider in the lower part than in the upper one.

(10) The endocranial braincase roof in lobe-fin fishes is quite closed except for the pineal opening. But in frogs it opens dorsally, this involving the large opening. In some forms tecta, developed to different extents, may bridge this opening. In adult labyrinthodonts probably a fairly large opening did not yet exist.

(11) The course of the *arteria occipitalis* in *Eusthenopteron* is closely related to the endocranium; in frogs, it was shifted more dorsally up to the level of the exocranium.

On the basis of the above mentioned changes on endocranium which occurred during the origin of frogs, the following main evolutionary trends may be assumed in the endocranial part of the skull, which took place in the further evolution of this group:

(1) Further reduction of the endocranium, particularly in the ethmoidal region.

(2) Regression of the ossified parts of the endocranium, manifested especially by their diminution or even disintegration into smaller parts.

(3) Reduction or disappearance of *lamina supraorbitalis*.

(4) Reduction of the size of the palatoquadrate.

(5) Gradual lowering of the braincase.

(6) Expansion of the openings in the braincase, particularly in its roof.

(7) Separation of the *arteria occipitalis* from the endocranium.

(8) Shift of morphological changes into earlier stages of ontogeny (e. g. disappearance of epipraemendibular cartilage, *copula I* etc.).

4.2 Exocranium of Pelobates fuscus

This part of the skull in *Pelobates* or at least some of its regions, has attracted scientists more than the endocranium did (Bayer, 1884; Boas, 1914; Bolkay, 1919;

Born, 1896; Reinbach, 1939b; Sewertzow, 1891). However, the mentioned authors only described the bones, or general shape of the exocranium. The reason for such a static description was the fact that the very strict relations between the endocranium and the exocranium were unknown, especially in the sense that the cartilago of some endocranial parts induces the origin of topographically corresponding exocranial elements (see e. g. Lebedkina, 1979: 137). This fact was verified experimentally and become the main clue for the homologization of exocranial elements.

As the topographical relations of the exocranium and endocranium with one another have already been described (see chap. 4.1.1 Endocranium of adults), only definitions of the exocranial bones, their descriptions and mutual relations will be given in the following text.

4.2.1 Exocranium of adults

The bones of the dorsal side of neural exocranium (praemaxilla, nasal, frontoparietal).

The praemaxilla (fig. 25 a-c) is a paired bone adjoining the anterior part of the endocranium; it bears the teeth, and it takes part in the formation of the tooth arch.

Brief notes on the morphology of this bone are by Bayer (1884) and Bolkay

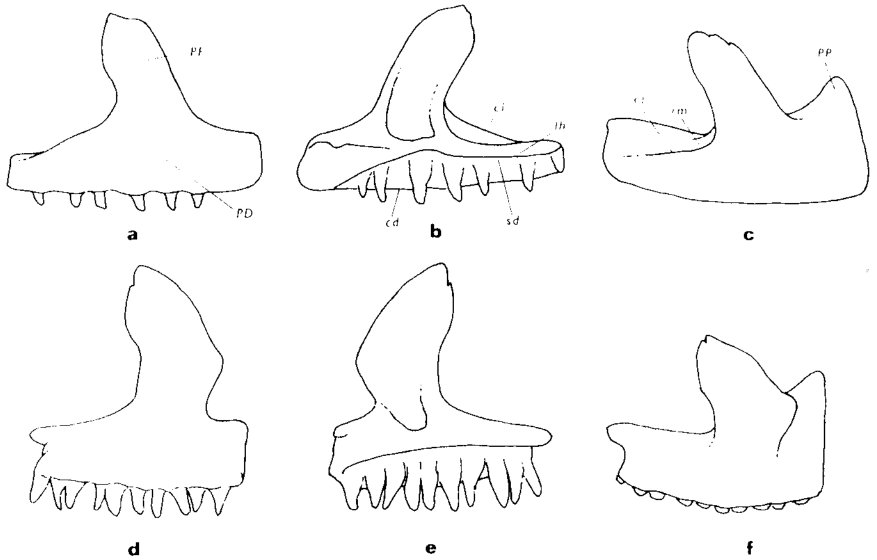


Fig. 25. General morphology of the praemaxilla of *Pelobates fuscus* (DP FNSP 6474; a - c) and *Pelobates varaldii* (DP FNSP 6328; d - f). a, d - anterior view; b, e - inner view; c, f - dorsal view; PD - *pars dentalis*; PF - *pars facialis*; PP - *pars palatina*; cd - *crista dentalis*; cl - *crista lateralis*; lh - *lamina horizontalis*; rm - *recessus marsupiatus*; sd - *sulcus dentalis*.

(1919). The basal, horizontally situated part of the praemaxilla is called the *pars dentalis.* Approximately in the middle of its dorsal margin a flattened outgrowth is given off called the *pars facialis* which is directed posterodorsally and slightly laterally. The outer surface of this outgrowth is smooth and convex, whereas on its inner surface there is an elongated concavity which deepens ventrally. Its bottom is at the level of the *lamina horizontalis.* A distinct *crista lateralis* runs down along the lateral part of the outer surface of the *pars facialis.* After reaching the dorsal surface of the *pars dentalis,* the *crista lateralis* gradually becomes lower, and entirely disappears close to the praemaxillo-maxillary suture. An edge which laterally borders the concavity on the inner surface of the *pars facialis* joins the *lamina horizontalis* dorsally. Thus, a depression arises between this edge and the *crista lateralis,* called the *recessus marsupiatus* by BOLKAY (1919: 286, fig. 8). Medially, the *pars facialis* is rounded.

The outer surface of the *pars dentalis* is slightly convex and smooth. Its ventral edge (*crista dentalis*) bears pleurodont teeth on its inner surface. The number of tooth positions ranges around 10 according to the age of the individual. BAYER (1884: 5) gives a tooth number 8—9; however this count represents probably only functional teeth, not the whole number of tooth positions. Teeth are completely lacking in the medial section of the *crista dentalis* close to the median symphysis. They are replaced in waves afflicting odd and even tooth positions separately. On the inner surface of the *pars dentalis* runs the *lamina horizontalis* at the level of the tooth bases. Its free margin is slightly turned ventrally so that a wide and shallow *sulcus dentalis* arises between this margin and the tooth bases. Medially, the *lamina horizontalis* begins to increase in width below the medial margin of the *pars facialis,* and passes into the *pars palatina.* From this point on the margin of *lamina horizontalis* a tiny ridge runs towards the most medial tooth position, which thus separates the tooth bearing section of the *crista dentalis* from the toothless one.

The *pars palatina* is represented by a thin horizontal lamina which is a continuation of the *lamina horizontalis.* Its margin forms a point at the place of contact with the *pars palatina* of the opposite praemaxilla.

Laterally, the *pars dentalis* adjoins the maxilla by a praemaxillo-maxillary suture (*symphysis maxillaris* sensu BOLKAY, 1919: 286), while medially both praemaxillae contact each other in a median symphysis. The medial margin of *pars dentalis* rather protrudes so that the contact between both praemaxillae is very tight in this place. Contrary to this, both *partes palatinae* are more free. The elastic tissue in both the praemaxillo-maxillary suture and median symphysis quarantee some mobility in the dorso-ventral direction of the whole complex of both praemaxilae as well as of each praemaxilla separately. The *cartilagines praenasales superiores* and *inferiores* serve in these movements as a leading pulley.

The distal section of the *pars facialis* is adjoined by septomaxilla. The space which is enclosed by the lateral margin of the *pars facialis praemaxillae, crista lateralis praemaxillae, lamina anterior maxillae,* and septomaxilla, is covered by a soft tissue, which completes an exocranial cover within this area.

The nasal (fig. 26a) is a flat dermal bone whose medial part covers the *tectum nasi,* while its lateral part covers the postnasal wall.

This bone in *Pelobates* is briefly mentioned by BOLKAY (1919: 290), but under the name *praefrontale.* The *facies dorsalis* is slightly convex and sculptured. The sculpture is formed by small nipple-like outgrowths or ridges. In the lateral part of the *facies ventralis* there is a shallow depression; this surface is otherwise more or less flat and smooth. The medial part of the nasal gives off anteriorwards a wide *processus anterior,* so that the *margo medialis* of this bone is quite long. The *processus anterior* takes part in bordering the *fenestra exonarina* which, however, is filled by *cartilago obliqua* in this area. The *pars lateralis* is rather broader. Anterolaterally it gives off an indistinct *processus parachoanalis* (sensu BOLKAY, 1919, fig. 12), while posterolaterally the pointed *processus paraorbitalis.* The margin of the nasal between the mentioned outgrowths is called *margo maxillaris.* The sculpture is lacking along the *margo maxillaris* and this unsculptured part of the *facies dorsalis* forms a part of the bottom of the groove for the *ductus nasolacrimalis.* The whole posterior margin of the nasal is called the *margo orbitalis.* It is slightly bent and serves as the anterior margin of the orbit. Between the *margo medialis* and the *margo orbitalis* the margin

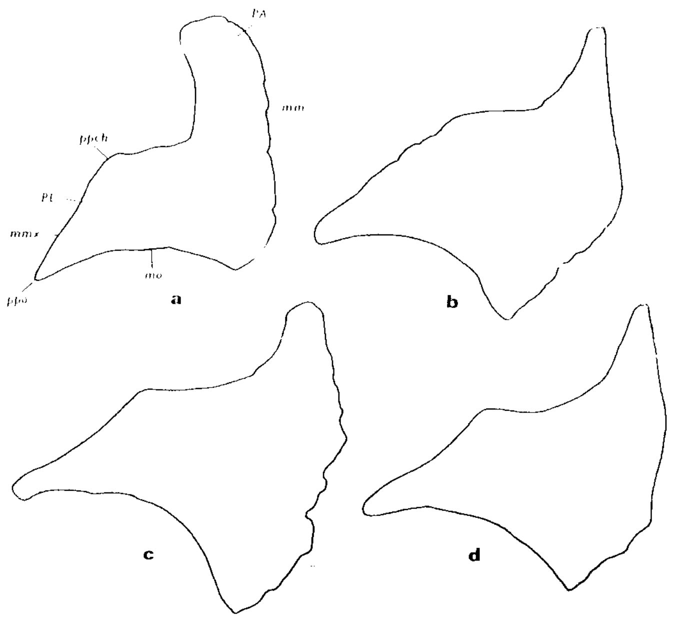


Fig. 26. Dorsal view of the left nasals in: a - *Pelobates fuscus* (DP FNSP 6474), b - *Pelobates varaldii* (DP FNSP 6328), c - *Pelobates cultripes* (DP FNSP 10002), and c - *Pelobates syriacus syriacus* (DP FNSP 2111). PA - *processus anterior*; PL - *processus lateralis*; mm - *margo medialis*; mmx - *margo maxillaris*; mo - *margo orbitalis*; ppch - *processus parachoanalis*; ppo - *processus paraorbitalis.*

of the nasal adjoins in a short section the frontoparietal in *sutura transversalis* (sensu Bolkay, 1919: 290). The length of this section varies according to whether or not the sphenethmoid is uncovered in this area. The nasal adjoins only the opposite nasal, maxilla and frontoparietal, but not the praemaxilla.

In the area among nasals and frontoparietal a tiny unpaired element may occur (fig. 29). For a more detailed discussion concerning this see chap. 4.2.3 Homologization of the exocranium.

The frontoparietal (fig. 27) is an unpaired flattened dermal element, covering the braincase dorsally in the whole extent of the orbitotemporal region, extending on the *tectum synoticum* in the posterior direction, and covering also a part of the roof of the otic capsule above the *canalis semicircularis anterior* and *ductus semicircularis posterior*.

This bone was studied by number of people who investigated it from different viewpoints (Bayer, 1884; Boas, 1914; Bolkay, 1919; Sewertzow, 1891). It is large and flat, comparatively thin anteriorly, while increasing in thickeness posteriorly. The *facies dorsalis* is sculptured similarly to the nasals. It is convex in its central part. Its margins (with exception of those parts which are connected with the nasals or with the uncovered part of the sphenethmoid) are rather elevated. The essential part of the lateral margin is represented by the *margo orbitalis* which laterally overhangs the braincase wall. This overhanging part of the frontoparietal is called the *tectum supraorbitale* (sensu Bolkay, 1919: 295). The *margo orbitalis* terminates

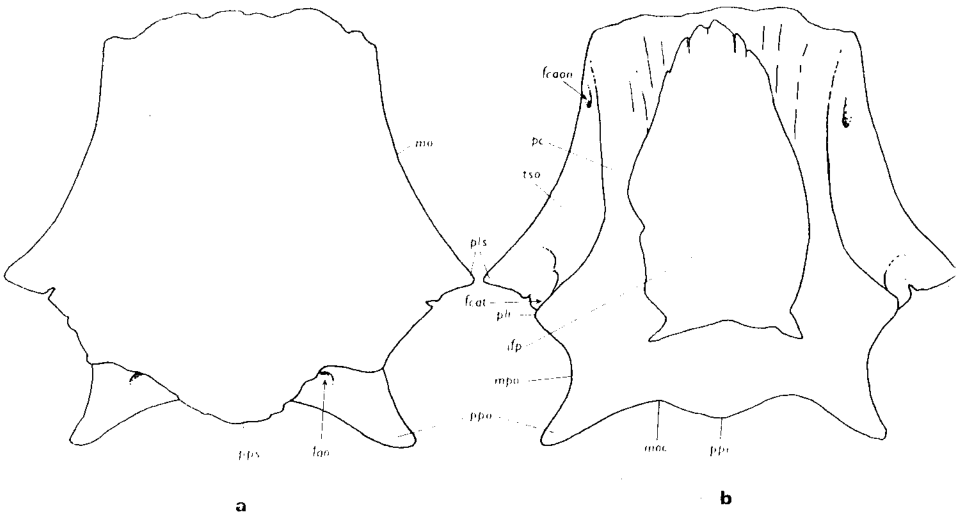


Fig. 27. Frontoparietal of *Pelobates fuscus* (DP FNSP 6474) in: a - dorsal view, b - ventral view. fao - *foramen arteriae occipitalis*; fcaon - orifice of *canalis arteriae orbitonasalis;* fcat - orifice of *canalis arteriae temporalis*; ifp - *incrassatio frontoparietalis*; moc - *margo occipitalis*; mpo - *margo prootica*; mo - *margo orbitalis*; pc - *pars contacta*; pls - *processus lateralis superior*; pli - *processus lateralis inferior*; ppo - *processus paraoccipitalis*; pps - *processus posterior superior*.

posteriorly on the *processus lateralis superior*. To this outgrowth is attached a narrow ligament called the *arcus postorbitalis*, which connects the frontoparietal bone with the opposite outgrowth of the squamosal. The margin of the *facies dorsalis* is directed from the *processus lateralis superior* posteromedially, and together with the corresponding margin of the opposite side forms the distinct *processus posterior superior*.

With the exception of its lateral parts, the *facies ventralis* is concave. It is possible to distinguish on it the ventral surface of the *tectum supraorbitale*, the part contacting the endocranium (*pars contacta*), and the central part filling the *fenestra frontoparietalis* (*incrassatio frontoparietalis*). The *pars contacta* and ventral surface of *tectum supraorbitale* meet each other in a rounded indistinct ridge running parallel with the *margo orbitalis* and terminating on the *processus lateralis inferior*. This outgrowth is not situated exactly below the *processus lateralis superior*, but rather more posteriorly and medially. Between both processes there is an opening of the *canalis arteriae temporalis* in a deep notch. From the *processus lateralis inferior* the margin of the *pars contacta* bends to the tip of the distinct *processus paraoccipitalis* (*margo prootica* sensu Bolkay, 1919, fig. 16), and from this point it runs to the *processus posterior inferior* situated at the mid-line (*margo occipitalis* sensu Bolkay, op. cit., fig. 16).

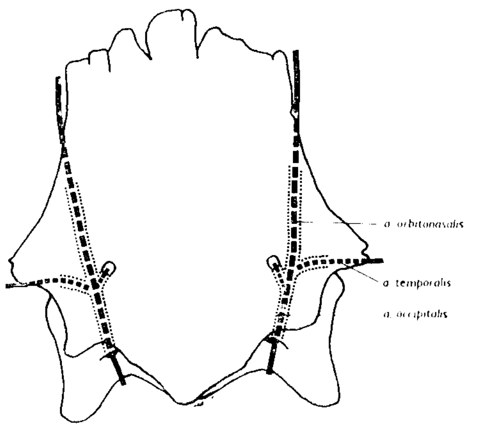


Fig. 28. Diagram to show courses of main vessels within frontoparietal, dorsal aspect.

Margins of *incrassatio frontoparietalis* (*superficies cerebralis* sensu Bolkay op. cit.: 295) are formed by a prominent ridge fitting into the *fenestra frontoparietalis* so that the incrassation and fenestra mutually correspond in shape.

The *facies posterior* is perpendicular, posterolaterally exposed part of the frontoparietal surface, which is situated posteromedially to the *processus lateralis inferior*. At about the middle of its length it gives off a long and pointed *processus paraoccipitalis* (sensu Bolkay, 1919: 295). Along its dorsal surface a low, indistinct ridge runs down from the margin of the *facies dorsalis*. There is a comparatively large *foramen arteriae occipitalis* (*foramen nutritium* sensu BOLKAY, op. cit.: 295) in the *facies posterior* medial to the mentioned process. This is the orifice of the canal continuing anteriorly (see fig. 28). The walls of the canal are pierced by tiny openings representing communications with irregular cavities in the bone. Dorsally, the canal splits off the narrow canals for branches of *arteria occipitalis* running into the subcutaneous space. At the level of the *processus lateralis inferior,* the *arteria occipitalis* splits into two branches: the *arteria orbitonasalis* running anteriorwards, and the *arteria temporalis* running laterad. Both run through similarly termed canals. The *canalis arteriae orbitonasalis* opens onto the ventral surface of the *tectum supraorbitale* approximately at the level of the posterior margin of the sphenethmoid. The *canalis arteriae temporalis* opens in the notch between the *processus lateralis superior* and *inferior*. The *arteria temporalis* then runs along the dorsal surface of temporal muscles, going obliquely below the *arcus postorbitalis.* The *arteria orbitonasalis* runs below the margin of the *tectum supraorbitale* along with the attachment of the orbital bedding anteriorwards, into the space below the *lamina supraorbitalis* of the sphenethmoid. It comes into the nasal cavity through the canal for the *ramus medialis n. ophthalmici.* In the vicinity of the branching of the occipital canal into the temporal and orbitonasal canals there is always present a short canal running to the dorsal surface of the bone, with a small branch of the *arteria occipitalis.*

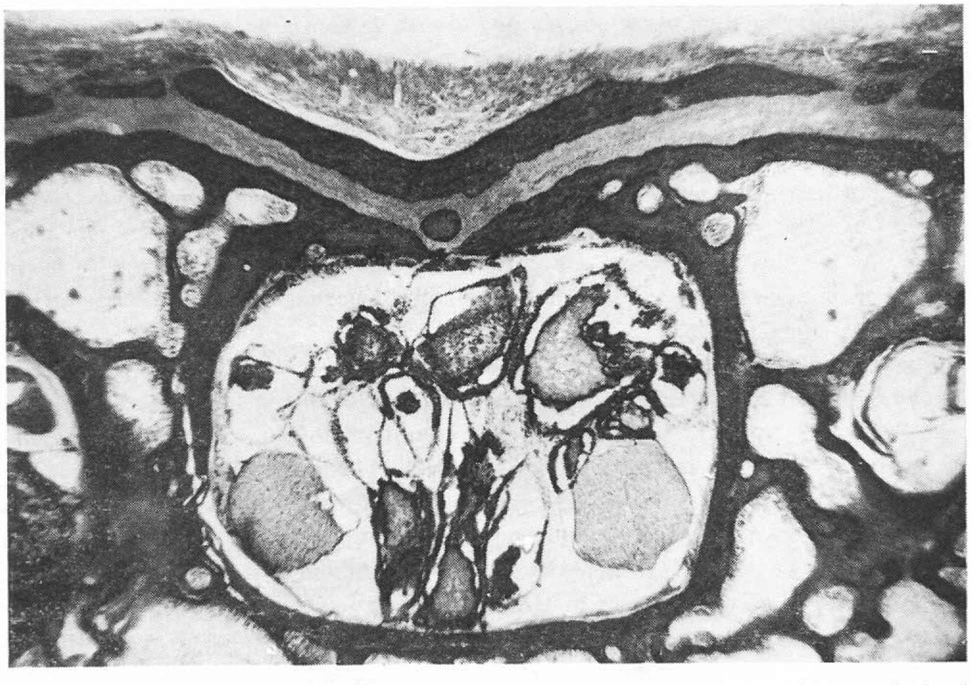


Fig. 29. Cross section through the neural endocranium of an adult *Pelobates fuscus* at the level of the anterior margin of the *fenestra frontoparietalis.* Note the tiny unpaired element located in the mid-line between the endocranial braincase roof and the frontoparietal.

The only exocranial elements contacting the frontoparietal bone are the nasals.

It is necessary to mention in connection with the dorsal exocranial bones a tiny unpaired element, embedded within the soft tissue between the frontoparietal and sphenethmoid close to the anterior margin of the *fenestra frontoparietalis* (fig. 29). With regard to its minute size it is possible to discover it only on the serial cross sections. It is characterized by its position at the mid-line, and in the tissue layer between the endocranial (i.e. *sphenethmoideum*) and exocranial (i.e. frontoparietal) elements. Its histology displays typical features of dermal bone. For further discussion see chap. 4.2.3 Homologization of the exocranium.

The bones of the cheek (septomaxilla, maxilla, squamosal, quadratojugal)

The septomaxilla (fig. 30) is a small bone of complicated structure, laterally adjoining the ethmoidal region of the endocranium. It borders the *fenestra exonarina* posteriorly and is pierced by the *ductus nasolacrimalis*.

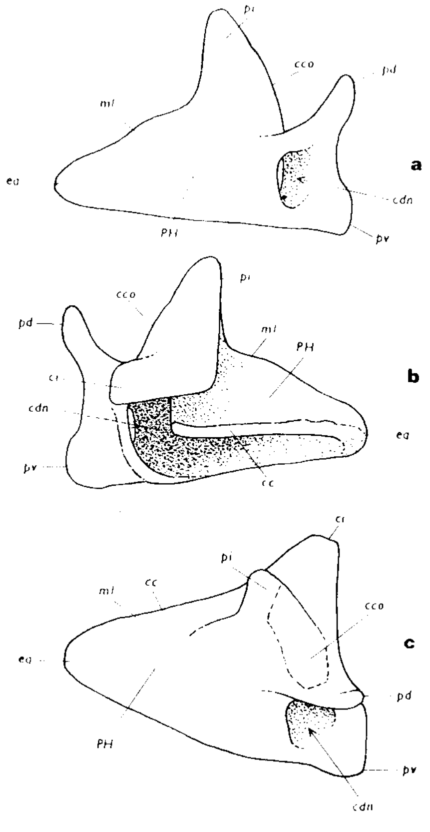


Fig. 30. General morphology of the septomaxilla of *Pelobates fuscus* in: a - lateral view, b - medial view, c - dorsal view. PH - *pars horizontalis*; cc - *crista contacta*; cdn - *canalis nasolacrimalis*; ci - *crista interna*; cco - area of contact with *cartilago obliqua*; ea - *extremitas anterior*; pd - *processus dorsalis*; pi - *processus intrafenestralis*; pv - *processus ventralis*.

The description of the bone in *Pelobates fuscus* (however, under the name *lacrimale*) is given by BORN (1876: 591), and in *Pelobates cultripes* by BOLKAY (1919: 288—290). For drawings see BOLKAY, 1933, tab. 10/5—9. This is a small element extending from the anterodorsal tip of maxilla into the *fenestra exonarina*. It was very often described under different names (for synonyms see STADTMÜLLER, 1936: 622; GAUPP, 1896: 53). Its descriptional terminology is as yet also considerably unstable.

Viewed laterally, the septomaxilla is seen to give off a big rounded outgrowth anteriorly (*extremitas anterior* sensu BOLKAY), directed into the space between the *cartilago alaris* and the *lamina inferior cristae intermediae* (fig. 11). The basal part of the septomaxilla is called the *pars horizontalis* (seu *corpus* sensu BOLKAY; for other synonyms see STADTMÜLLER, 1936: 622). The posterior part of the *pars horizontalis* gives off the *processus intrafenestralis* (for synonyms see STADTMÜller, op. cit.: 622) directed dorsally. In its anterior part the *pars horizontalis* is rounded dorsally (*margo libera* sensu BOLKAY, 1919, fig. 11). Medially, this part of the *pars horizontalis* is bordered by a thin horizontal ledge (*crista contacta*), adjoining the *lamina superior cristae intermediae*. Posteriorly, this ledge is terminated by a sharp apex which is directed into the nasal cavity. The ventral surface of *pars horizontalis* is plain, passing laterally onto the *facies externa* by a comparatively sharp ridge. The medial margin of the mentioned surface is bordered by a horizontal ledge parallel to the *crista contacta,* lying on the *lamina inferior cristae intermediae*. The *pars horizontalis septomaxillae* is deeply concave between both mentioned ledges, thus forming a lateral wall of the *recessus medius*. Dorsally, the *pars horizontalis* gives off the *processus intrafenestralis* which adjoins the *cartilago obliqua* by part of its posterior surface. It supports the posterior margin of the external nostril. Its basal part gives off medially a rather sharp ledge (*crista interna*), separating the *diverticulum principale* from the *diverticulum medium*. In its posterior part the *lamina horizontalis* is pierced by the *canalis nasolacrimalis* (cf. BORN 1876: 594), and terminated by dorsal and ventral processes adjoining the *planum terminale*.

The septomaxilla is connected with other parts of the exocranium only by the maxilla.

The maxilla (fig. 31) is a dermal bone laterally adjoining the ethmoidal region and the anterior part of the palatoquadrate; it bears the teeth thus forming anterolateral and lateral sections of the tooth arch.

The bone is briefly mentioned by BAYER (1884) and BOLKAY (1919). It is elongated in shape, and its ventral tooth-bearing edge is called the *crista dentalis*. The teeth are pleurodont, and the total count of tooth positions varies between 40—50 according to the age of animal. The method of tooth replacement is the same as with the praemaxilla. The *lamina horizontalis* similar to that in the praemaxilla is also present; it is narrow close to the praemaxillo-maxillary suture, but it increases in width posteriorly and its margins gradualy increase in thickness. Between this margin and the tooth bases there is the *sulcus dentalis*. The *lamina horizontalis* is terminated by a distinct *processus pterygoideus* which is in contact with the pterygoid. This outgrowth is situated comparatively posterior in aged specimens, which is associated with an increase in the number of tooth positions in the course of life. A low ridge runs down from the base of this outgrowth to the *crista dentalis*, thus separating the posterior toothless section of the crista. This toothless section of the *crista dentalis*

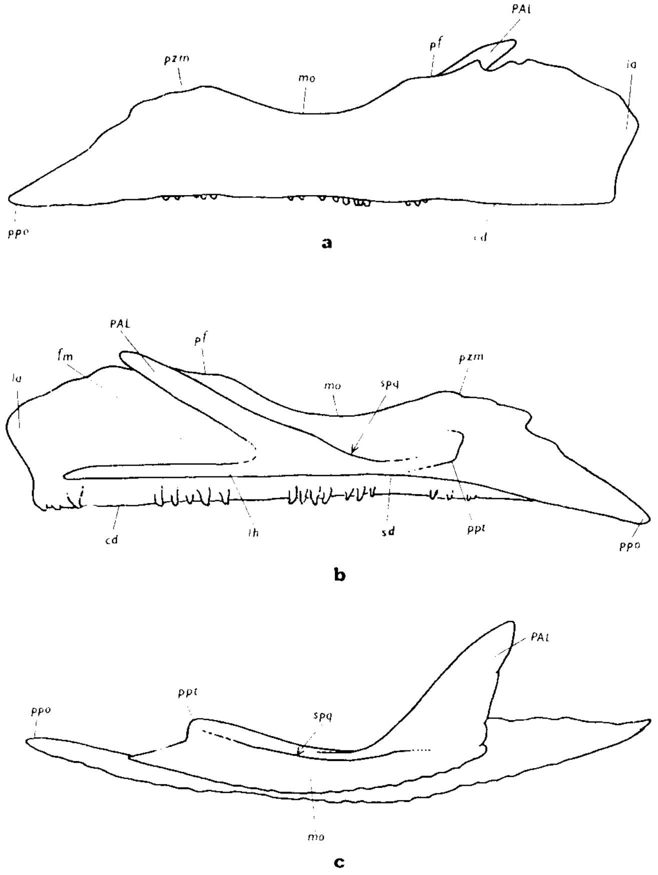


Fig. 31. General morphology of the maxilla of *Pelobates fuscus fuscus* (DP FNSP 6474) in: a - lateral aspect, b - medial aspect, c - dorsal aspect. PAL - *processus palatinus*; cd - *crista dentalis*; fm - *fossa maxillaris*; la - *lamina anterior*; lh - *lamina horizontalis*; mo - *margo orbitalis*; pf - *processus frontalis;* pt - *processus pterygoideus*; pzm - *processus zygomatico-maxillaris*; sd - *sulcus dentalis*; spq - groove for *pars palatina palatoquadrati*.

is terminated posteriorly by the *processus posterior* by which the maxilla contacts the quadratojugal. If viewed laterally, other outgrowths may also be distinguished: the *processus zygomatico-maxillaris* (sensu BOLKAY, 1919, fig. 9), directed posterodorsally, and the indistinct *processus frontalis* on the dorsal margin of the anterior half of the maxilla. The latter process lacks sculpture along its dorsal margin, for it takes a part in the formation of a groove for the *ductus nasolacrimalis*. The dorsal margin of the bone between the *processus zygomatico-maxillaris* and the *processus frontalis* is concave and rounded, thus forming the *margo orbitalis*. The most anterior part of the maxilla is the widely rounded *lamina anterior* which exceeds the level of anterior end of the *crista dentalis*. The *lamina anterior* is in contact with the septomaxilla. The whole outer surface of the maxilla is sculptured.

On the inner surface of the maxilla there is a long, slender outgrowth directed anteromedially and slightly dorsally, called the *processus palatinus*. Already Sewertzow (1891: 153) pointed out that this represents the *palatinum* fused with the maxilla. Down its dorsal surface runs a groove which passes onto the dorsal surface of the posterior section of the *lamina horizontalis*. It is filled by the *processus antorbitalis* and the adjacent section of the palatoquadrate. Between the proximal part of the *processus palatinus* and the anterior part of the *lamina horizontalis* there is a depression called the *fossa maxillaris*.

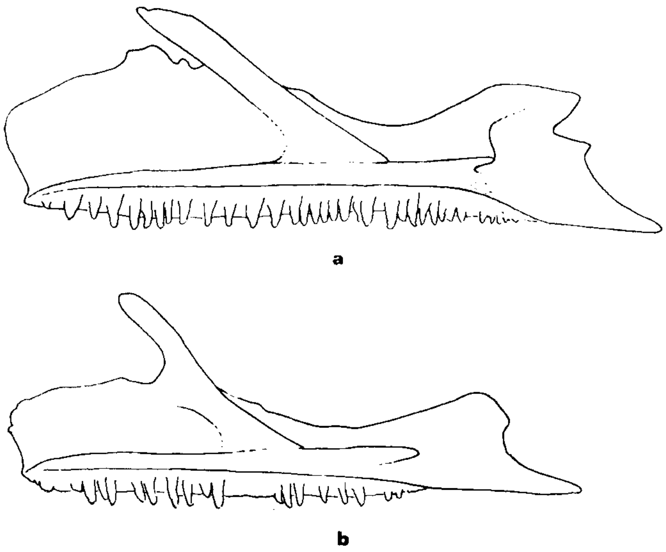


Fig. 32. Maxillae of a - *Pelobates syriacus syriacus* (DP FNSP 2111) and b - *Pelobates varaldii* (DP FNSP 2122) in medial view.

The maxilla is immediately connected with the praemaxilla, septomaxilla, nasal, pterygoid, squamosal and quadratojugal.

The squamosal (fig. 33) is a dermal bone laterally adjoining the otic capsule above the level of the *fenestra ovalis,* and covering also the *pars quadrata palatoquadrati*.

Besides Bayer (1884) and Bolkay (1919) (both mentioned this bone under the name *os tympanicum*), also Boas (1914) presented some data on this element. Its central part is flattened and rhomboid in shape. This part of the bone is called the *lamella alaris* according to BOLKAY (1919, fig. 17). Its outer surface is sculptured, while the inner surface is smooth. It is connected by its short ventral margin (called the *processus zygomaticus squamosi* sensu BOLKAY 1919) with the *processus zygomatico-maxillaris maxillae*. Along the line of their mutual contact there is rather long and firm squamoso-maxillary suture. Thus, both processes form a bone bridge which is called by BOAS (1914: 253, fig. 17) simply »Brücke zwischen der Augenöffnung und dem seitlichen Fenster«, while BOLKAY (1919: 296) called it incorrectly the *arcus zygomaticus*. The anterodorsal margin of *lamella alaris* represents the *margo orbitalis,*

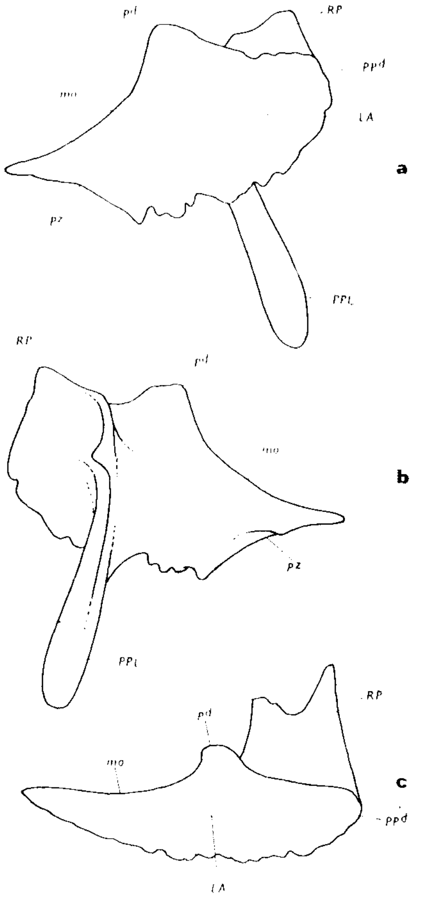


Fig. 33. Squamosal of *Pelobates fuscus fuscus* (DP FNSP 6474) in a - lateral aspect, b - medial aspect, c - dorsal aspect. LA - *lamella alaris*; PPL - *processus posterolateralis*; RP - *ramus paroticus*; mo - *margo orbitalis*; pd - *processus dorsalis*; ppd - *processus posterodorsalis*; pz - *processus zygomaticus*.

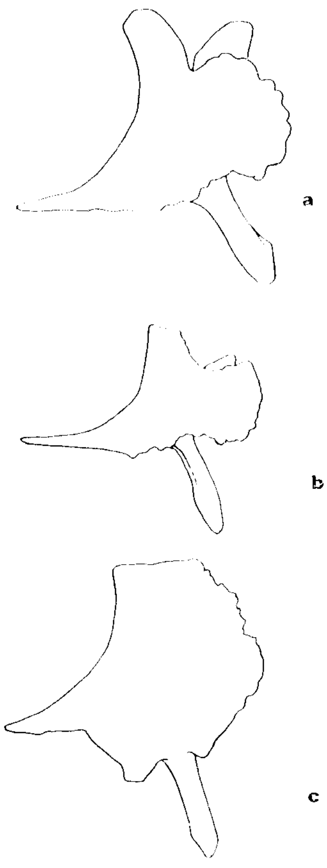


Fig. 34. Squamosals of a - *Pelobates syriacus syriacus* (DP FNSP 2111), b - *Pelobates varaldii* (DP FNSP 2122), and c - *Pelobates cultripes* (DP FNSP 10002), in lateral aspect.

and is terminated by the *processus dorsalis,* to which the *arcus postorbitalis* (a narrow ligament running from the *processus lateralis superior ossis frontoparietalis*) is attached. The dorsal margin of the *lamella alaris* is concave, and is terminated posteriorly by a big *processus posterodorsalis.* From its inner dorsal surface the *ramus paroticus* is given off, and this dorsally and laterally adjoins the *crista parotica.* A slender *processus posterolateralis* runs out from the base of the *ramus paroticus* (approximately in the middle of the posteroventral margin of the *lamella alaris* in lateral aspect) posterolaterally (BAYER, 1884: 7, tab. I/1 considered this outgrowth an independent bone *symplecticum*). On its medial surface there is a groove which in situ is complemented by a similar groove on the *ramus posterior pterygoidei* in the canal storing the *pars quadrata palatoquadrati.* In other frogs the *anulus tympanicus* is present in the space between the *processus posterodorsalis* and the *processus posterolateralis,* although it is lacking in *Pelobates.*

Hence, the squamosal is in contact with the maxilla and pterygoid; moreover the distal part of the *processus posterolateralis* is also in contact with the quadratojugal.

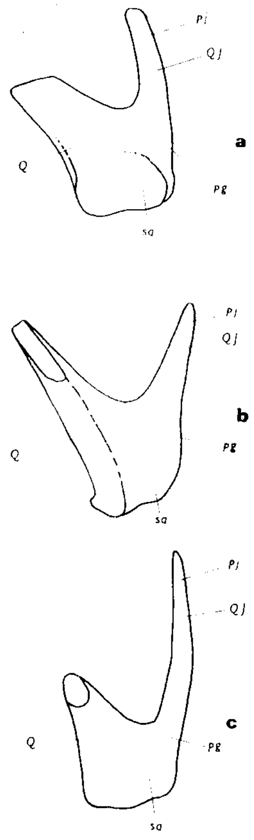


Fig. 35. Ossified quadrate + quadratojugal complex in ventral aspect. a - *Pelobates fuscus fuscus* (DP FNSP 6474), b - *Pelobates syriacus syriacus* (DP FNSP 2111), c - *Pelobates varaldii* (DP FNSP 2122). Q - *quadratum*; QJ - quadratojugal; pg - *pars glenoidalis ossis quadratojugalis*; pj - *pars jugalis ossis quadratojugalis*; sa - area taking part in articulation with the articular.

The quadratojugal (fig. 35) is a short rod-like dermal bone posterolaterally adjoining the distal ossified section of the *pars quadrata palatoquadrati* (*os quadratum*), and fusing with it synostotically. STADTMÜLLER (1936: 633) erroneously considers the whole quadratojugal-quadratum complex as the quadratojugal: »Bei Anuren tritt in einem Bande ... eine Bindegewebsverknöcherung auf, die sich später bis auf den Knorpel des Palatoquadrats ausdehnt und in diesen eindringt, d. h. einen Mischknochen bildet«.

It is a short rod-like element which can be distinguished according to BOLKAY (1919: 287) into the *pars jugalis* directed anteriorly, and the *pars glenoidalis* adjoining the *os quadratum*. The distal section of the *pars jugalis* is terminated by an oblique facet exposed ventrolaterally; it is in contact with the *processus posterior maxillae*. The *pars glenoidalis* makes contact dorsally with the distal part of the *processus posterolateralis squamosi*. Thus, the maxilla and squamosal are the only exocranial elements contacting the quadratojugal.

The dermal bones of the palate (vomer, palatine, parasphenoid, pterygoid)

The vomer (fig. 36) is a paired dermal bone bearing the teeth, ventrally covering the *solum nasi* medially to the *fenestra endochoanalis*.

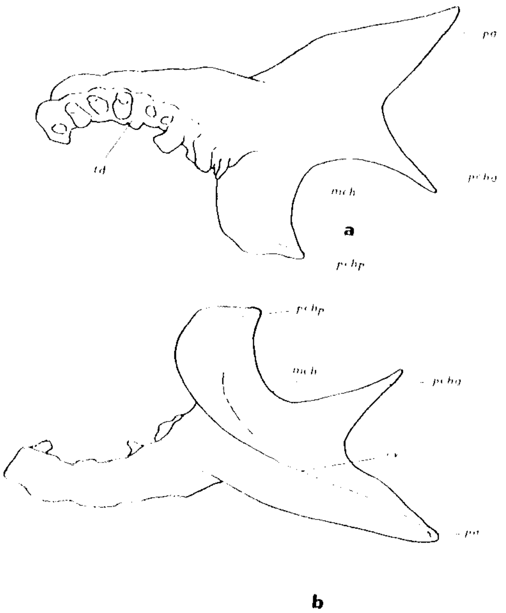


Fig. 36. Left vomer of *Pelobates fuscus* (DP FNSP 6474). a - ventral view; b - dorsal view. cv - *crista vomeri*; mch - *margo choanalis*; pa - *processus anterior*; pcha - *processus choanalis anterior*; pchp - *processus choanalis posterior*; td - *torus dentigerus*.

Huxley (1873, ex Stadtmüller, 1936: 638) stated erroneously that this bone is lacking in *Pelobates*. Bolkay (1919: 300) distinguishes on the vomer its antero-posteriorly flattened part directed medially, which bears on its ventral edge (*torus dentigerus*) 7—9 tooth positions. The tooth row is arch-like, convex anteriorly. The presence of replacement teeth in some positions, as well as the resorbed bases of some teeth suggest that teeth are replaced also in the vomer. Teeth seem to be acrodont, with their pedicels fused with each other thus forming a mound. However, the base of each tooth is marked by an opening directed posteriorly which is caused by the process of resorption. Thus the pedicel is gradually resorbed from its posterior surface, which finally results in a shedding of the upper tooth part. The replacement tooth starts to develop in the shallow vertical groove between the two adjacent pedicels, and is a derivative of the membranous *lamina dentalis*; only during further development does it ankylose to the bone. The tooth crowns are slender, and their hook-like tips are directed posteriorly.

The thin, lateral part of the vomer gives off three outgrowths. The *processus anterior* is directed anterolaterally, to the praemaxillo-maxillary suture. The *processus choanalis anterior* is directed laterally, approximately in the long axis of the *torus*

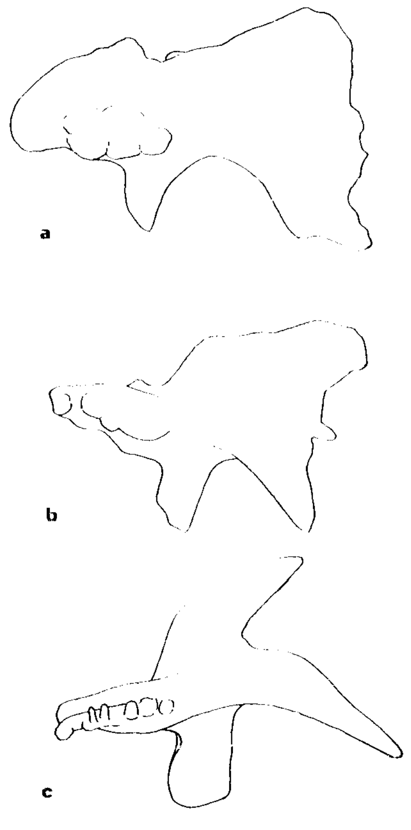


Fig. 37. Left vomers in ventral aspect. a - *Pelobates cultripes* (DP FNSP 10002); b - *Pelobates varaldii* (DP FNSP 6328); c - *Pelobates syriacus syriacus* (DP FNSP 2111).

dentigerus. From the margin of the vomer between both these processes a flat membranous ligament runs to the inner surface of the *lamina anterior maxillae*. It thus completes the lacking part of the palate. The *processus choanalis posterior* is the third outgrowth, directed posterodorsally. The margin between both choanal processes is called the *margo choanalis,* and bounds the *fenestra exochoanalis*. Owing to the posterodorsal position of the *processus choanalis posterior,* the choana opens into the mouth cavity posteroventrally. Its posterior margin is rather submerged below the level of the *processus palatinus maxillae*.

On the dorsal surface of vomer there is a distinct *crista vomeri* taking part in a fixation of the bone to the lateral margin of *solum nasi*. This ridge runs from the *processus choanalis posterior* to the *processus anterior*. The vomer is entirely isolated from all other exocranial elements. The course of its lateral margin between both mentioned processes considerably varies (differences between left and right vomers exist also).

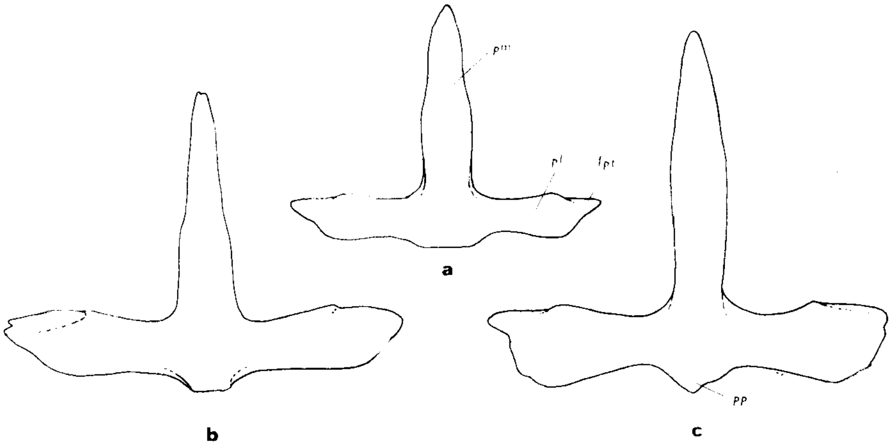


Fig. 38. Parasphenoids in ventral view. a - *Pelobates fuscus fuscus* (DP FNSP 6474); b - *Pelobates syriacus syriacus* (DP FNSP 2111); c - *Pelobates cultripes* (DP FNSP 10002). ftp - area of contact with pterygoid; pl - *processus lateralis*; pm - *pars medialis*; pp - *processus posterior*.

The palatine is a flat elongated dermal bone adjoining the postnasal wall ventrally, thus forming the posterior margin of *fenestra endochoanalis*. In *Pelobates* it is fused with the maxilla, forming the *processus palatinus maxillae* (fig. 31, 59 a, b).

The parasphenoid (fig. 38) is an unpaired, flat, T-shaped bone, which adjoins the braincase ventrally in the otic and orbitotemporal regions, covering also the floors of the otic capsules.

In accordance with the terminology introduced by Bolkay (1919: 301—303) (who called this bone the *parabasale*) it is possible to distinguish the following parts of the bone: the *pars medialis,* directed anteriorly, and two lateral outgrowths (*processus lateralis dexter et sinister*). The dorsal surface of *pars medialis* is concave, forming a wide groove parallel with its longitudinal axis, while the ventral surface is correspondingly convex. This modellation is in accordance with the general shape of the braincase floor. Approximately in the middle of the length of the free part of the *pars medialis* there is a rounded outgrowth on the left and right margins; anteriorly to these processes the *pars medialis* gradually narrows. Both *processus laterales* are directed not only laterally, but also rather ventrally, in accordance with the slanting bases of the otic capsules. The dorsal surface of *processus laterales* is rather concave and rough, while the ventral surface is smooth and convex in the plane perpendicular to the long axis of the processus. Both anterior and posterior margins of *processus lateralis* rather diverge in their proximal sections, whereas in their distal thirds they break to converge, so that the *processus laterales* are pointed. The distal third of the anterior margin is in contact with the pterygoid.

The medial section of the posterior margin of the bone (where the *processus posterior* is present in some other genera, e. g. *Bufo*) is only slightly convex. BOLKAY (1919: 302) mentioned that in aged specimens of *Pelobates fuscus* and *Pelobates cul-*

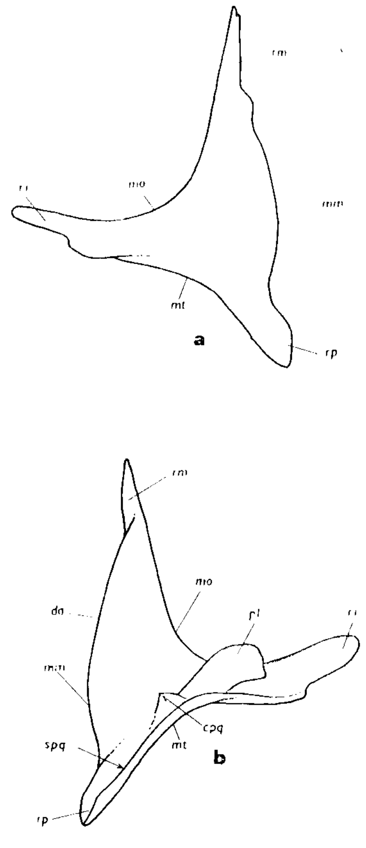


Fig. 39. Left pterygoid of *Pelobates fuscus fuscus* (DP FNSP 6474). a - ventral view; b - dorsal view. cpq - orifice of canal filled with that part of the palatoquadrate which is housed within the *ramus maxillaris*; da - *dilatatio alaris*; mt - *margo tympanicus*; mm - *margo mandibularis*; mo - *margo orbitalis*; ri - *ramus interior*, rm - *ramus maxillaris*; rp - *ramus posterior*; pl - *processus lingualis*.

tripes (see also p. 130) there is a low ridge on the ventral surface of the *pars medialis*, bearing a row of tooth-like outgrowths.

The pterygoid is the only exocranial bone which is in contact with the parasphenoid.

The pterygoid (fig. 39) is the element adjoining the posterior part of palatoquadrate ventrally; besides, it adjoins the neural endocranium in the limited area of the anterolateral wall of the otic capsule.

A rather modified terminology of BOLKAY (1919: 303—305) will be used in the following description. However, it must be noted that fig. 26 in BOLKAY'S paper which shows the left pterygoid of *Pelobates cultripes* in dorsal aspect is incorrectly designated as the right pterygoid in ventral aspect (similarly also figs 27—29 of the paper cited). In dorsolateral aspect, it is possible to distinguish the central part of the bone giving off three outgrowths: the *ramus maxillaris* directed anteriorly, whose distal section medially adjoins the posterior part of the inner surface of the maxilla, the *ramus posterior* directed posterolaterally, and the *ramus interior* directed dorsomedially. A sharp, ventrally directed edge (*margo mandibularis*) connects the *ramus maxillaris* and the *ramus posterior*; it is extended by a distinct *dilatatio alaris* approximately in the middle of its length. The margin between the *ramus maxillaris* and the *ramus interior* (*margo orbitalis*) is rounded, forming part of the palatal margin of the orbit. The *ramus interior* is shaped like a cornet, and adjoins the anterolateral part of otic capsule. Its lower margin is in contact with the anterior margin of the distal third of the *processus lateralis parasphenoidei*, and passes by a flexure (*margo tympanicus*) onto *ramus posterior*. In contrast to this, the upper margin of the *ramus interior* runs out dorsolaterally as the *processus lingualis*. This tongue-like outgrowth does not belong the *margo tympanicus*, but both represent two adjacent lamellae connected synostotically. The lateroventral edge of the *processus lingualis* slants along the laterodorsal surface of the bone to its centre where it breaks its course to continue as an indistinct ridge onto the *ramus posterior*. This broken edge bounds an opening which is mistakenly (see below) interpreted by Bolkay as »sinus pro tuba Eustachii«. The stripe of bone between the mentioned indistinct ridge and the *margo tympanicus* represents that part of the pterygoid which medially completes the canal (formed laterally by a groove on the surface of the *processus posterolateralis squamosi*) for the cartilaginous part of the *pars quadrata palatoquadrati*. The *processus pterygoideus palatoquadrati* runs through the canal in the *ramus maxillaris pterygoidei*. The palatoquadrate branches within the pterygoid into its characteristic outgrowths; one of them (*pars quadrata palatoquadrati*) runs out from the bone through the opening called incorrectly by BOLKAY »sinus pro tuba Eustachii«.

The medioventral surface of the pterygoid is smooth and besides three processes visible in both dorsolateral and medioventral aspects it displays no other morphological particularities.

Of the exocranial elements only the maxilla, the parasphenoid and the squamosal contact the pterygoid.

The dermal bones of free parts of the visceral endocranium (dentary, praearticular, parahyoid)

The dentary is an elongated dermal bone laterally adjoining the anterior part of Meckel's element, and contacting the corresponding opposite element in median symphysis.

The morphology of the bone is very simple: it is a considerably thin, elongated bone lamella which forms an anterolateral section of the lower jaw arch. Its ventral edge is even, while the dorsal one is slightly convex; the top of this convexity is in that half of the bone which adjoins the symphysis.

The dentary of adults is fused with the vestigial and ossified *cartilago labialis inferior* (mentomandibular). Thus a bone complex of both enchondral and endesmal origin arises.

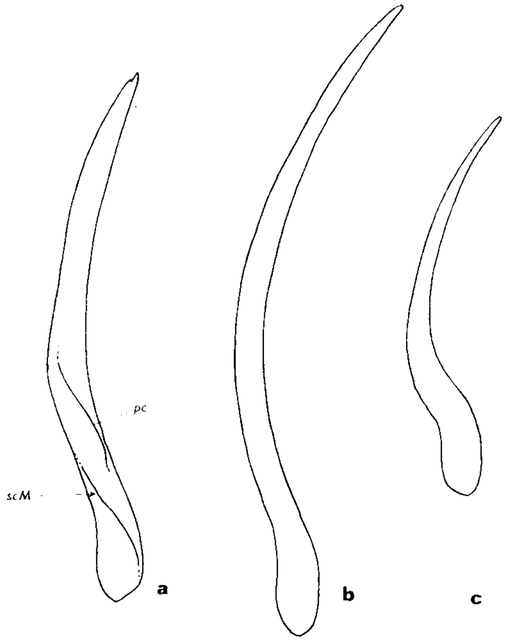


Fig. 40. Left praearticular of *Pelobates fuscus fuscus* (DP FNSP 6474). a - in dorsal aspect; b, c - imprints of praearticulars of *Eopelobates bayeri* (DP FNSP 183 b, 9641 b). pc - *processus coronoideus*; scM - sulcus for Meckel's element.

The praearticular (fig. 40) is an elongated dermal bone adjoining the posterior section of Meckel's element medially and ventrally.

It follows from the survey of the names used for the designation of this element by earlier authors (gonial, angular, amphibienangular, postopercular, postsplenial, dermarticular, praearticular, coronoid, splenial, angulosplenial) that some uncertainty concerning the homology of this element existed in the past. Similarly to the dentary, it is a thin elongated bone which is slightly S-shaped if viewed dorsally. A distinct *sulcus pro cartilago Meckeli* runs on the lateral surface of the anterior section of the bone, while in its posterior section this groove comes onto the dorsal surface, and close to its posterior end it considerably increases in width. In that section where Meckel's element comes onto the dorsal surface of the bone there is an indistinct *processus coronoideus*.

The dentary adjoins the praearticular along its outer surface, covering Meckel's element laterally.

The parahyoid is a diminutive ossification arising inconstantly on the ventral hyoid surface. Its occurrence in *Pelobates* (see p. 34) is probably associated with the age of an animal.

Exocranial openings

The largest openings in the exocranial roof are the orbits, which are completely bounded by dermal bones in *Pelobates cultripes* (Boas, 1914, fig. 16, 18; Bolkay, 1933, tab. I/1), while in *Pelobates fuscus* this circumorbital ring is interrupted posteriorly (Boas, op. cit.: 17, 19; Bolkay, op. cit., tab. I/2; 1919, fig. 6). However, even in *Pelobates cultripes* neither the squamosal nor the frontoparietal intimately adjoin the dorsal surface of the prooticooccipital; hence, a space remains here which is connected with the orbit anteriorly, while posteriorly it is opened by the so-called »posterior temporal fenestra« (see Boas, 1914: 249, fig. 18). This space is an analogue of the *fossa bridgei* in *Eusthenopteron*.

In pelobatids there is another opening in the skull roof between the quadratojugal and the squamosal which is called by Boas (op. cit.: 249, fig. 16, 17) the »lower temporal fenestra«. The *fenestra exonarina* and an unpaired opening through which the *processus praenasalis medius* comes onto the skull surface are other openings in the exocranial roof.

The exocranial mouth cavity roof is much more reduced. In the area of the orbits the palate is entirely lacking so that the orbits are separated from the mouth cavity only by a thin membrane in living individuals. The exocranial elements of other parts of the palate are reduced and completely isolated in some cases (e. g. vomers) so that the endocranial elements remain uncovered. Besides the orbits, also the *fenestrae exochoanales* and the so-called »ventral opening of lower temporal fossa« (see Boas, 1914, fig. 22) which is bounded by the quadratojugal, pterygoid and praemaxilla occur. Chewing muscles originating on the *processus coronoideus* of praearticular come into this fossa. The space of the »lower temporal fossa« also has a communication with the orbit.

4.2.2 Ontogenetic development of the exocranium

The ontogeny of the exocranium of *Pelobates fuscus* was treated by Sewertzow (1891) and partly also by Reinbach (1939b). In the following description only the most important data will therefore be given.

Ossification of exocranium begins in the areas of the frontoparietal and parasphenoid; it starts earlier than indicated by any signs of ossification which can be ascertained on the endocranium. The frontoparietal ossifies first (fig. 43; see also Luther, 1914, figs 16—20) from two ossification centres above the lateral parts of the braincase in the orbitotemporal region. Their ossification advances medially and only later also posteriorly above the otic region. In the area of the future frontoparietal also the third unpaired element, which is situated on the *tectum synoticum*, begins to develop (see also Jarvik, 1967: 196, pl. III/A). At the beginning it develops quite independently, but later, in consequence of its growth anteriorly, it adjoins the anterior elements; this takes place when these anterior parts are not yet joined together. Just before metamorphosis, yet a further ossification appears on the medial parts of the otic capsules, separated from the above-mentioned element by the *arteria occipitalis*. These elements extend from the anterior margin of the *prooticum* to the posterior margin of the capsules. The process of fusing of these ossifications has been described by Reinbach (1939b, figs 2—5) and it has also been mentioned by Sewertzow (1891: 151—152, fig. 7). On the definitive frontoparietal, the above-mentioned elements represent those parts which lie laterally from the *arteriae occipitales*, i. e. inclusive of the *processus paraoccipitales*. The inconspicuous unpaired ossification centre may be discerned just in front of the anterior paired elements meet each other medially, in the area above the anterior margin of the *fenestra frontoparietalis*. This centre expands partly posteriorly where it fuses with the main part of the complex, partly anteriorly where it closes to different extents the area between the posteromedial margins of the nasals. This element markedly influences the variability of shape of the anterior margin of frontoparietal.

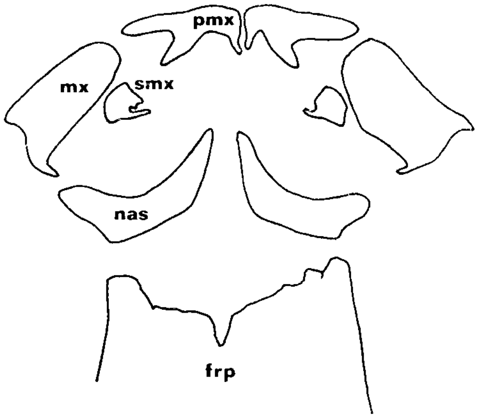


Fig. 41. Ethmoidal region of a metamorphosing *Pelobates fuscus* tadpole in anterodorsal view o show the degree of ossification of respective exocranial elements. frp - frontoparietal; mx - maxila ; nas - nasal; pmax - praemaxilla; smx - septomaxilla.

The parasphenoid is the second in the ossification sequence. But from the very beginning it has an approximately definitive shape. The sole difference consists in that the posterior margin of the *pars medialis* is deeply incised. During metamorphosis, further exocranial bones also begin to develop (fig. 41). The anterior part of the maxilla arises in its section anterior to the level of the postnasal wall and the praemaxilla on which the *pars dentalis* is developed at first and only later does the *pars facialis* attain its final size. BORN (1876: 608) however described an inverse ossification sequence in the praemaxilla, and LEBEDKINA (1968: 327, 328) similarly did with *Rana ridibunda*. It is worthy of note that the septomaxilla inclusive of its *processus intrafenestralis* is already well developed near the anterior upper angle of the maxilla; in relation to the praemaxilla and maxilla it is larger than that in the adult individual. It is in this stage that the vomers begin to ossify.

At the final stages of metamorphosis and immediately after it, the maxilla attains its definitive shape, and the squamosal, pterygoid, praearticular and dentary arise. Among the last bones of the exocranium to ossify are the quadratojugals (cf. CARROLL and HOLMES, 1980: 7); this takes place at the time when the quadrate is already well ossified. The palatines arise as independent ossifications, but they soon fuse with the maxillae.

4.2.3 Homologization of the exocranium

In the last decades particular attention has been directed to the homologization of the exocranium in lower vertebrates, especially in connection with the problems concerning the interpretation of the bones of the cranial roof (for a survey see e. g. JARVIK 1967: 181—184; LEBEDKINA, 1979: 157—160). The respective discussion was focused particularly on the problem of the choice of the criteria for homologization. Homologization based on the course of sensoric lines (for a survey see PARRINGTON, 1949: 65—68) is a relatively reliable method, as ossification centres arise around accumulations of neuromasts. The disadvantage of this criterion consists in the fact that it can be used only for water and the most archaic terrestrial vertebrates which still possess sensoric lines. This is why further criteria have been sought for homologization of the bones of water and terrestrial vertebrates. One such criterion may be seen in the topographical relation of the exocranial elements to the brain; that is why the position of the pineal opening in fossil vertebrates became fairly important, as it is according to this that the proportions and the position of the brain may be determinated, at least approximately. But the significance even of this criterion diminished when consideration was given to the ontogenetic and individual variability of the pineal opening's position, which property resulted from the disproportional growth of the brain in relation to the neurocranium (e. g. GEIGER, 1956); this criterion also became less suitable because pineal openings in various groups of vertebrates are filled with different (pineal or parapineal) organs (JARVIK, 1967: 185, 186), and that therefore these openings are not homologous.

The most reliable criterion for homologization of the exocranium has hitherto been revealed in its topographical relation to the endocranium. This relation may even be verified experimentally. It has been found that certain fields of the cartilage of the endocranium directly induce the origin of dermal bones. If the given field of the endocranium is experimentally disturbed, the dermal bone belonging to it does not develop. From this it may be inferred that the topographical correlation between the endocranium and the exocranium is very close (LEBEDKINA, 1979: 137). However, the individual elements of the exocranium retain their original position even after the partial reduction of the respective field of the endocranium during ontogeny, or after the complete disappearance of such a field (e. g. the frontals in urodeles - LEBEDKINA, 1979: 139).

The topographical relations of the exocranium to the endocranium in *Pelobates fuscus* have already been described in detail above. Below, only the most important data will be given on the position of the exocranial bones.

The most anterior part of the endocranium is covered lateral and ventral to the *processus praenasalis medius* by the praemaxilla, whose *pars dentalis* bears teeth and extends dorsally into the *pars facialis* and whose *pars palatina* is ventrally adjacent to the *processus praenasalis medius*. In *Eusthenopteron*, this area of the endocranium is covered by a number of minute elements which in some individuals may fuse with one another. These elements are the medial rostral, the praemaxilla, several postrostrals and the most anterior of the nasal series (JARVIK, 1942: 346—347). But this original state is found only very rarely, as the medial rostral mostly fuses with the praemaxilla forming the rostropraemaxillare, and sometimes even the most anterior of the nasals is incorporated in this complex. This suggests that this bone is of a composite origin, and this is why this bone is termed the nasorostropraemaxillare (JARVIK, 1942: 347, figs 34, 68 A, D, E). Hence it is clear that the praemaxilla in *Eusthenopteron* is only a partial homologue of the similarly termed element of frogs. It is important to note that in *Eusthenopteron* the praemaxilla proper is not in a direct contact with the endocranium but lies below its level, being separated from it by the *processus palatini* of the medial and lateral rostrals. From this it may be inferred that the praemaxilla of *Eusthenopteron* corresponds to the *pars dentalis praemaxillae* of frogs. As in *Eusthenopteron* no further exocranial element posteriorly adjoins either the praemaxilla or the *processus palatinus* of the medial rostral lying between it and the endocranium (the endocranium is exposed in this area), there is no doubt that the *pars palatina praemaxillae* of the frog is a homologue of the *processus palatini* of the medial and lateral rostrals. In contrast, the *pars facialis praemaxillae* forms a prominent dorsal process sitting on the *cartilago praenasalis superior* which is an evolutionarily new form. From the topographical relationship with the *fenestra endonarina* it may be concluded that a further nasal or nasals from the nasal series could be concerned here (at least nasal 2) which during evolution fused with the praemaxilla. This assumption is supported by observations concerning the ontogeny of praemaxilla, according to which it seems that the *pars facialis* and *pars dentalis* appeared independently of each other. However, these observations have not been verified histologically. Jarvik (1942: 497, 498) homologizes the *pars facialis praemaxillae* of frogs only with an analogous process on the nasorostropraemaxillare in *Eusthenopteron*. With regard to this, the above-mentioned statement that the *cartilago praenasalis superior* forming the support of the dorsal part of *pars facialis* of the praemaxilla in frogs is an evolutionarily new formation which did not exist in *Eusthenopteron* is of great significance. There is a diminished probability that the dorsal parts of the facial process in *Eusthenopteron* and frogs would be homologous. Jarvik (1942: 497) also calls attention to the fact that the nasorostropraemaxillare in *Eusthenopteron* reaches laterally up to the level of the *fenestra endochoanalis* and also forms part of its boundaries, whereas the *pars dentalis praemaxillae* in frogs is fairly reduced in the direction from the praemaxillo-maxillary suture.

From the above discussion the conclusion may be drawn that the praemaxilla in frogs is most probably a homologue not only of the nasorostropraemaxillare of *Eusthenopteron*, but also of the anterior nasal or nasals of the nasal series.

The nasal of *Pelobates* arises above the lateral margin of the *tectum nasi*, and extends posterolaterally onto the postnasal wall. During ontogeny, it expands partly in a medial direction, so that it comes into contact with the nasal of the opposite side, forming a comparatively long median suture, partly laterally, so that it also partially covers the *cartilago obliqua*. It also forms part of the boundaries of the *fenestra exonarina*. In *Eusthenopteron* (Jarvik, 1942: 349—351, 448—449, 549—550, fig. 34) the *nasalia* 3—7, *tectalia anterior et posterior* and also the *supraorbitale anterior* are developed in this exocranial area. The nasals show a strong tendency to fuse with one another. The anterior tectal forms the dorsal boundary of the *fenestra exonarina anterior*. In addition, it also covers the dorsal part of the lateral wall of the nasal capsules (dorsally and laterally from the mentioned opening), and the adjacent part of the *tectum nasi*. It bears a medial process on its inner side, which reaches into the nasal cavity. The posterior tectal shows a tendency to fuse with the *supraorbitale anterior* into the so-called supraorbitotectal.

Jarvik (1942: 345, 549) homologizes the nasal of frogs only with the *tectale anterior*. This would correspond to the fact that this bone embryonically develops from a single centre, showing a striking tendency to expand medially. But it does not seem probable that all the other above-mentioned bones would have disappeared throughout. For example, in *Triadobatrachus* a well discernible element remains preserved on the site of the supraorbitotectal, which evidently ceased to exist as late as during the further development (see also Piveteau, 1937: 145, 153, fig. 7; Watson, 1940: 221, fig. 18). In urodeles, the nasal is certainly of composite origin. Lebedkina (1979: 157, fig. 52) has found that this bone in urodeles ossifies from two centres; between both these ossification centres is inserted the long *pars facialis praemaxillae*, which at early stages of ontogeny reaches up to the anterior margin of the frontal (see also Bjerring, 1977, fig. 33 A). As has already been indicated in the context of homologization of praemaxilla, this condition could be interpreted such that the *pars facialis* has become longer due to the incorporation in it of a certain number of further nasals. The hind-most nasal really adjoins the frontal. In anurans, this process could take place to a lesser extent than in urodeles. The lateral ossification is homologized by LEBEDKINA with the nasal, and the medial one with the postrostral (SÄVE-SÖDERBERGH has interpreted this element in a similar way - see JARVIK, 1967: 194). If the hypothesis of gradual incorporation of nasals into praemaxilla were accepted, then Lebedkina's interpretation should be somewhat corrected in the sense that the lateral ossification corresponds to the *tectale anterior,* as no other element except this tectal occurs laterally of the nasal series in the above-mentioned area. Such an interpretation would partly correspond to the opinion of JARVIK (1942: 415), who however does not consider in connection with homologization of the nasal in urodeles any other element except for one or several *tectalia anterior.* It is interesting that in interpreting the medial ossification as postrostral, LEBEDKINA in fact supports Jarvik's theory on the origin of the urodeles from *Porolepiformes,* as only in this group is the most posterior postrostral paired (on the assumption that the pineal plate is not included among the postrostrals; cf. JARVIK, 1942, fig. 33; 1972, fig. 36 D), whereas in *Osteolepiformes* the series of posterior postrostrals (at the level where in urodeles the above-mentioned medial ossification is developed) ends with a single unpaired element.

Let us return to the interpretation of the nasal in *Pelobates.* It seems to be most probable that it represents a complex originated by fusion of the *tectale anterior* and several posterior nasals.

In *Pelobates* the dorsal part of the braincase in the orbitotemporal region and in the major part of the otic region is covered by a large element usually called the frontoparietal. This bone starts to develop as a paired ossification above the posterior section of the lateral walls of the braincase in the orbitotemporal region (fig. 43 a; LEBEDKINA, 1979, fig. 85 B) and a little later as an unpaired element which develops above the *tectum synoticum*; finally, a further paired element arises above the medial parts of otic capsules. The paired ossification in the orbitotemporal region gradually expands anteriorly and medially, so that it soon reaches, by its lateral parts, the level of the anterior margin of the orbit, and medially fuses with the corresponding opposite ossification by a suture. But this suture is shorter than the antero-posterior length of the lateral part of the above- mentioned ossifications, so that at this developmental stage the anterior part of the future frontoparietal is wedge-like incised (fig. 43 c). It is only later that this area becomes closed by a more or less independent unpaired ossification (fig. 43 d) which, in addition, runs variously up to the angle between the posteromedial margins of both nasals, either filling this space or leaving a variously large part of it exposed (fig. 12). This is also responsible for the variation of the anterior margin of the definitive frontoparietal.

It is generally well known that in fishes (e. g. *Amia, Esox*; see LEBEDKINA, 1979: 160—162, figs 81, 82) three paired ossifications arise in the orbitotemporal region, which soon fuse into a single bone, usually termed the frontal (frontal 1 + frontal

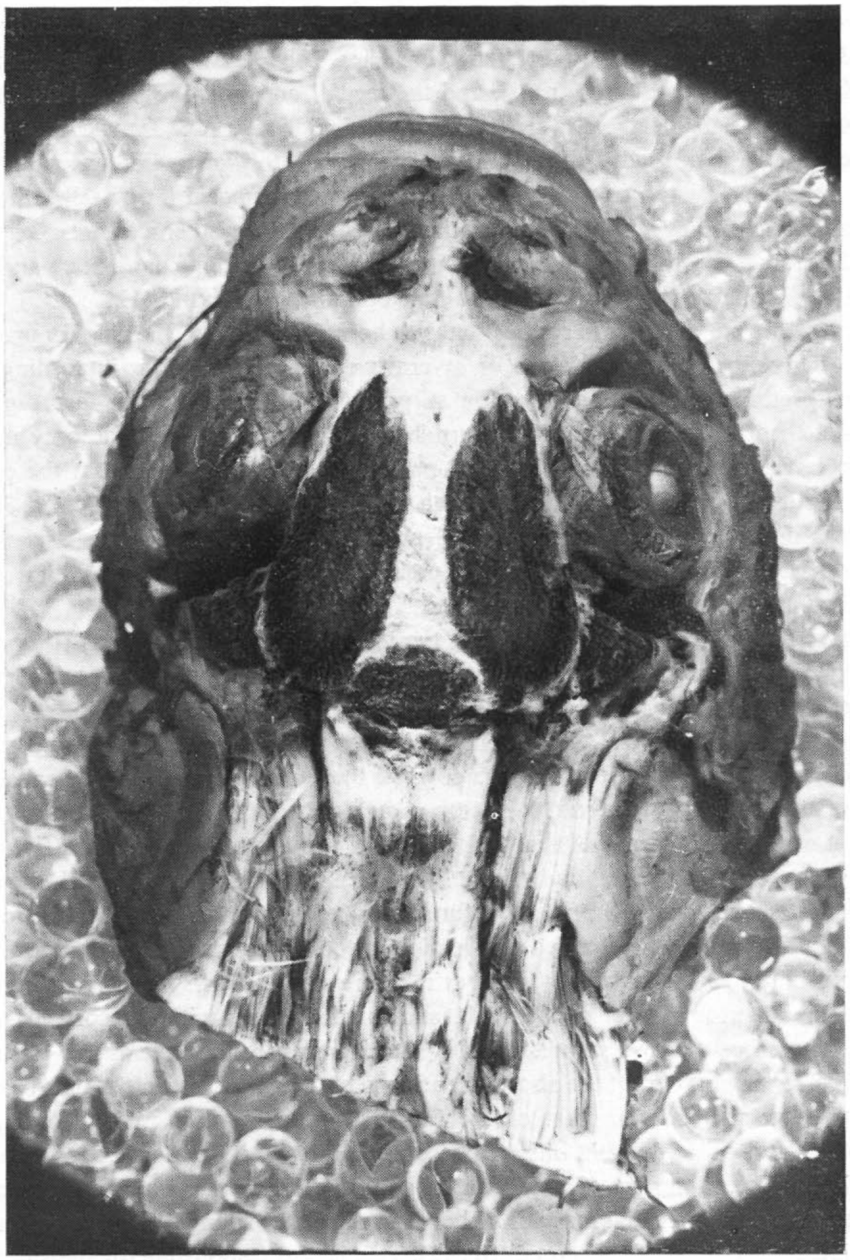


Fig. 42. Dorsal aspect of the skull of a *Pelobates syriacus* tadpole after removal of the skin. The frontoparietal hitherto divided into three parts is well visible (Photograph by courtesy of the Swedish Museum of Natural History, Stockholm).

2 + frontal 3). This resulting condition (i. e. composite frontal) may be observed also in *Eusthenopteron*. As the first ossification in the area of the future frontoparietal in *Pelobates* arises above the posterior section of the orbitotemporal region, Lebedkina (1979: 165—167) homologizes, undoubtedly correctly, this initial formation with frontal 3. This expands anteriorly into the area where in some fishes independent frontals 1 and 2 still exist, and also posteriorly into the otic region where in other frogs the parietal arises as an independent ossification. However, during ontogeny the expansion of this element, which would proceed by the fusion of independent three frontals with the parietal cannot be observed. This may be conceived such that in contrast to fishes the exocranium is initially very retarded in its development, but later it develops very rapidly, practically during and shortly after metamorphosis. The stages of the bone development may then follow in close succession, which gives the impression of a continuous growth of the bone. On this assumption it is therefore possible to interpret the anterior paired ossification of *Pelobates as* a frontoparietal sensu stricto, and it may be inferred that its anterior part represents not only a homologue of the original frontal 3 but at least also frontal 2. As it is usually not possible to encounter such a developmental stage where both ossifications representing frontal and parietal would still be separated, the impression arises that the frontoparietal sensu stricto develops from one sole ossification centre (see e. g. Griffithhs 1954a, pl. 1). Long discussions have attempted to answer the question whether this

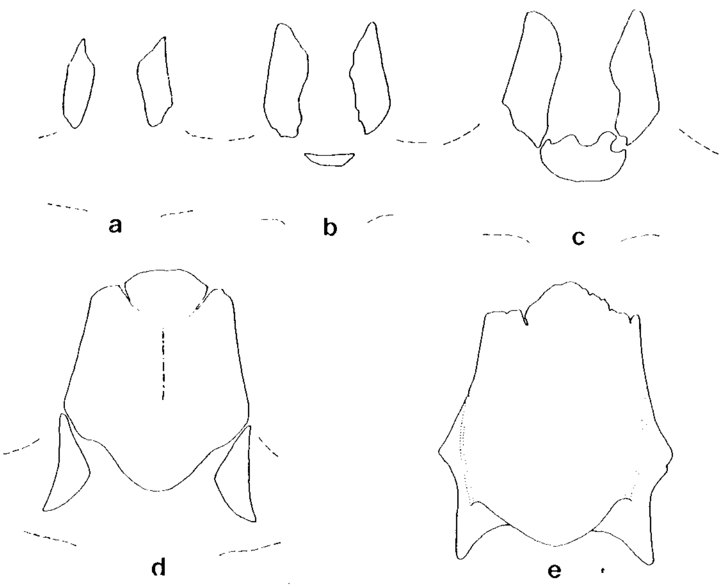


Fig. 43. The main stages of the development of the frontoparietal complex in *Pelobates fuscus*. The outlines of the otic capsules are indicated by a broken line, the courses of the canals for the *arteria occipitalis* and *arteria orbitonasalis* are dotted.

seemingly single ossification represents the frontal (EATON, 1939; 1942; SEDRA, 1949) or frontoparietal (GRIFFITHS, 1954a).

In *Eusthenopteron* (JARVIK, 1942, fig. 34; 1980, fig. 121A) a single paired bone called the frontal is developed above the orbitotemporal region, and partly reaches onto the ethmoidal region. The posterior margin of the bone extends onto the area close to level of the intracranial juncture apparatus. Irrespective of whether it represents all or some initial ossifications of the bone it is undoubtedly a homologue of the anterior part of the frontoparietal of ranids (see JARVIK 1942: 343—344; 1967: 194; LEBEDKINA, 1979, fig. 84; 1968, fig. 9) as well as a homologue of the anterior part of the frontoparietal sensu stricto in *Pelobates*. In *Eusthenopteron,* the parietal adjoins from behind each frontal. It is beyond doubt that this is a homologue of the posterior part of the frontoparietal in ranids as well as of the posterior part of the frontoparietal sensu stricto in *Pelobates* (see also JARVIK, 1967: 194).

Above the *tectum synoticum,* an unpaired median ossification arises in *Pelobates* tadpoles (see also LUTHER, 1914, figs 17, 18; SEWERTZOW, 1891: 149, fig. 7; JARVIK, 1967: 196, pl. III A). In *Eusthenopteron,* a median extrascapular occurs in the same area, anteriorly adjoining both parietals*). The above-mentioned unpaired element

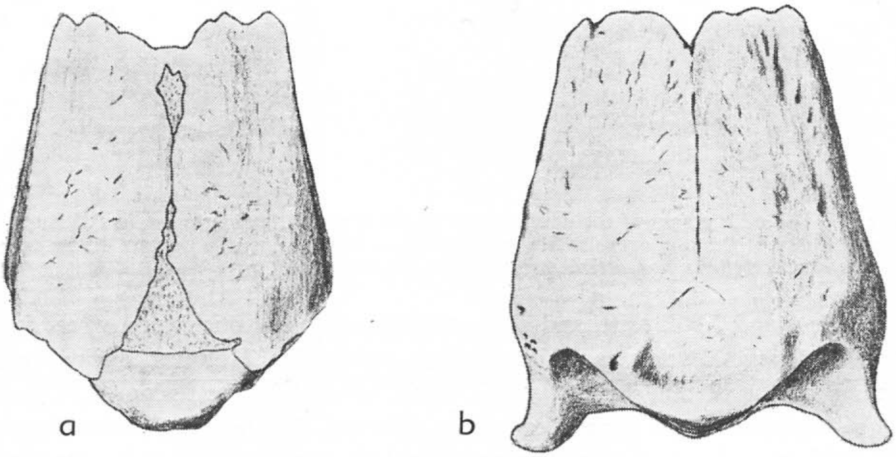


Fig. 44. The frontoparietal complex of *Pelobates syriacus syriacus*. a - tadpole in metamorphosis (DP FNSP 2118—1); b - tadpole at the final stages of metamorphosis (DP FNSP 2116—1)l Note the gradual incorporation of the median unpaired element into the future frontoparieta. complex.

---

*) In *Ichthyostega* the condition is somewhat different, as the otic region of the endocranium is fairly shortened as compared with the prootic parts of the skull; this may be inferred from a comparison with *Lyrocephalus* (SÄVE-SÖDERBERGH 1936, fig. 14; 1937, fig. 1 C-F). According to JARVIK (1967: 203, fig. 11 C, D) the posterior median element represents here the parietoextrascapular. But in frogs the proportions of the endocranium in the antero-posterior direction rather resemble those of *Eusthenopteron*; for this reason, in homologizing the posterior part of the cranial roof, the condition in *Ichthyostega* may be regarded as specializad already (cf. JARVIK, 1967: 207).

in *Pelobates* therefore represents most probably a homologue of the median extrascapular. The problem of homologization of the paired ossification arising above the medial parts of the otic capsules was dealt with by REINBACH (1939b); SEWERTZOW (1891: 151, fig. 7) however already knew of its existence. Considering that an ossification is concerned which lies on the roof of the otic capsule, and which is also the only element located between the squamosal and parietal, REINBACH concluded that this ossification is a supratemporal. In contrast, GRIFFITHS (1954b: 45) maintained that this element represents the postorbital. But REINBACH'S conclusions seem to be more correct - if we do not consider the possibility that also lateral extrascapular may play a role in the origin of this paired posterior ossification (cf. JARVIK, 1967: 203, fig. 11 C, D). This is supported by its topographical relations to the endocranium (the *processus paraoccipitales* in *Pelobates fuscus* cover approximatelly the same area of the endocranium as do the *extrascapularia lateralia* in *Eusthenopteron*; see JARVIK, 1975, fig. 11 A, D) as well as by its relation to the *arteria occipitalis*. For the sake of completeness it should be noted that BOAS (1914: 248) was of the opinion that the *canalis arteriae occipitalis* is a remnant of a cavity (»Schläfenhöhle«) which was originally emplaced here. However, there is no evidence to support his opinion.

The last ossification arising independently in the area of the future frontoparietal fills the space between the divergent anteromedial margins of the frontoparietal sensu stricto. This ossification is developed above the anterior margin of the *fenestra frontoparietalis,* and above the roof of the anterior part of the braincase; it reaches also into the ethmoidal region. It may even cover all of this originally exposed parts of the sphenethmoid between the posteromedial margins of the nasals*). In *Eusthenopteron* (JARVIK, 1942, fig. 34) this area is covered by the hindmost one from the series of postrostrals, i. e. by the large unpaired *postrostrale mediale* occupying the median position. It could therefore be a homologue of the anterior unpaired ossification in the area of the frontoparietal (cf. JARVIK 1968: 508, fig. 2). REINBACH (1939a: 321) has found a similar element in *Calyptocephalus.* But in connection with the homologization of the anterior part of the frontoparietal bone in *Pelobates* some interest is deserved by an independent tiny ossified element (fig. 29) which has been found under the anterior part of the frontoparietal in the specimen investigated by the means of serial sections. The question may be raised what is represented by this element. This tiny ossification is undoubtedly of endesmal origin, however, its homologization with some of originally independent exocranial elements is hindered by its position below the level of the other dermal bones. Thus it would be more probable to homologize the *postrostrale mediale* of *Eusthenopteron* with the median unpaired ossification in the area of the anterior margin of the frontoparietal.

It may be concluded briefly that the frontoparietal of *Pelobates* represents a com-

---

*) This evidently depends on the age of the individual. Basoğlu and Zaloğlu (1964: 236, figs 13—16) found in younger individuals of *Pelobates syriacus* the sphenethmoid still exposed while in older ones it is covered throughout.

posite structure due to the fusion of the frontals, parietals, supratemporals, median extrascapular, median postrostral and possibly also of lateral extrascapulars (cf. JARVIK, 1967: 196).

The septomaxilla of anurans has been interpreted in detail by JARVIK (1942: 516, 529, 532—535, 549; 1967: 194) who has drawn the conclusion that it may be homologized with the *processus dermintermedius* and adjacent parts of the *rostrale laterale* of *Eusthenopteron*. According to the latter author, the comparatively intricate configuration of this bone in frogs arose secondarily in connection with the expansion of the *recessus medius*.

The maxilla is an element which in *Eusthenopteron* is located from about the level of the *fenestra endonarina* to the posterior end of the *pars autopalatina palatoquadrati*. However, the maxilla is in immediate contact neither with the ethmoidal region (JARVIK, 1942: 349) nor with the *pars autopalatina*, but is situated below the level of their lower margin. In addition, the maxilla is separated from the *pars autopalatina* by the dermopalatine and ectopterygoid. In *Pelobates*, a relatively extensive element, also called the maxilla, is in similar relations. But its relations to the palatoquadrate are slightly different, as it closely adjoins the latter. But it is necessary to take into consideration that the size as wellas the proportions of the palatoquadrate in *Pelobates* and frogs in general became modified in consequence of the phylogenetic changes which this part of the visceral endocranium underwent. This originally comparatively large element (see BJERRING, 1977, fig. 26; JARVIK, 1954, fig. 23 B) became a relatively subtle in relation to the endocranium, because its main function of support was transferred to the dermal bones (maxilla, pterygoid, squamosal). It may therefore be assumed that the maxilla as a dermal bone which had taken over the palatoquadrate's original fuction of support for the substantial part of the upper dental arch either becomes more robust or at least retains its original size. Due to this, the adjacent less significant elements may be reduced or disappear throughout. In spite of the above-mentioned differences in topographical relations to the palatoquadrate, the homology between the maxilla of *Eusthenopteron* and that of frogs is beyond any doubt. In addition, in both cases the maxilla is a bone bearing part of the dentition of the outer dental arch, which fact in this case may also be regarded as the proof of the homology between both these elements.

The palatine of *Pelobates fuscus* appears in the ontogeny as an independent ossification, but soon fuses with the maxilla. It is clear that the palatine of frogs is a homologue of that part of the dermoplatine in *Eusthenopteron*, which participated in the formation of the posterior margin of the *fenestra exochoanalis*.

In contrast, there is a more intricate problem as to the interpretation of the squamosal in frogs. This is a bone whose one part laterally covers the *pars quadrata palatoquadrati*, and another part adjoins *crista parotica* of the otic capsule. Thus, it covers on the one hand the element of the visceral endocranium, and on the other, part of the neural endocranium. However, in *Eusthenopteron* the corresponding part of the palatoquadrate (i. e. the posteroventral part of the *pars pterygoquadrata*) is covered by the *praeoperculum,* whereas the squamosal proper does not reach up to here (see BJERRING, 1979, fig. 4). The squamosal itself covers the central part of the *pars pterygoquadrata* but, in addition, its dorsal process adjoins the lateral commissure of the otic region (whose dorsal part at least is a homologue of the *crista parotica*; see chap. 4.1.3. Homologization of the endocranium). From the above facts it follows that the squamosal in frogs should correspond to the complex of squamosal and praeoperculum of *Eusthenopteron.* In this case, the praeoperculum would be represented on the squamosal of frogs by the *processus posterolateralis.* The results of this topographical comparison are confirmed by studies of the ontogeny of dermal bones within this area. It should be noted that squamosal in frogs arises from two ossification centres of which the dorsal one displays close relations to the *crista parotica,* whereas the ventral appears in the area laterally to the *pars quadrata palatoquadrati,* i. e. having topographical relations to the endocranium identical with those of the squamosal and praeoperculum in *Eusthenopteron.* During further development, both these ossifications fuse, constituting one unit. This has already been stated by REINBACH (1939b), but he erroneously regarded the dorsal ossification as supratemporal; this was apparently influenced by his find of a similar element in *Pelobates fuscus* which however develops above the medial part of the otic capsule. REINBACH (op. cit.: 173) then wondered how it was possible that both these elements which he regarded as homologous could originate on different parts of the otic capsule, and why it was possible that in *Pelobates* the above-mentioned element was incorporated into the frontoparietal, whereas in *Calyptocephalus* it was incorporated into the squamosal (REINBACH, 1939a). SEDRA (1949: 633—639) has also stated the existence of two ossifications in the area of the future squamosal also in some ranids and bufonids. The latter author however considered that only that ossification which adjoins the *pars quadrata palatoguadrati* represents the squamosal. He homologized the dorsal ossification with the postfrontal (seu *supraorbitale* sensu JARVIK). GRIFFITHS (1954b: 38) has also found that in Bufonidae and Atelopodidae two ossifications arise in the area of the future squamosal, which later fuse with each other. Like SEDRA, GRIFFITHS regarded only the lower of these ossifications as the squamosal, and the upper one was homologized by him with the supratemporal (op. cit.: 48) .He considered REINBACH's supratemporal to be postorbital. The finds of two ossifications in the area of the future squamosal have also been confirmed in ranids by LEBEDKINA (1979, fig. 99). All this permits the assumption that in all groups of frogs, and therefore also in pelobatids, the squamosal arose in the same way. In urodeles (LEBEDKINA op. cit., fig. 24) the squamosal is similarly composed of two centres and under equal topographical conditions as is the case in frogs and *Eusthenopteron.* The topographical relations to the endocranium sufficiently confirm LEBEDKINA's conclusions (op. cit.: 172) that in urodeles the squamosal represents a bone of a composite origin (squamosal + praeoperculum). For the same reason, this interpretation may also be extended to the squamosal of frogs.

The quadratojugals in frogs and *Eusthenopteron* correspond one another in topographical relations to the palatoquadrate, but with the mere difference that in frogs the quadratojugal is considerably reduced. The homology between these two elements is therefore doubtless. In the vomer the case is similar. In *Eusthenopteron,* just as in frogs, the endocranium is exposed between the vomer and the praemaxilla or nasorostropraemaxillare (»anterior palatal fenestra«). Both in frogs and *Eusthenopteron* the vomers are situated on the *solum nasi* slightly overlapping by their lateral part the *fenestra endochoanalis.*

The parasphenoid in *Pelobates* ventrally adjoins the orbitotemporal and otic regions. In the latter, it gives off sideways the robust *processus laterales* adjoining the bases of the otic capsules. In addition, the free margins of the *pars medialis parasphenoidei* possess inconspicuous, rounded processes directed dorsoventrally and situated closely behind the level of the exit of the *nervus opticus* from the braincase. In contrast, the parasphenoid of *Eusthenopteron* (Jarvik, 1954, figs 25, 30 B, E) covers the endocranium only within the orbitotemporal and partly also ethmoidal regions. That part of the otic region which in frogs is covered by the parasphenoid is in *Eusthenopteron* overlain by prootic, subotic and spiracular dental plates. According to Jarvik, the variability of the shape of the parasphenoid is due to the fusion of a varying number of these originally independent dermal elements. From this it follows that the parasphenoid of *Eusthenopteron* is a homologue of only that part of the parasphenoid in frogs which covers the orbitotemporal region (i.e. approximately the free part of the *pars medialis*). According to the above-mentioned Jarvik's theory on the origin of the parasphenoid by the fusing of dental plates, it would also be possible to explain a certain variability in the formation of the medial part of the posterior margin of this bone which is some frog groups projects into a median process directed posteriorly (in *Eusthenopteron,* the suboccipital dental plates are located in this area).

The parasphenoid in frogs develops very rapidly; this gives the impression that there is only one ossification centre. In urodeles the conditions are similar. However, in the latter, Lebedkina (1979: 50, 153—154, figs 20, 21) has found that the parasphenoid arises from two ossification centres, one in the orbitotemporal region, whereas the other is beneath the otic region. Both these centres fuse with each other very soon. Lebedkina homologizes the anterior centre with the parasphenoid of the lobe-fin fishes, and the posterior one with their paraotic dental plates. It may be assumed that after examination of the earlier developmental stages of the parasphenoid in frogs a similar conclusion might be drawn for them.

In fishes, the *processus ascendens anterior parasphenoidei* projects dorsolaterally at the level of the basipterygoid process of the neural endocranium. In frogs, on this site of the parasphenoid a rounded more or less conspicuous process also exists. The *processus ascendens posterior,* which in *Eusthenopteron* was not developed due to the absence of parasphenoid in the otic region (neither in *Ichthyostega*; Jarvik, 1954: 69), developed convergently in several evolutionary lines (paleoniscids, Holostei, post-Devonian tetrapods), and covers a fairly large part of the lateral wall of their otic regions. It is beyond any doubt that the *processus laterales parasphenoidei* in frogs are homologous with the *processus ascendens posteriores* of the above-mentioned groups. The changes in the position of these processes are due to the lateral expansion of the otic capsules, so that the posterior processes of the parasphenoid are then directed laterally or even lateroventrally, not dorsally.

In *Pelobates,* the pterygoid covers the palatoquadrate medially (i. e. the substantial part of its *pars palatina,* and - with the exception of the ossified *quadratum* - also the whole *pars quadrata*); in addition, it adjoins the anterolateral part of the otic capsule. In *Eusthenopteron* (Jarvik, 1954, fig. 16 C; 1972, fig. 73 B; 1980, fig. 124 A), the homologous part of the palatoquadrate is covered medially by a large entopterygoid. This element displays topographical relations with the *pars quadrata palatoquadrati* which are completely equal to such relations displayed by the pterygoid of frogs (Jarvik, 1975, fig. 11 A, D). In *Eusthenopteron,* the ectopterygoid and dermopalatine cover the *pars autopalatina* which is homologous with the *processus antorbitalis* in frogs, i.e. with that part of the palatoquadrate which already lies outside the pterygoid in them. It may therefore be concluded that the pterygoid of frogs is homologous with the entopterygoid of *Eusthenopteron* (cf. Jarvik 1975, fig. 11 A, B, D).

The dentary in *Pelobates* is a slender bone laterally covering the anterior part of Meckel's element. In *Eusthenopteron,* an equally named bone occupies a similar position. The series of four infradentaries is linked with the dentary, but these infradentaries already lie ventrally to Meckel's element. In some fishes (e.g. *Amia*), the infradentaries show a strong tendency to fuse with the dentary (see Jarvik, 1980, fig. 37 A, C). Thus, either the dentaries of both *Eusthenopteron* and frog are homologous or the dentary of the frog represents a complex dentoinfradentary. If this is the case, then most probably the first two infradentaries are involved.

There are more problems as to the praearticular. In *Pelobates,* the anterior part of this bone medially adjoins Meckel's element; its posterior part joins it ventrally or even also ventrolaterally. The praearticular of *Eusthenopteron* occupies a similar position in relation to Meckel's element, adjoining it only medially. In *Eusthenopteron,* the third and fourth infradentaries (seu angular and surangular; see Miles 1971, fig. 6.6 A) are adjoined in the area corresponding to the *pars articularis* of Meckel's element in frogs. With respect to the clear tendency of the dermal bones of the lower jaw to fuse with each other, it is probable that the praearticular of frogs is a complex arisen from originally independent praearticular and infradentaries 3 and 4.

Concerning the *parahyoideum,* which according to Fuchs (1929: 429, figs 20—26, 27 D) is a dermal bone adjoining the ventral side of the hyoid, the interpretation is considerably difficult. During ontogeny, this element arises as a paired ossification (Fuchs, op. cit.: 435) on the posterior half of the *corpus hyoidei,* e.e. in the area arisen by transformation of the posteromedial parts of the hypobranchial plates. These parts have been homologized with the hypobranchials of the posthyoid visceral arches (see p. 70). Consequently *parahyoideum* may represent a remnant of dermal ossifications covering the branchial arches of archaic forms (in *Eusthenopteron* they are already reduced being restricted to infrapharyngobranchials or to a minor extent also to epibranchials; see JARVIK, 1954, figs 31 A, 35 C).

4.2.4 Changes in the exocranium occurring during the evolution of frogs from their ancestors corresponding by their anatomy to Eusthenopteron

On the basis of a comparison of homologous formations of the exocranium in frogs with those in *Eusthenopteron,* it is possible to determine the evolutionary changes occurring during the origin of frogs as an independent group. Similarly as in the case of the endocranium, the determination of these changes helps in recognizing the assumed transitional forms and in judging the evolutionary trends manifested in various lineages of frogs. The evolutionary changes considered are as follows:

(1) The fusion of some originally relatively small dermal bones into larger units, or the expansion of a certain element at the expense of some adjacent elements. This is due to the substantial reduction of the endocranium, so that the dermal bones took over the function of some parts of the latter. This »centralization« of the exocranium manifested especially in the following areas:

a) The area of the *pars autopalatina palatoquadrati.* The *pars autopalatina* (= *processus antorbitalis* in frogs) and the *pars pterygoquadrata* became fairly reduced and remained joined to each other by a thin and subtle *pars palatina palatoquadrati.* Originally, the palatoquadrate had the function of the main supporting element of the upper jaw. But in frogs this function passed to the maxilla which in consequence of this became markedly more robust. This was manifested particularly by its expansion anteriorly at the expense of the praemaxilla which diminished proportionally to the former (JARVIK, 1942: 497). The expansion of the maxilla in the posterior direction took place at the expense of the quadratojugal. The maxilla also took over the function of some dermal bones which became reduced or disappeared; e.g. the lacrimal and jugal disappeared throughout due to the widening of the orbit, the dermopalatine diminished because of the restriction of the extent of the mouth palate; the same is true of the ectopterygoid.

b) The area of the *pars quadrata palatoquadrati.* In *Eusthenopteron* this part was attached to the neurocranium by means of the paratemporal, basal and suprapterygoid articulations, and in addition it was supported medially by a large entopterygoid. The squamosal, praeoperculum and quadratojugal adjoined the *pars quadrata* laterally. In frogs the *pars quadrata* became reduced to a subtle rod-like process ossifying only in its terminal part; in addition its attachment to the neurocranium became less firm (i.e. by a syndesmosis). Due to this, the dermal bones became the main support of the jaw joint. The entopterygoid remained the main medial supporting element which in addition also came in contact with the neurocranium (see below under point 2), while the squamosal and praeopercular become lateral supporting elements. The quadratojugal diminished with increasing maxilla, partly because it occupied a position precluding any role in the fixation of the jaw joint to the neurocranium (this position was occupied by the praeoperculum and squamosal), partly also because it freed the space necessary for the contraction of the *adductor mandibulae posterior subexternus* muscle (see LUTHER, 1914, fig. 20) or possibly also for further mandibular adductors (CAROLL and HOLMES, 1980: 32—33). One solitary element was suitable for the fixation of the jaw joint to the neurocranium, and therefore the praeoperculum fused with the squamosal. The initial phases of the reconstruction of the posterolateral exocranial cover may be seen in *Ichthyostega* (SÄVE-SÖDERBERGH, 1932, figs 15, 16; JARVIK, 1952, fig. 35). In this case the quadratojugal is still large and the lower temporal fenestra has not yet developed (it may be assumed that the mandibular adductors were attached to the inner surface of the squamosal, as in Palaeozoic labyrinthodonts; CAROLL and HOLMES, 1980: 28, 29, fig. 25). The praeoperculum and squamosal of *Ichthyostega* were still independent, fusing only during their further development.

c) The area of the nasal capsule. The walls of this capsule in which there were originally only three openings permitting passage onto the surface of the skull (the *fenestra endonarina anterior et posterior* and *fenestra endochoanalis*), are fairly reduced in frogs, particularly in the lateral part. In connection with this, the bones of corresponding part of the exocranium fused into one central unit (the anterior tectal + posterior nasals into the composite »nasal« of frogs) and the other smaller elements were reduced or disappeared. For example, the nasal complex of rostral and supraorbitotectal disappeared throughout. But in *Triadobatrachus,* the supraorbitotectal probably still remained preserved (see also PIVETEAU, 1937: 145—146, fig. 7; WATSON, 1940: 221, fig. 18). The lateral rostral also underwent reduction, but did not disappear completely, as it took over the function of the lateral cover of the *recessus medius.*

d) The area of the skull roof. In this part of the skull, the tendency of the initially independent bones to fuse was already manifested at lower phylogenetic stages than is the case in *Eusthenopteron.* The functional »centralization« appeared here in two directions - in the first, represented by *Pelobates,* the bones had fused, so that a complex, unpaired and fairly large element arose which after incorporation of further bones (e.g. the supratemporal) could to a fairly large extent reach into the orbit. The second direction represented e.g. by the genera *Bufo, Rana* etc., is characterized by a fusion of the parietal and frontal only; at this stage the whole process of fusion is finished and does not continue by a further fusion into one unpaired unit. The adjacent elements (extrascapular series, supratemporal, postorbital etc.) disappeared throughout. It would seem that according to this criterion *Pelobates* and its related forms could be considered to be at a lower evolutionary level as compared with the representatives of the second direction of development, because at least during the early stages of ontogeny they retain their archaic nature; but this is not the case. As early as in *Triadobatrachus* - which up to the present time is believed to display the anatomical condition representing the level of an immediate ancestor of frogs - the frontoparietal is composed in the same way as that in the representatives of the above-mentioned second direction, inclusive of the median suture reaching up to the posterior margin of this bone (see also PIVETEAU, 1937: 145). This suggests that e. g. the extrascapular series had already ceased to exist in the course of earlier phylogenetic stages, the median extrascapular not being incorporated into the frontoparietal complex of this form. The same may also be assumed as to the further adjacent elements in the otic region. With regard to this character it may be inferred that the evolution of pelobatids may have followed a line independent of *Triadobatrachus*.

In *Ichthyostega* all elements are still preserved in the same state as those in *Eusthenopteron* (SÄVE-SÖDERBERGH, 1932: 74—79, figs 15, 16; JARVIK 1952, fig. 35 B; 1967, fig. 11; in the last cited paper the posterior unpaired element has bęen interpreted as parietoextrascapular).

e) The area of the lower jaw. Here, the dermal bones have taken over the function of Meckel's element, similarly as did the maxilla in the case of the upper jaw receiving the function of the palatoquadrate. Of the larger number of elements only two (dentary and praearticular) remained here. The tendency to fusion is also manifested in this area by the synostosis of the mentomandibular and dentary.

(2) Originally, the entopterygoid was closely associated by its function with the palatoquadrate, and it seems that it was not in contact with the neurocranium (JARVIK, 1954, figs 24, 25). However, in *Pelobates* the pterygoid is immovably attached to the anterolateral part of the otic capsule. Some primitive frogs still display a mobile junction between the pterygoid and the base of the otic capsules (CAROLL and HOLMES, 1980: 6).

(3) In connection with the widening of the orbit, the bones of the circumorbital ring (jugal, postorbital, dermosphenotic, supraorbital, posterior tectal and lacrimal) ceased to exist. In *Ichthyostega* and further Palaeozoic labyrinthodonts, the orbits are still relatively small and the elements of the circumorbital ring are well developed (*Ichthyostega* even possesses two supraorbitals, which suggests that in this recpect it is more archaic than *Eusthenopteron*). In *Triadobatrachus*, some elements seem to have been preserved as vestiges at this stage of phylogeny (e.g. supraorbitotectal).

(4) With the increasing volume of the orbit, the mouth palate became reduced. The dermopalatine was restricted only to the ventral cover of the postnasal wall, and the ectopterygoid disappeared throughout. The entopterygoid was reduced to a comparatively subtle but firm triradiate element. Hence, throughout its extent the orbit communicates with the mouth cavity.

(5) The regressive development of the exocranium was manifested not only by the lower number of its elements (be it fusion or complete disappearance) and by the diminution of their size (in connection with the appearance or widening of the openings in the endocranium), but also by the exposure of further parts of the endocranium. This appeared especially in the dorsal cover of the otic capsules, in the

area of the *processus praenasalis medius,* the lateral walls of the nasal capsules (large parts of the *cartilago obliqua* and *cartilago alaris* are uncovered), on the ventral surface of the ethmoidal region (where the vomers were fairly reduced), in the dorsal surface of the ethmoidal region (where the space between nasals and frontoparietal is uncovered), in the area of the anterolateral part of the orbit (part of the *processus antorbitalis* is uncovered), and in the area of the lower jaw (where Meckel's element is exposed in the area of the dentary as well as of the praearticular). The question to what extent the dermal cover of the otic region in *Pelobates cultripes* indicates the archaic state will be discussed below in chap. 5 Outlines of the phylogeny and systematics of the family Pelobatidae. A reduction of the dermal cover of the dorsal parts of the otic capsules also appeared during the phylogeny of urodeles (Caroll and Holmes, 1980: 15). This progressive trend is apparently associated with the dorsal cervical muscles becoming more massive in terrestrial tetrapods; these muscles were originally attached within the *fossa bridgei* whose area was restricted.

(6) The parasphenoid increased in size; in frogs it covers also a large part of the ventral surface of the otic region. This undoubtedly occurred in consequence of the disappearance of the intracranial juncture apparatus. In *Ichthyostega* where a trace of the division of the endocranium into anterior and posterior moieties is still retained, the parasphenoid too is still short. But as early as in the Palaeozoic labyrinthodonts, which had already lost this division, the parasphenoid reaches into the otic region and has its *processus ascendens posterior* well developed (Jarvik, 1954: 69). In frogs, the course of the posterior margin of parasphenoid has not yet been stabilized, which is manifested by the presence or absence of the *processus posterior* or even of the posterior lateral processes (e.g. Pipidae; Sokol, 1977: 360). This part of the parasphenoid also arises as the latest during ontogeny. It is worthy of note that in some Palaeozoic labyrinthodonts (Shishkin, 1973) the same as in primitive urodeles (Caroll and Holmes, 1980), the parasphenoid has a massive *processus posterior* reaching up to the posterior margin of the skull, into the area between the *condyli occipitales.* Both are therefore more advanced in this respect than are some frogs.

(7) The *arteria occipitalis* originally ran so that it penetrated from behind into the endocranium (*canalis arteriae occipitalis*), then emerging on its dorsal surface, and passed further in a groove up to the *fenestra anterolateralis,* and from here further anteriorly, being covered dorsally by the *lamina supraorbitalis* (Jarvik, 1967: 196; 1975, figs 8 A, C, 9). It therefore was in close relation to the endocranium. In pelobatids, this state is indicated only in early ontogeny, but in them this vessel never passes through a canal in the endocranium. A sign of the latter appears only in pipids (*Pipa carvalhoi*; Sokol 1977: 361, fig. 2) and in *Calyptocephalus* (Reinbach, 1939a, b). In most frogs, simultaneously with the development of the definitive frontoparietal this arteria become separated from the endocranium, which results in the formation of a narrow canal in the bone (e.g.; in pelobatids, discoglossids) or the

arteria even runs in a groove or freely on the surface of the bone (e.g. bufonids; JARVIK, 1975, fig. 11 c). The fact that the shift of the course of the *arteria occipitalis* in the dorsal direction may indicate a certain phylogenetic trend was already pointed out by REINBACH (1939b: 176).

(8) Some dermal bones (e.g. opercular series) disappeared in frogs in connection with the reduction and modification of the postmandibular part of the visceral endocranium. But *Ichthyostega* still retains a vestige of the suboperculum (JARVIK, 1952, fig. 35 A). As there are some doubts as to the homologization of the parahyoid ossification (see p. 108), only the degree of the changes in the dermal cover of the individual arches may be estimated. Nevertheless it may be assumed that the covering elements on visceral arches were fairly reduced as early as in *Eusthenopteron* and that they disappeared throughout in frogs. Only the *os parahyoideum* may be an exception. This element has been well preserved in *Triadobatrachus* (PIVETEAU, 1937: 148), and its presence may be regarded as an archaic character (cf. FUCHS, 1929: 436—439).

(9) The original relations in the proportions between the maxilla and praemaxilla of *Eusthenopteron* changed in frogs to the advantage of the expanding maxilla. This fact has already been pointed out by JARVIK (1942: 497). During the phylogeny of frogs, the relationship between maxilla and quadratojugal changes at the expense of the quadratojugal which in some groups (e.g. scaphiopodids) may even disappear throughout.

(10) CAROLL and HOLMES (1980: 17, 33) regard the otic notch on the squamosal of frogs as an important character. It was not yet formed in *Eusthenopteron* and was also lacking in some very archaic amphibians (e.g. the Lower Carboniferous *Greerpeton*; CAROLL and HOLMES, op. cit.: 17; *Dvinosaurus primus*; SHISHKIN, 173, fig. 2). But in *Ichthyostega* a sign of this notch on the squamosal already existed (SÄVE-SÖDERBERGH, 1932, fig. 7; JARVIK, 1952, fig. 35).

(11) Whereas in *Eusthenopteron* and Palaeozoic labyrinthodonts the jaws are still provided with the full number of teeth (although the inner dental arch gradually disappeared), the dentition was fairly reduced in frogs.

(12) The originally richly sculptured dermal bones in *Eusthenoptern* lost their sculpture during the phylogeny of frogs: it remains preserved only in some groups of them (e.g. in *Pelobates*, *Scaphiopus*).

(13) The lower jaw of *Eusthenopteron* and probably also of Palaeozoic labyrinthodonts had the shape of a regular arch. However, in frogs the praearticular is mostly typically S-shaped.

Some of the above-mentioned specializations occurred during the origin of frogs, and could not continue further during their phylogeny either because they would have taken place at the expense of the functional-mechanical properties of the skull, or simply because their extreme stage had already been attained (e.g. reduction of the bones of the circumorbital ring). But there are changes which may be assumed to continue further. These are as follows:

(1) »Centralization« of the exocranium manifested by the fusion of originally independent elements.

(2) Further reduction of the praemaxilla and quadratojugal, with the maxilla becoming more massive.

(3) Reduction of the exocranial cover of the endocranium (especially in the ethmoidal region and on the dorsal surface of the otic capsule).

(4) Expansion of the openings in the exocranium (particularly the *fenestra exonarina* or also the orbit).

(5) Expansion of the area where the pterygoid adjoins the otic capsule.

(6) Increase of the parasphenoid in a posterior direction.

(7) Shift of the course of the *arteria occipitalis* to the level of the dorsal skull cover.

(8) Shift of the appearance of the ossification centres of the dermal bones into earlier stages of ontogeny.

(9) Diminution and disappearance of the parahyoid bone.

(10) Reduction of dentition.

(11) Complete disappearance of sculpture.

(12) The S-shaped curvature of praearticular becoming more pronounced.

4.3 Comparison of Pelobates fuscus*) with some Cretaceous and Tertiary forms considered to be pelobatids, and with other representatives of the genus Pelobates

This chapter presents those characters which can be evaluated according to the evolutionary trends stated in previous chapters (p. 75, 113). It also presents those which distinguish the nominate form *Pelobates fuscus* from other representatives of the genus *Pelobates,* and from some other forms which were hitherto considered to be closely related to that genus. However, it must be emphasized that the characters given are of different values, as a certain variability must be supposed especially in those forms where only a limited number of specimens was available. The survey of forms is given in chronological order. Other data on the material investigated can be found in chap. 2 Material.

4.3.1 *Eopelobates leptocolaptus* BORSUK-BIALYNICKA, 1978

(figs 45—47)

1978 — *Eopelobates leptocolaptus* sp. n.; M. BORSUK-BIALYNICKA: *Eopelobates leptocolaptus* sp. n. - The first Upper Cretaceous pelobatid frog from Asia, p. 58, fig. 1, pl. 15

Geological age: Upper Cretaceous (? Middle Campanian)

---

*) For the sake of this comparison the nominate form *Pelobates fuscus fuscus* was taken.

The sphenethmoideum. The degree of preservation of this element allows to find following differences against *Pelobates fuscus:*

a) The *lamina orbitonasalis* larger. This is situated horizontally, not directed laterodorsally as that in *Pelobates fuscus*. It covers the anteromedial part of the orbit. It may be supposed its much larger extent in living animal, due to the completion with cartilage.

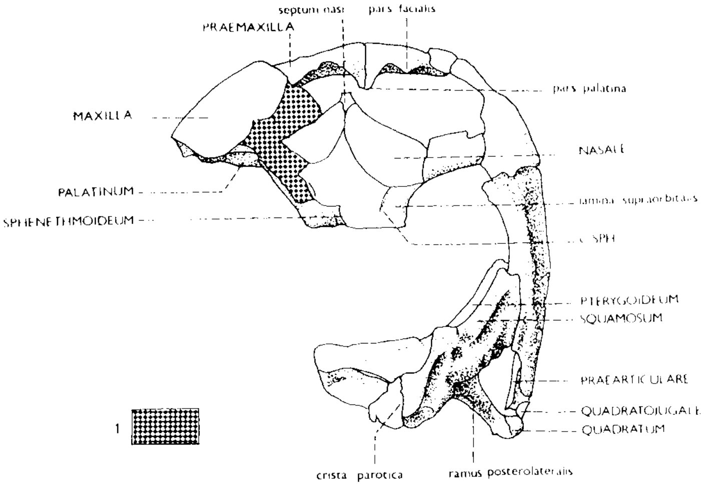


Fig. 45. The skull of *Eopelobates leptocolaptus*, dorsal view. 1 - area covered by sediment; c. SPH - ridge on the dorsal surface of sphenethmoid.

b) The *canalis pro ramus medialis nervi ophthalmici* continues into the orbit by a wide groove on the ventral surface of the *lamina supraorbitalis*. A similar groove is lacking in *Pelobates fuscus* due to the different position of the *lamina supraorbitalis* (see previous item).

c) There are distinct ridges on the dorsal surface of the sphenethmoid, diverging from each other, and running parallel with the margins of both *laminae supraorbitales*. They are lacking in *Pelobates fuscus*. It is impossible to interpret them as *cristae frontoparietales*, as the latter pass into the marginal edges of the *laminae supraorbitales*.

d) The area between both nasals is slightly depressed and unsculptured, the latter condition suggesting that this part was covered by the frontoparietals.

e) The anterior margin of the *fenestra frontoparietalis* is located posterior to the level of the postnasal wall, which can be deduced from the fact that the mentioned margin in the specimen investigated is not found (perhaps it would be identical with a part of the break surface). In *Pelobates fuscus* this opening reaches the level of the postnasal walls.

f) The sphenethmoid is more flattened dorsoventrally than that in *Pelobates fuscus*. It is impossible to decide if it is a natural condition or a deformation.

The prooticooccipitals and mentomandibulars are preserved only as dislocated fragments which prevent any conclusions.

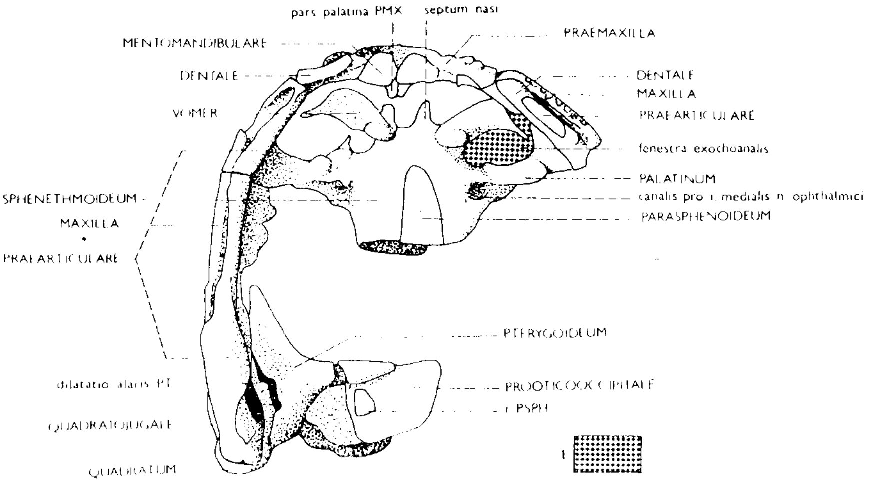


Fig. 46. The skull of *Eopelobates leptocolaptus* in ventral view. 1 - area covered by sediment; r. PSPH - fragment of parasphenoid.

The praemaxilla is comparatively well preserved, only its *pars facialis* is broken away.

a) The number of tooth positions probably amounts up to 12, and the tooth row reaches up to the median symphysis. Contrary to this, teeth are lacking in *Pelobates fuscus* in that part of the *crista dentalis* which is adjacent to the median symphysis.
b) Instead of the *crista lateralis* occurring in *Pelobates fuscus* there is only an indistinct ridge running from the basis of *pars facialis* which, however, becomes gradually more distinct laterally. The dorsal surface of the *pars dentalis* breaks along this ridge passing into an almost perpendicular anterior surface. The *recessus marsupiatus* is entirely lacking. The medial part of the *pars dentalis* bears a similar ridge so that the median suture runs horizontally, breaks almost at a right angle, and continues vertically.

The nasal. The right nasal is preserved almost completely, while most of the left one is broken away except for its anteromedial part.

a) The *sutura medialis* where both nasals contact each other is very short if compared with the condition in *Pelobates fuscus*.
b) The anterolateral margin which takes part in the bounding of the *fenestra exo-*

narina is only slightly concave, while it is deeply concave in *Pelobates fuscus.*

c) The dorsal surface was probably sculptured but not to such a degree as is the case with squamosal (fig. 47). In spite of this, the sculpture is more robust than that in *Pelobates fuscus.*

The maxilla of the right side is preserved almost completely.

a) There are remnants of the robust sculpture on its outer surface.

b) There is a distinct mound along the *margo orbitalis,* while it is poorly developed in *Pelobates fuscus.*

c) The most anterior part of maxilla is not formed by its *lamina anterior,* which is the condition in *Pelobates fuscus,* but by the anterior end of the *pars dentalis.*

d) The *processus zygomatico-maxillaris* is lacking, so the squamoso-maxillary suture runs as a continuation of the margo *orbitalis.*

e) The *processus posterior* is short and massive, while long and slender in *Pelobates fuscus.*

The squamosal (fig. 47) is almost completely preserved; it is only impossible to ascertain the shape and extent of its *ramus paroticus.*

a) The *lamella alaris* is massively sculptured on its outer surface. The sculpture is represented by a few fossae separated by rounded ridges. In *Pelobates fuscus* it is mammilar-like.

b) The margin between the *processus dorsalis* and the *processus posterodorsalis* is almost straight, while concave in *Pelobates fuscus.* This margin is accompanied by a distinct mound which is similar to that accompanying the *margo orbitalis maxillae.*

c) A distinct outgrowth is present on the posterior margin of the *lamella alaris* ventrally to the *processus posterodorsalis.* In *Pelobates fuscus* there is an indistinct convexity instead.

d) In the lateral aspect, the posteroventral margin of the *lamella alaris* and the long axis of the *processus posterolateralis* form an obtuse angle. In *Pelobates fuscus* this angle is much sharper.

e) The widest part of the *processus posterolateralis* is in its proximal section, while it narrows distally. Quite the opposite condition occurs in *Pelobates fuscus.*

The quadratojugal is situated within a considerably destroyed area of the skull (especially the *processus posterolateralis squamosi* is interrupted by several fractures; see fig. 47). Despite this it seems that the quadrate and the quadratojugal are independent. However, some doubts exist as to whether the dividing line represents the suture or the fracture.

The vomer is well preserved at least on the left side. The right vomer is moved somewhat beyond its original position.

a) There is a flat outgrowth medial to the *torus dentigerus*; it is lacking in *Pelobates fuscus.* As this process reaches up to the mid-line, both vomers were originally in mutual contact. In *Pelobates fuscus* both vomers are widely separated.

The palatine

a) It is separated from the maxilla by a suture.

The parasphenoid is preserved as a mere tip of the *pars medialis,* and as a tiny fragment on the ventral surface of the otic capsule.

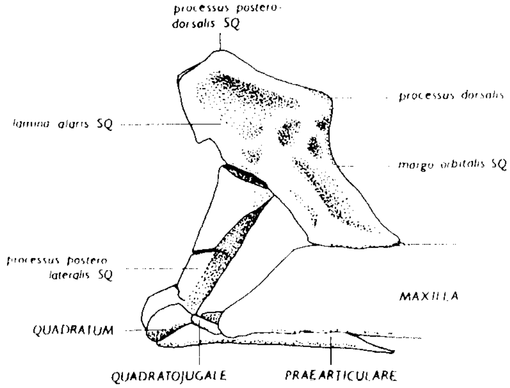


Fig. 47. *Eopelobates leptocolaptus.* Lateral view of the posterolatera part of the skull.

a) There is a distinct keel on the ventral surface of *pars medialis* which diminishes anteriorly, and disappears close to the anterior tip. In *Pelobates fuscus* the ventral surface of the *pars medialis* is flat or slightly convex only.

The pterygoid is preserved in its original shape, though it is fractured.

a) In the ventral aspect, the *margo orbitalis* is only slightly concave, while in *Pelobates fuscus* the *ramus maxillaris* and the *ramus interior* almost form a right angle.
b) The central part of the ventral surface of the bone is rather concave which results in a triangular-shaped depression. In *Pelobates fuscus* this part of the surface is flat.

The praearticular is considerably destroyed by fractures, but its general shape is preserved.

a) It is regularly bent in dorsal or ventral aspect, not S-shaped as in *Pelobates fuscus.*

The state of preservation of other cranial elements, though they be present at least as fragments (e.g. dentary) does not allow a reconstruction either of their original shape or of their accurate topographical relations.

4.3.2 Hitherto undescribed form from the locality Khermeen Tsav, Mongolia

Geological age: Upper Cretaceous (?Middle Campanian)

This differs from the form described as *Eopelobates leptocolaptus* in the following characters:

(1) The sphenethmoid is not flattened dorsoventrally, and the anterior part of the braincase has similar proportions as in *Pelobates fuscus*.

(2) A sculpture is present on the preserved part of the left nasal (the area of *processus paraorbitalis*), as well as on the posterior two thirds of the outer maxillary surface, and on the surface of the *lamella alaris squamosi*. This sculpture is made up of numerous irregular fossae isolated by rounded ridges. This conditions represent a quite different type of sculpture which is much more subtle if compared with that of *Eopelobates leptocolaptus*. By no means is it possible to suppose that these differences are due to the degree of ontogenetical development.

(3) The distinct suborbital mound running parallel with the *margo orbitalis maxillae* is lacking, while present in *Eopelobates leptocolaptus*.

(4) The quadratojugal is considerably long, while it is only a minute element in *Eopelobates leptocolaptus*.

(5) The *processus dorsalis squamosi* is widely rounded and not protruding in such an extent as is the case with *Eopelobates leptocolaptus*.

(6) The margin of the *lamella alaris* between the *processus dorsalis* and the *processus posterodorsalis* is not accompanied by a distinct mound as is the case with *Eopelobates leptocolaptus*.

(7) The squamosal proportions are different in both forms. The longest diameter of *lamella alaris* approximately equals the length of the *processus posterolateralis*, while this process is comparatively more robust and shorter in *Eopelobates leptocolaptus*.

(8) The *margo orbitalis squamosi* is only slightly concave which is a condition connected with the shape of the *processus dorsalis* described above. In *Eopelobates leptocolaptus* there is a distinct flexure of the margin close to the base of the mentioned process (fig. 47).

(9) The praearticular is very distinctly S-shaped. In *Eopelobates leptocolaptus* it has the shape of a regular arch.

Both forms are identical in the following characters:

(1) The dorsal surface of the sphenethmoid is quite flat.

(2) The quadratojugal and quadrate are probably separated by a suture.

(3) The *processus zygomatico-maxillaris maxillae* is lacking. Hence the course of the squamoso-maxillary suture is a straight continuation of the *margo orbitalis maxillae*.

(4) There is a distinct keel on the ventral surface of the *pars medialis parasphenoidei*.

(5) The anterior margin of the dorsal opening of the braincase is situated posterior to the level of the postnasal walls.

These differences and conformities would probably be more numerous if other parts of the skull were also available. However, it follows also from such a limited comparison that this form and *Eopelobates leptocolaptus* are closely related but not identical as for their cranial anatomy.

Hitherto undescribed form from the Cretaceous of Mongolia differs from *Pelobates fuscus* in the following characters:

The sphenethmoid is either not preserved throughout (in 1 specimen), or it is embedded in sediment to such an extent that important characters are not visible. Despite this, it is possible to state the following:

a) The anterior margin of the braincase roof opening is situated posterior to the level of the postnasal walls.

The prooticooccipital is visible only in its dorsal aspect. Similarly to *Pelobates fuscus* there is a large but shallow depression on its dorsal surface.

a) Both prooticooccipitals are separated dorsally from each other by a wide cartilaginous stripe (forming a part of the *tectum synoticum*). The disappearance of this cartilage during the fossilization results in the dorsal margin of the *foramen magnum* bearing a distinct incision in the mid-line.

The frontoparietals are nearly complete; merely both anterior tips are broken away and rather dislocated. The part of the left element adjacent to the fracture is lacking. In minor specimens, only the posterior parts of frontoparietals are preserved. The *processus paraoccipitales* and *foramina pro arteriae occipitales* are well developed.

a) It is a paired element. There is a distinct median suture along the mutual contact of both frontoparietals, including also the *facies posterior*.
b) Between the anterior two thirds of both elements there is a large fontanelle.
c) In a larger specimen, the sculpture is present merely along the lateral margins; the minor specimen has preserved parts of both frontoparietals without any sculpture.
d) The type of sculpture is different from that in *Pelobates fuscus*. It is made up of large fossae and small pits separated by rounded ridges. The sculpture of the same nature, though rather more subtle, occurs also on the fragment of the nasal, and on the maxilla and squamosal.

The maxilla of the left side is nearly completely preserved. Similarly to *Pelobates fuscus*, its *lamina anterior* reaches before the most anterior tip of the *pars dentalis*. The groove for the *ductus nasolacrimalis* is well developed. Differences are as follows:

a) The *processus frontalis* is very poor'y developed (however, in some *Pelobates fuscus* specimens this outgrowth is slightly developed or also lacking throughout).
b) The *processus zygomatico-maxillaris* is lacking.
c) Owing to the poor development or absence of both mentioned processes the dorsal margin of the maxilla is quite straight.
d) Sculpture is lacking in that part of the maxillary surface which is situated anterior to the orbit.
e) The *processus posterior* is massive, not running out in a slender point functionally substituting a part of the quadratojugal.

The squamosal is rather beyond its original position in relation to the maxillary;

however, it is completely preserved. Besides the different type of sculpture (see notes on frontoparietal above), the following differences can also be found:

a) The dorsal margin of *lamella alaris* between the *processus dorsalis* and the *processus posterodorsalis* is straight, not concave.

b) The *processus dorsalis* is widely rounded, not terminated by an acute, dorsomedially directed point.

The quadratojugal is rather moved beyond its original relative position against the maxillary; however, it is complete.

a) It is highly probable that the quadratojugal and quadratum are separated by a suture.

b) It is relatively larger than that in *Pelobates fuscus* where it is partly substituted functionally by the long and slender *processus posterior maxillae*.

The parasphenoid is nearly complete. Only the anterior tip of the *pars medialis* is lacking.

a) Approximately at the level of the posterior margin of sphenethmoid the *pars medialis* suddenly becomes indentedly narrower.

b) There is a rounded but distinct keel on the ventral surface of *pars medialis*.

c) The *processus posterior,* which is the most posterior part of the bone, is well developed, almost reaching the margin of the *foramen magnum*.

The pterygoid of the left side is preserved only, and its *ramus interior* is detached by a big fracture which together with the fracture running across the maxilla causes the entire posterolateral part of the skull to be broken away and dislocated.

a) The central part of its ventral surface has a triangular depression.

The praearticular is preserved only in its posterior section.

a) It is only very indistinctly S-shaped.

The other cranial elements are destroyed to such an extent that they cannot afford any diagnostic data.

4.3.3 *Macropelobates osborni* NOBLE, 1924

(fig. 48; see also NOBLE, 1924, fig. 1; ESTES, 1970, fig. 27)

1924 — *Macropelobates osborni* gen. et sp. n.; G. K. NOBLE: A new Spadefoot Toad etc., p. 1, fig. 1, 2 B, 3 B, C, E, G
1956 — *Macropelobates osborni*; R. G. ZWEIFEL: Two Pelobatid frogs etc. p. 12, fig. 7 C
1970 — *Macropelobates osborni*; R. ESTES: New Fossil Pelobatid Frogs etc., p. 324
Geological age: boundary between the Lower and Middle Oligocene (ESTES 1970: 324)

The sphenethmoid (ESTES, 1970. figs 4 c, 7 B) has its larger part of the *tectum nasi* broken away; however, the postnasal wall and most of the *solum nasi* including the untouched margin of the *fenestra endochoanalis* are preserved.

a) The surface of the postnasal wall exposed into the nasal cavity is not vertical as in *Pelobates fuscus* but it is slanting anteroventrally, passing in the *solum nasi* in a wide groove.

b) The margin of the *solum nasi* bounding the *fenestra endochoanalis* is thickened which is reminiscent of the condition in *Pelobates fuscus*. However, this marginal thickening does not continue posteriorly up to the base of postnasal wall, but it is confined to the medial margin of *fenestra endochoanalis*.

c) The dorsal surface of the intact part of the *tectum nasi* and the braincase roof in the adjacent area of the orbitotemporal region is flat, not concave transversally as is the case with *Pelobates fuscus*.

d) The *lamina supraorbitalis* is large, forming the roof of the anteromedial part of the orbit. Its dorsal surface is smooth and situated horizontally so that it passes without any break in the dorsal surface of the braincase roof.

e) Despite the fact that the anterior part of the frontoparietal is largerly broken away, the uncovered surface of sphenethmoid does not display any sign of the

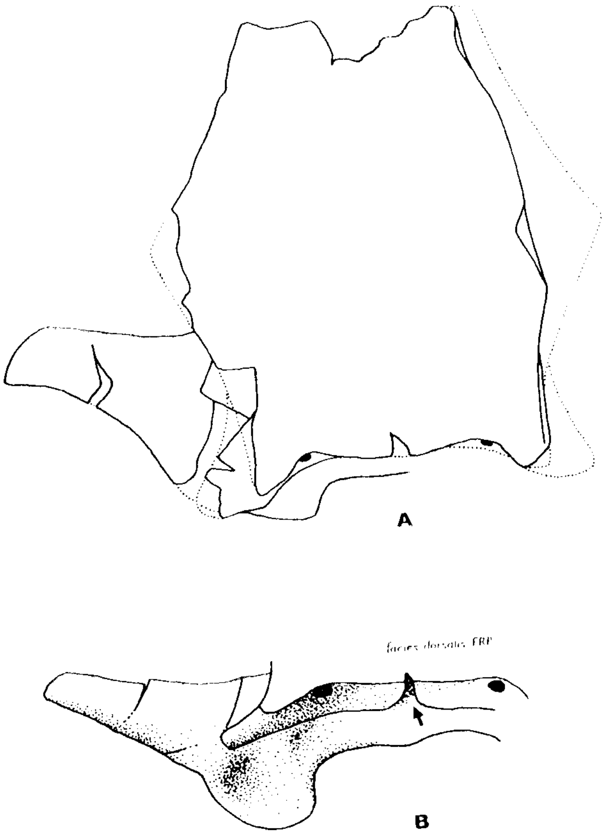


Fig. 48. *Macropelobates osborni*. A - frontoparietal and left prooticooccipital in dorsal view; B - *facies posterior frontoparietalis* and left prooticooccipital in posterodorsal view. Reconstructed outline of frontoparietal is indicated by dotted line. The location of the symmetrical incision in the *facies posterior frontoparietalis* is indicated by the arrow.

anterior margin of the *fenestra frontoparietalis* or homologous opening. Hence, this fenestra is assumed to be less extensive than that in *Pelobates fuscus*.

The prooticooccipital has its ventral part embedded within the sediment, but its dorsal surface (except the part covered by frontoparietal) is well visible.

a) In the dorsal aspect, the lateral part adjacent to the *crista parotica* is slender in comparison with that in *Pelobates fuscus* (see fig. 48).

The detailed morphology of the posterior surface of occipital region approximately corresponds with that in *Pelobates fuscus*.

The nasal is preserved only as a dislocated fragment, close to the left part of the sphenethmoid.

a) The sculpture of the dorsal surface consists of numerous and regular pits, separated by acute ridges. This type of sculpture is rather reminiscent of that in the hitherto undescribed form from the Cretaceous of Mongolia, but it is quite different from that in *Pelobates fuscus*.

The frontoparietal (fig. 48; cf. Estes, 1970, fig. 27) is sufficiently preserved, including the base of the left *processus paraoccipitalis*. However, the marginal parts are mostly broken away. The original position of the element is also preserved.

a) The *margo orbitalis* is slightly lifted dorsally, so that the central part of the dorsal surface is rather depressed. The only sign of surface convexity is in the posterior part. In contrast to this, the central part of frontoparietal is distinctly convex in *Pelobates fuscus*.
b) The sculpture is of the same nature as is the case with the nasal.
c) The sculptured part of the frontoparietal surface passes gradually into the smooth surface of the *processus paraoccipitales*, not by the acute indentation which occurs in *Pelobates fuscus*.
d) The posterior margin of the *facies dorsalis* between both *processus paraoccipitales* is only slightly convex not forming the distinct and sometimes pointed *processus posterior superior* (»occiput«) occurring in *Pelobates fuscus*.
e) The posterior margin of the *facies dorsalis* is interrupted in the middle of its length by a small but distinct notch which is rather asymmetrical in dorsal aspect. It would seem as if this were a small marginal part broken away (fig. 48 A). However, careful investigation of the *facies posterior* (fig. 48 B) reveals that this notch is quite symmetrical and divides the facies posterior into the two symmetrical moieties. This suggests that the mentioned notch is not an artefact, but the remainder of a formerly paired nature of the frontoparietal. It follows from this fact that the frontoparietal bone of this form could not arise in the same way as it does in *Pelobates fuscus* (i.e. by incorporating the unpaired median element adjoining the *tectum synoticum*).

The squamosal (see Estes, 1970, fig. 18 e) is dislocated. However, except for the distal part of *processus posterolateralis* and the anterior part of *lamella alaris*, its surface is well visible.

a) The sculpture is of the same type as that in the nasal and frontoparietal.

b) The *processus posterodorsalis* is not developed.

c) The dorsal margin of the *lamella alaris* posterior to the *processus dorsalis* is straight, not concave as is the case with *Pelobates fuscus*.

d) The entire posterior margin of *lamella alaris* is convex, not giving out any process.

The pterygoid consists of separated fragments, and tips of all outgrowths are lacking throughout. This results in the original shape of bone being destroyed. Moreover, the whole complex of fragments is moved out from it original position.

The praearticular is preserved only in its posterior third.

a) The preserved part is nearly straight, not S-shaped as in *Pelobates fuscus*. Only the groove for Meckel's element is S-shaped due to its turning from the dorsal surface of the bone onto the lateral one.

The other cranial elements are either lacking or are covered by sediment.

4.3.4 *Eopelobates bayeri* Špinar, 1952

(fig. 49; Špinar, 1952, fig. 2; 1972, tab. 153, 154, 155, 158/1, 2; Estes, 1970, fig. 2)

For synonymy see Špinar (1972: 199).

Geological age: Oligomiocene

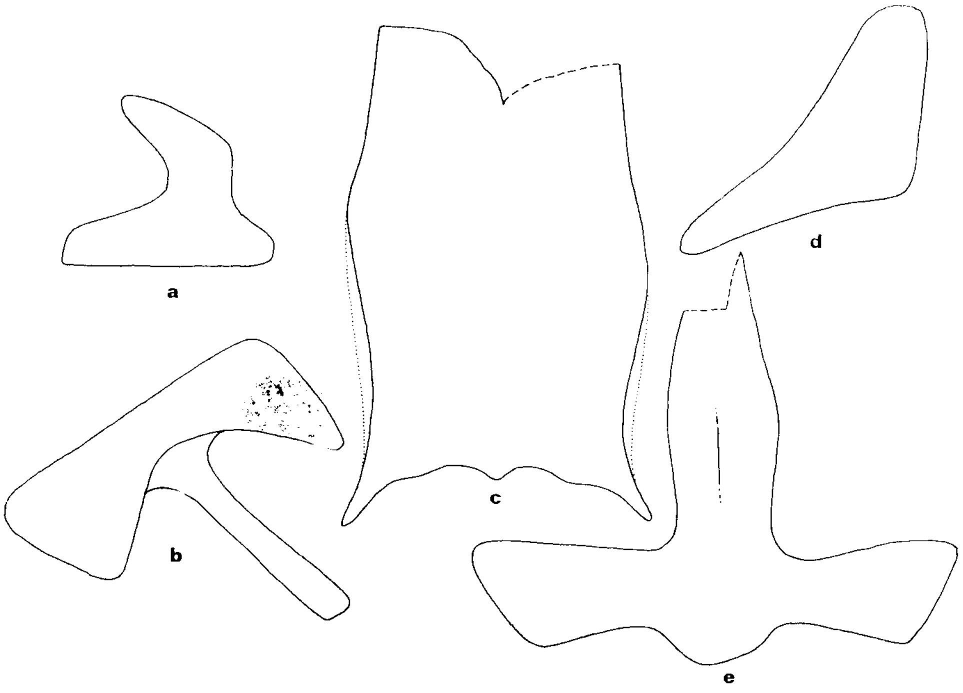


Fig. 49. *Eopelobates bayeri*. a - imprint of praemaxilla; b - imprint of squamosal; c - imprint of frontoparietal (the outline of *facies ventralis* is indicated by dotted line); d - nasal; parasphenoid.

The sphenethmoid is preserved only as a negative imprint in a few specimens (see Špinar, 1972, fig. 84), which allows only to determine its general shape and proportional relations against other cranial elements.

a) The ossified interior of *processus praenasalis medius* is developed to a lesser extent than that in *Pelobates fuscus,* so that it forms only an indistinct outgrowth.

b) The postnasal walls were probably ossified to a lesser extent, as they are preserved only in the form of short lateral processes.

The praemaxilla (fig. 49 a)

a) The medial margin of *pars facialis* has a distinct convexity terminated with an obtuse point, which is reminiscent of the condition in *Pelobates varaldii* (see below).

b) According to Špinar (1972: 200) it bears 12 teeth.

The nasal (fig. 49 d; Špinar, 1972, fig. 81 A; Estes, 1970, fig. 12 B)

a) The sculpture on the dorsal surface is made up of numerous pits separated by rounded ridges.

b) The *pars lateralis* is represented by a considerably slender, laterally narrowing process, directed posterolaterally. Both the *processus parachoanalis* and *processus paraorbitalis* are not developed.

c) The *margo orbitalis* is either straight or merely slightly concave.

The frontoparietal (fig. 49 c; Špinar, 1952: 462; 1972: 201—202, figs 81, 82 A; Estes, 1970, fig. 12 B)

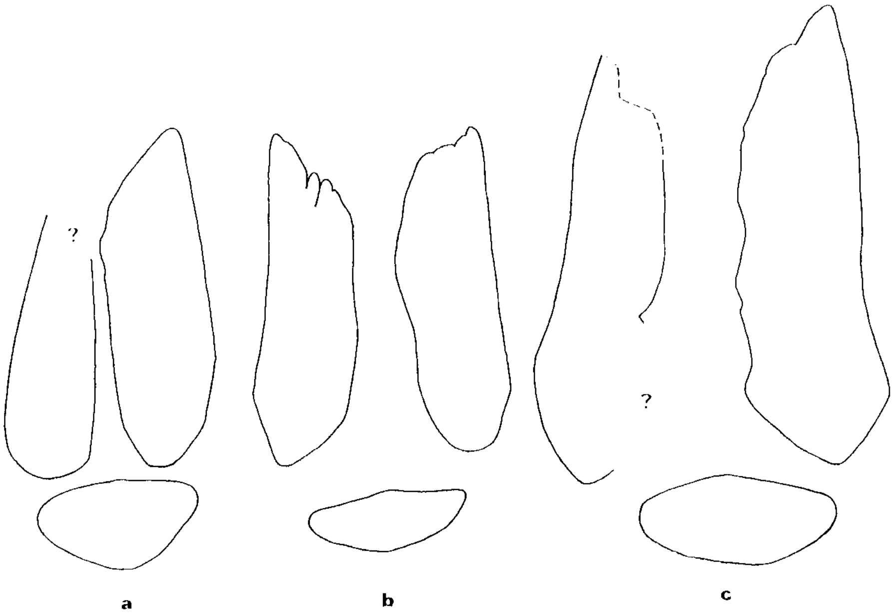


Fig. 50. Embryonic stage of the development of the frontoparietal complex in *Eopelobates bayeri* tadpole. a - DP FNSP 6002; b - DP FNSP 4349; c - DP FNSP 9651.

a) The sculpture is similar to that in the nasal. However, it is less distinct in the centre of the interorbital section of the bone.
b) The lateral margin is slightly convex.
c) The *processus posterior superior* is represented only by an indistinct and obtuse point.
d) The *facies dorsalis* is approximately oblong; from its posterolateral corners the slender and comparatively short *processus paraoccipitales* are given off.

It must be stressed that the embryonic development of the frontoparietal bone is identical with that in *Pelobates fuscus* (see fig. 50). That is to say that in a certain number of tadpoles (see also ŠPINAR, 1972, tab. 171/2) the unpaired median element adjoining the *tectum synoticum* is more or less preserved. However, in most other specimens this median element is imprinted to the centre of the posterior part of the parasphenoid, which causes conditions not providing an easy survey.

The maxilla
a) The sculpture is of the same nature as that in the nasal, frontoparietal and squamosal.
b) According to ŠPINAR (1972: 200) the *processus frontalis* is not well developed.

The squamosal (fig. 49 b; ESTES, 1970, fig. 20 a; ŠPINAR, 1972, fig. 83).
a) The sculpture is of the same type as that in the nasal, frontoparietal and maxilla; however, there are signs that the pits are arranged into rows.
b) The *margo orbitalis* is straight.
c) The only dorsal outgrowth is situated posterior to the level of the base of the *processus posterolateralis.*
d) The posterodorsal and posteroventral margins of the *lamella alaris* meet each other at a comparatively sharp angle, thus forming a distinct process.
e) The posterior section of the posteroventral margin and the long axis of the *processus posterolateralis* form a sharp angle.
f) The whole posteroventral margin of the *lamella alaris* is deeply concave. In contrast to this, this margin is convex in *Pelobates fuscus.*

From what has been said it follows that the shape of the *lamella alaris squamosi* is different from that in *Pelobates fuscus.* It is not possible to find whether squamosal and frontoparietal were in contact.

The parasphenoid (fig. 49 e; ŠPINAR, 1972, fig. 85 A, B, B', tab. 156, 157, 169, 175/1,2, 176)
a) There is a narrow but acute keel along the *pars medialis.*
b) The *processus posterior* is well developed both in tadpoles and adults.
c) There is a sign of an indistinct sculpture which could be considered as vestigial teeth on the posterior part of the *pars medialis*; these unevenesses become less distinct in adults.
d) Processes on the lateral margin of the anterior part of *pars medialis* vary in size. Remarkably, in one specimen (DP FNSP 9641 b) it seems as if two such outgrowths on each side are developed.

The praearticular is typically S-shaped (fig. 40 b, c).

a) The posterior part of most specimens investigated is considerably wide, in contrast to the condition in *Pelobates fuscus*.

The other cranial elements are either not preserved or imprints are so indistinct that thorough morphological investigation is impossible.

4.3.5 *Pelobates fuscus insubricus* CORNALIA, 1873

For synonymy see GORHAM (1966: 24)
Geological age: Recent

The sphenethmoideum

a) The ventral surface of the postnasal walls bears an acute ledge.
b) The area covered by the *processus palatinus maxillae* is bounded by disctinct ridges; one of them is identical with the section of the acute ledge mentioned in the previous item.
c) Similar ridges bound the area covered by the *pars medialis parasphenoidei*. In the nominate form *Pelobates fuscus fuscus* these ridges are not so distinct.

The prooticooccipital

a) An acute ridge runs from the surface of the *prominentia ducti semicircularis posterioris* to the lateral margin of the *foramen magnum*.

The praemaxilla

a) The number of tooth positions is 13.
b) The ridge running in continuation of the *lamina horizontalis* below the *pars facialis* is directed to the median suture, not obliquely to join the *crista dentalis*.
c) The *crista lateralis* and *recessus marsupiatus* are not developed.

The frontoparietal

a) The *processus posterior superior* is represented by an elevated and sharply convex medial section of the posterior margin of the *facies dorsalis*.
b) The opening of the *canalis pro arteria orbitonasalis* is located approximately in the middle of the *margo orbitalis*. In the nominate form it is shifted more anteriorly. A groove runs anteriorwards along the ventral surface of *tectum supraorbitalis* from the mentioned opening, where the *arteria orbitonasalis* is stored.

The maxilla

a) The margin between the *processus zygomatico-maxillaris* and the *processus posterior* is deeply concave.

The squamosal

a) The *processus dorsalis* is less distinct than that in *Pelobates fuscus fuscus*.
b) The *lamella alaris* is more narrow than that in the nominate form.
c) The anterior tip of the *processus zygomaticus* is longer than that in the nominate form, which also causes a prolongation of the *margo orbitalis squamosi*.

The parasphenoid

a) The middle section of the posterior margin is widely convex and gradually passes into the posterior margins of both *processus laterales*.

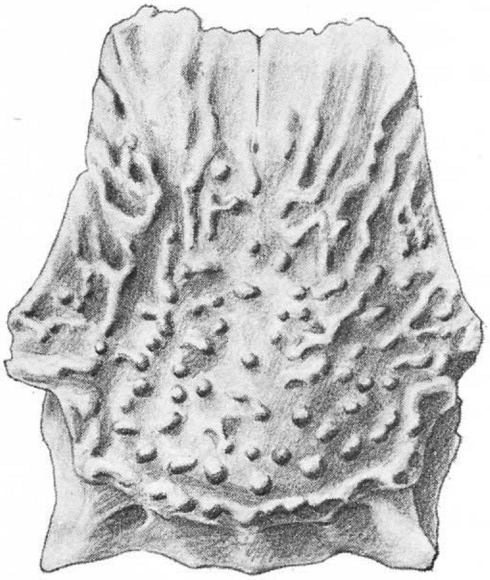


Fig. 51. Frontoparietal of *Pelobates cf. fuscus* (AF 10/64/a PAN Krakow); Pliocene, Rebielice Krolewskie, Poland.

The pterygoid

a) The margin of the *ramus interior* is neither interrupted by a notch nor S-shaped as is the case with the nominate form in connection with the occurrence of pterooccipital fissure.

No other important diagnostic differences were found.

4.3.6 *Pelobates cultripes* (CUVIER, 1829)

(fig. 57/1; BOAS 1914, figs 16, 18, 22; MERTENS 1923, fig. 4)

For synonymy see GORHAM (1966: 23).

Geological age: Recent

The following are diagnostic characters ascertainable on the non-disarticulated skull (see also Mertens 1923: 118—119).

The sphenethmoid

a) That part which is situated anterior to the level of the *fenestrae nasobasales* is not ossified.
b) The *lamina supraorbitalis* is larger, and its lower surface covering the opening for the *ramus medialis nervi ophthalmici* dorsally is nearly horizontal.

The prooticooccipital

a) There is a distinct ridge on the surface of the *prominentia ducti semicircularis posterioris,* which is a continuation of the similar ridge on the surface of the *processus paraoccipitalis* of the frontoparietal bone. This ridge runs lateroventrally, and by a sudden break it joins the posterior margin of the otic capsule roof, covering the *fossa fenestrae ovalis* dorsally. Another ridge runs from the tip of the *processus paraoccipitalis,* although this soon turns medioventrally to the lateral margin of the *foramen magnum*.

The praemaxilla

a) The number of tooth positions is higher (11—12).
b) The tooth row reaches the median symphysis.
c) The *lamina horizontalis* is narrower than that in *Pelobates fuscus*.
d) The *sulcus dentalis* is not developed.
e) Medially, the *lamina horizontalis* is represented by an indistinct ledge situated ventral to the *pars palatina* and reaching the median symphysis. Therefore, it does not pass into the *pars palatina* as is the case with *Pelobates fuscus*.
f) The *crista lateralis* and consequently also the *recessus marsupiatus* are not developed.

The nasal

a) The *processus anterior* is short and narrow.

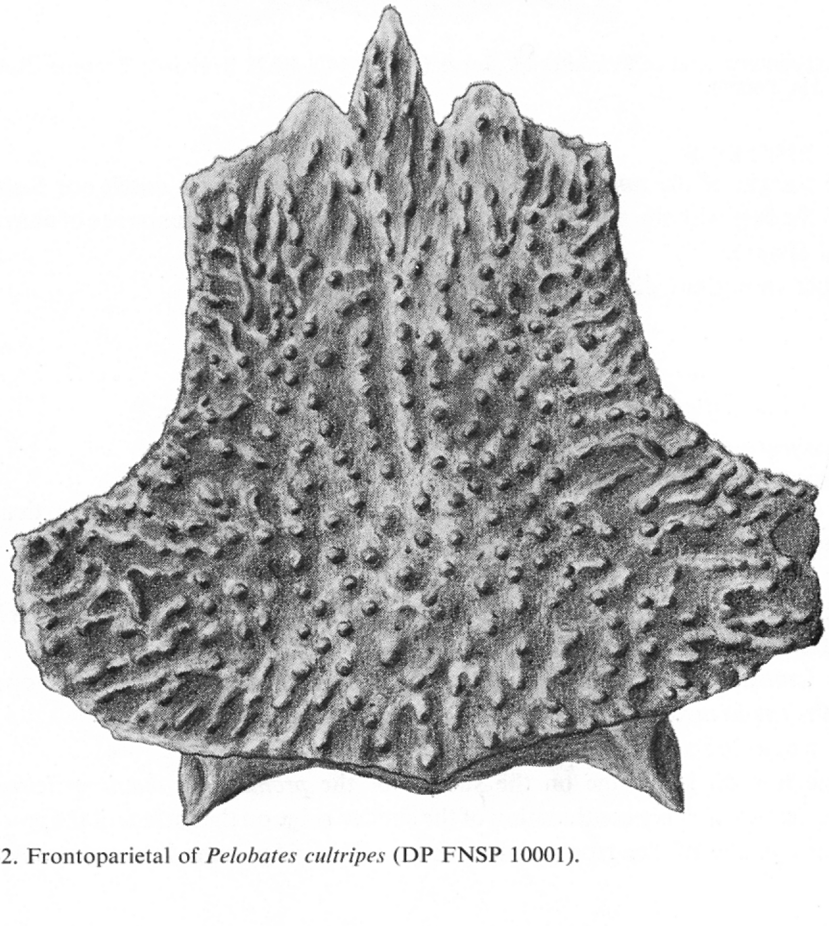


Fig. 52. Frontoparietal of *Pelobates cultripes* (DP FNSP 10001).

b) It gives off a well developed posteromedial outgrowth reaching far behind the level of the *processus paraorbitalis* (fig. 57/1). Hence, it forms more than one third of the medial margin of the orbit.

The frontoparietal (fig. 52, 57/1)

a) The *margo orbitalis* borders only the posteromedial part of the orbit.

b) The *facies dorsalis* is almost flat transversally in its interorbital section, and poor convexity occurs only in its posterior part. The margins of *facies dorsalis* are not elevated.

c) The *tectum supraorbitale* becomes gradually wider posteriorly so that it considerably overlaps the posteromedial flat of the endocranial orbit (see Boas 1914, fig. 22)

d) The frontoparietal is in contact with the *lamella alaris squamosi* in a considerably long suture (fig. 57/1; see also Boas, 1914, fig. 16).

e) The *facies posterior* is only slightly convex in its section between both *processus paraoccipitales*.

f) Similarly to this, also the posterior margin of the *facies dorsalis* is slightly convex. The *processus posterior superior* is poorly developed.

g) The ridge running down the dorsal surface of the *processus paraoccipitalis* is more pronounced than that in *Pelobates fuscus*.

h) The *facies posterior* is very low (see also Boas, 1914, fig. 18).

The maxilla

a) This is comparatively higher than that in *Pelobates fuscus*.

b) The *margo orbitalis* is more deeply concave; hence the *processus frontalis* and *processus zygomatico-maxillaris* are pronounced.

c) In lateral aspect, the posterior margin of maxilla is situated vertically, and slender and unsculptured *processus posterior* is given off as a prolongation of *crista dentalis*, adjoining laterally the oblique facet on the quadratojugal.

d) The *lamina horizontalis* is narrow and less prominent than that in *Pelobates fuscus* (similarly as is the condition with praemaxilla).

e) The *processus palatinus* reaches much farther medially than is the case with *Pelobates fuscus* (up to the level of the opening of *canalis pro ramus medialis nervi ophthalmici*; see Boas, 1914, fig. 22).

The squamosal (fig. 57/1; Estes, 1970, fig. 18 d)

a) The margin between the *processus dorsalis* and the *processus posterodorsalis* is connected by suture with the adjacent part of the frontoparietal bone.

b) The margin of the *lamella alaris* runs from the *processus posterodorsalis* anteroventrally with the result that this process forms a sharp point. This however is well visible if the skull is viewed laterally, not dorsolaterally.

c) The mentioned posteroventral margin of the *lamella alaris* and *processus posterolateralis* form an obtuse angle (when the skull is viewed laterally). In *Pelobates fuscus* this angle is always much sharper (approximately 90°) (cf. Estes 1970, fig. 18 a-c).

d) Owing to the large extent of the *lamella alaris* (and also of the posterior part of maxilla), the lower temporal fenestra is reduced.

e) The greatest diameter of *lamella alaris* is approximately twice the length of the *processus posterolateralis*.

The vomer (fig. 37 a)

a) There is a comparatively large and flat process medial to the *torus dentigerus*; however, these outgrowths of both opposite vomers need not be in mutual contact.

b) A thin osseous lamina is extended between the *processus anterior* and *processus choanalis anterior* which results in both these processes not forming slender points as is the case with *Pelobates fuscus*. Owing to this, the vomer is considerably large (see also Boas 1914, fig. 22).

c) The base of the *torus dentigerus* is comparatively large and low.

The parasphenoid (fig. 38 c)

a) The *pars medialis* is more slender than that in *Pelobates fuscus*.

b) A distinct *processus posterior* is developed which even overlaps the ventral margin of *the foramen magnum* (see BOAS, 1914, fig. 22).

c) In ventral view, the suture between the pterygoid and *processus lateralis parasphenoidei* is directed laterally, whereas posterolaterally in *Pelobates fuscus*.

d) The rounded outgrowth borne by the margin of the free section of the *pars medialis* is shifted anteriorly, approximately to the level of posterior margin of sphenethmoid.

The pterygoid (see BOLKAY, 1919, fig. 26)

a) There is a small foramen on the ventral surface close to the *margo tympanicus*, which was erroneously called by BOLKAY (1919, fig. 26) the »sinus pro tuba Eustachii«. In *Pelobates fuscus* it is substituted functionally by a notch with an opening in its bottom, visible in dorsal view.

The praearticular

a) The *processus coronoideus* has no sharp margins, and is bent medially.

In other parts of the skull either essential differences are lacking or it is impossible to find them on the non-disarticulated skull.

4.3.7 *Pelobates varaldii* PASTEUR et BONS, 1959

1959 — *Pelobates varaldii*; C. PASTEUR et J. BONS: Les Batraciens du Maroc. Trav. Inst. Sci. chérif., sér. zool., 17, p. 117, tab. 2

Geological age: Recent

The sphenethmoid has its *laminae supraorbitales* morphologically identical with those in *Pelobates fuscus*. However, it differs in the following characters:

a) The most anterior section of the *septum nasi* with adjacent parts of the *solum* and *tectum nasi*, and *processus praenasalis medius* are not ossified.

b) The dorsal surface of the sphenethmoid is flat in transversal section. Only both *laminae supraorbitales* are rather elevated so that they are directed dorsolaterally.

The prooticooccipital

a) The *crista frontoparietalis* is represented only by an indistinct ridge which is even lacking on the dorsal surface of the *prominentia ducti semicircularis posterioris* (also in adults).

b) That part of the *crista parotica* which is above the *fossa fenestrae ovalis* is not represented by a sharp edge, but is rounded.

c) The ventral margin of the *fenestra ovalis* in adults bears a deep and wide notch from which a groove runs medially, filled with cartilage in living animals. In *Pelobates fuscus* there is only a sign of the mentioned notch.

d) The pterooccipital fissure does not cause any incision into the ossified part of the *prooticum*. An outgrowth which in other forms represents the ventral side of this fissure is lacking, and thus the lateral margin of the *prooticum* is quite even.

The praemaxilla

a) The tooth row reaches almost up to the median symphysis.

b) The *lamina horizontalis* is narrow and its margin is widely rounded. Due to this, the *sulcus dentalis* is not developed.

c) The medial margin of the *pars facialis* gives off a rounded but distinct outgrowth directed posteromedially.

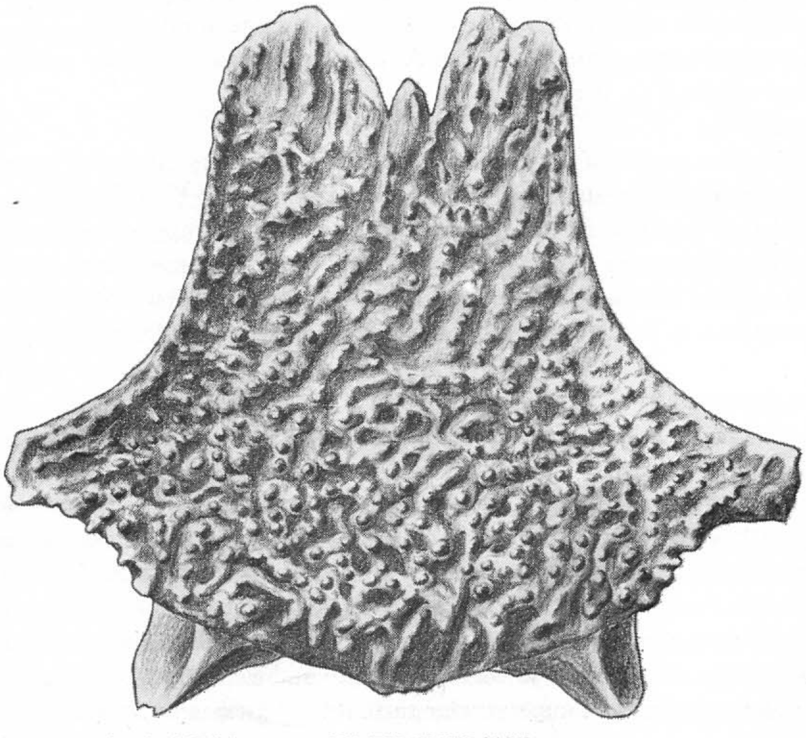


Fig. 53. Frontoparietal of *Pelobates varaldii* (DP FNSP 2122).

d) Both *crista lateralis* and *recessus marsupiatus* are not developed.

The nasal

a) It has a large posteromedial outgrowth whose lateral margin takes part in the formation of the medial margin of the orbit, however, to a lesser extent than that in *Pelobates cultripes.*
b) The *processus anterior* is short, narrow, and is terminated by a rounded point.

The frontoparietal (fig. 53)

a) The *tectum supraorbitale* is only slightly elevated.
b) The frontoparietal takes part in the formation of only three quarters of the medial margin of the orbit.
c) The central part of the facies dorsalis is only slightly convex.
d) The opening of the *canalis pro arteria orbitonasalis* is approximately in the middle of the antero-posterior diameter of the bone, whereas it is on the boundary between the first and second quarters of this dimension in *Pelobates fuscus.*
e) *Tectum supraorbitale* gradually becomes wider posteriorwards so that it considerably extends into the posteromedial part of the orbit.
f) The facies posterior is very low.
g) Only a sign of the *processus posterior superior* is developed.
h) The *processus paraoccipitales* are small in relation to other parts of the bone.
i) Two instead of one distinct ridges run down the dorsal surface of the *processus paraoccipitales,* which only nearly to its point join one another.
j) The frontoparietal contacts the *lamella alaris squamosi* in a short suture in the section adjacent to the orbit.

The maxilla

a) The posterior margin of the maxilla is vertical in its dorsal section, and approximately in the middle of its length it is broken, running out by a pointed *processus posterior*. In contrast to this, the margin between the *processus zygomatico-maxillaris* and *processus posterior* is nearly straight in *Pelobates fuscus.*
b) The *processus palatinus* reaches much farther medially than that in *Pelobates fuscus* (up to the level of the opening of *canalis pro ramus medialis nervi ophthalmici).*

The squamosal

a) The *lamella alaris* is in contact with the frontoparietal in a short suture adjacent to the orbit.
b) The posterior margin of the *lamella alaris* runs by the concave arch onto an outgrowth which is probably a homologue of the *processus posterodorsalis.* This margin is located much more dorsally than the dorsal surface of *ramus paroticus.*
c) From the *processus posterodorsalis* the margin of the *lamella alaris* runs ventrally by the widely convex arch, so that this margin and the long axis of the *processus posterolateralis* form an angle similar to that in *Pelobates fuscus* (cf. Estes 1970, fig. 18 a).

d) In place of the base of the *processus posterolateralis* the margin of *lamella alaris* bears a wide notch.

e) The *processus zygomaticus* gives off anteriorly a slender and unsculptured point which adjoins the medial margin of posterior section of the *margo orbitalis maxillae*.

The quadratojugal corresponds by its size and shape to that in *Pelobates fuscus*.

The vomer

a) There is a thin osseous lamina between the *processus anterior* and the *processus choanalis anterior,* but both mentioned processes distinctly protrude from it, though not to such an extent as in *Pelobates fuscus*.

The parasphenoid

a) Each lateral process bears on its ventral surface a rounded ridge which turns anteriorly within the area of attachment of the lateral process to the *pars medialis,* then joining each other. In some specimens the sole unpaired ridge arising by the fusion of the above described ones may continue anteriorly along the surface of the *pars medialis*.

b) The *processus posterior* is developed, but it does not reach the ventral margin of the *foramen magnum*.

The morphology of other cranial elements is within the variation range of that in *Pelobates fuscus*.

4.3.8 *Pelobates syriacus syriacus* BOETTGER, 1889

(MERTENS, 1923, fig. 3; BASOĞLU and ZALOĞLU, 1964, figs 7—16, 20, 21)

For synonymy see GORHAM (1966: 25)
Geological age: Recent

For diagnostic differences against *Pelobates cultripes* see MERTENS (1923: 119—121), for those against *Pelobates fuscus* see BOETTGER (1889: 145—146).

The sphenethmoid

a) The *processus praenasalis medius* is not ossified to such an extent as in *Pelobates fuscus*. The *septum* is ossified up to the level of the *fenestra nasobasalis.*

b) That section of the margin of the *solum nasi* which takes part in the bordering of the *fenestra endochoanalis,* is considerably elevated. This elevation is manifested by a corresponding depression on the ventral surface of the *solum nasi.*

c) The dorsal surface of the *tectum nasi* and of the adjacent part of the braincase roof is nearly flat. However, the *laminae supraorbitales* are directed dorsolaterally, similarly to *Pelobates fuscus*.

d) The *fenestra frontoparietalis* reaches by its most anterior part to the level of the posterior end of the marginal cartilaginous stripe bordering the *laminae supraorbitales*. It reaches more anteriorly in *Pelobates fuscus.*

The prooticooccipital

a) The *crista frontoparietalis* is represented by an elongated elevation only, or it is lacking throughout.

b) There is distinct *crista frontoparietalis posterior* which, however, does not turn ventrally down along the posterior surface of *prominentia ducti semicircularis posterioris,* but continues laterally and joins the marginal edge dorsally covering the *fossa fenestrae ovalis.*

c) The ventral part of the ossified margin of the *fenestra ovalis* is interrupted by a deep notch. Only a sign of the latter occurs in *Pelobates fuscus.* The groove runs medial from this notch, filled with cartilage in living animals. It reaches up to the margin of the cartilaginous part of the braincase floor in the otic region.

d) The medial wall of the otic capsule is more convex into the braincase cavity than that in *Pelobates fuscus.*

The quadrate (fig. 35 b)

a) A more extensive part of the *pars articularis palatoquadrati* ossifies in comparison with the condition in *Pelobates fuscus,* so that this outgrowth is more robust than the ankylosed quadratojugal.

The praemaxilla

a) The tooth row reaches up to the medial margin of the *pars dentalis.*

b) The tooth positions number is 14.

c) The dorsal surface of the *pars dentalis* is much more extensive than the anterior surface which is very low and rounded.

d) In connection with this, the *crista lateralis* is very indistinct, and the *recessus marsupiatus* is lacking throughout.

e) The medial margin of the *pars facialis* bears distinct though rounded outgrowth.

f) The *pars facialis* is comparatively slender and terminated by an acute point.

The nasal (fig. 57/2)

a) That part of its margin which takes part in bordering the *fenestra exonarina* is regularly concave, whereas the margins of the *processus parachoanalis* and *processus anterior* meet approximately at a right angle in *Pelobates fuscus.*

b) The *processus anterior* forms a distinct point.

c) The *margo orbitalis* is distinctly concave, which condition is associated with the presence of a pointed posteromedial process.

The frontoparietal (fig. 54, 57/2)

a) The *facies dorsalis* is slightly and regularly convex transversally. However, in the lateral view, the radius of the convexity somewhat varies (BASOǦLU and ZALOǦLU, 1964: 236, figs 7, 8, 11, 12).

b) The *tectum supraorbitale* is developed approximately to the same extent as that in *Pelobates varaldii.*

c) The squamoso-frontoparietal contact is also developed, but to a lesser extent than in *Pelobates varaldii.* However, according to BASOǦLU and ZALOǦLU (1964: 236, figs 13—16) its length considerably varies, which condition is explained

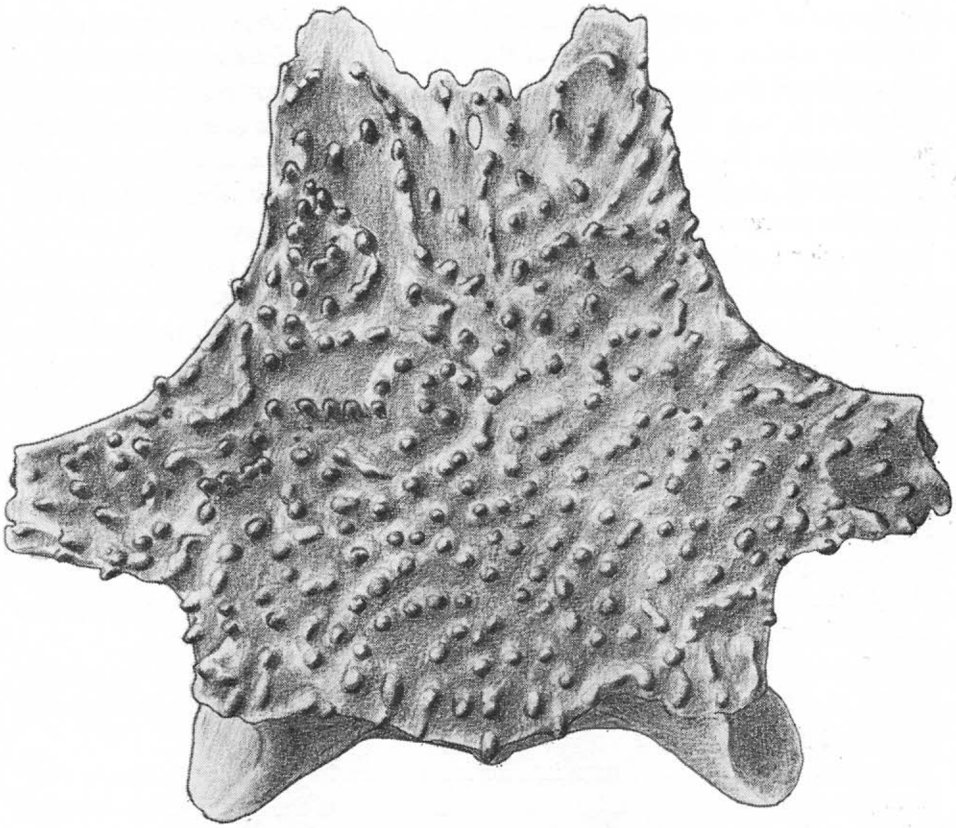


Fig. 54. Frontoparietal of *Pelobates syriacus syriacus* (DP FNSP 2111).

by the dependence on age (the older the individual is, the longer suture occurs).

d) The *processus posterior superior* is represented only by a small point which is located in the middle of the convex posterior margin of the *facies dorsalis* (in younger individuals there is a distinct transversal mound in this place) (see fig. 44).

e) A similar outgrowth is developed also on the margin of the *facies ventralis*.

f) The *processus paraoccipitales* are not pointed, but widely rounded.

The maxilla

a) The posterior margin between the *processus zygomatico-maxillaris* and the *processus posterior* is deeply concave.

b) It is comparatively higher than that in *Pelobates fuscus*.

c) The *processus palatinus* reaches further medially than that in *Pelobates fuscus*.

The squamosal

a) This is in contact with the frontoparietal by a short suture.

b) Only a short section of the dorsal margin of the *lamella alaris* takes part in the formation of this suture.

c) Between the most posterior point of this suture and the *processus posterodorsalis*, the margin of the *lamella alaris* is deeply concave; the lower-most point of this concavity reaches up to the level of the dorsal surface of the *ramus paroticus*.

d) The margin of the *lamella alaris* runs from the *processus posterodorsalis* ventrally to another process where it breaks to continue towards the base of the *processus posterolateralis*. In *Pelobates fuscus* this additional process is lacking.

e) The posterior section of the ventral margin of the *lamella alaris* and the long axis of the *processus posterolateralis* form a sharp angle.

f) The anterior section of the ventral margin of *lamella alaris* passes by means of a ridge onto the outer surface of the *processus posterolateralis*.

g) The anterior section of the ventral margin of the *lamella alaris* meets the base of the *processus posterolateralis* at a more ventral level than the posterior section.

h) The *processus posterolateralis* represents approximately half of the greatest diameter of the *lamella alaris*.

The vomer

a) The *processus choanalis posterior* is widely rounded.

The parasphenoid (fig. 38 b)

a) The *processus posterior* is developed in adults, whereas it is lacking in young individuals and in tadpoles.

b) In metamorphosing tadpoles a rounded ridge occurs lengthwise along the anterior section of the ventral surface of the *pars medialis*. It is lacking in adults.

The pterygoid

a) The vertical margin of the *ramus interior* is even, not folded as is the case in *Pelobates fuscus* where this condition is associated with the pterooccipital fissure being well developed.

The remaining cranial elements do not display any other diagnostic differences.

4.3.9 *Pelobates syriacus balcanicus* KARAMAN, 1928

(BASOĞLU and ZALOĞLU, 1964, figs 26, 27)

For synonymy see GORHAM (1966: 25)

Geological age: ? Pliocene - Recent

The following survey only treats those characters which differentiate this subspecies both from *Pelobates syriacus syriacus* and *Pelobates fuscus*.

The sphenethmoid

a) The depression on the ventral surface of the *solum nasi* which is caused by the dorsal convexity of the margin of the *fenestra endochoanalis* into the nasal cavity is more pronounced.

The prooticooccipital

a) The dorsal overhang of the *fossa fenestrae ovalis* and its continuation onto the posterior surface of *prominentia ducti semicircularis posterioris* is not sharp as is the case in *Pelobates syriacus syriacus* but rounded. However, despite this it is very distinct.

The praemaxilla

a) The number of tooth positions is 15.
b) The outgrowth borne by the medial margin of the *pars facialis* is directed posteriorly so that it is almost invisible in the anterior aspect.
c) The *pars dentalis* is considerably high if compared with that in nominate form, and narrow in its lateral part. In this character the condition is very similar to that in *Pelobates fuscus*.

The nasal

a) The *processus anterior* and *processus parachoanalis* are more rounded in comparison with those in the nominate form.

The frontoparietal (see also ESTES, 1970, fig. 27)

a) The central part of the *facies dorsalis* in its interorbital section is slightly depressed. The *tecta supraorbitalia* are directed dorsolaterally.

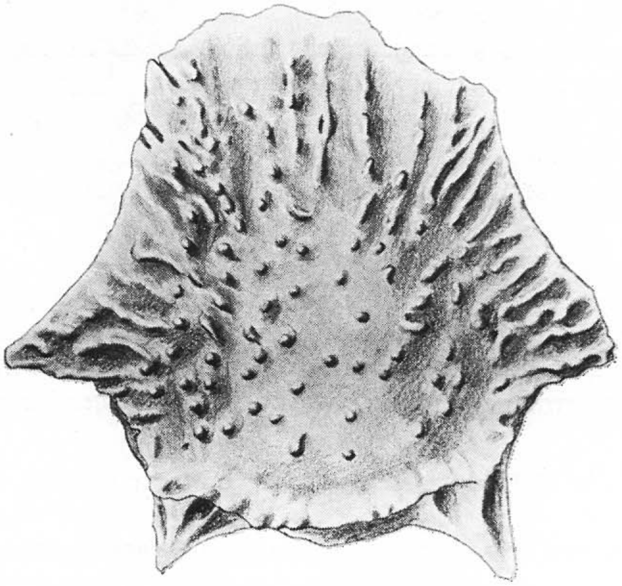


Fig. 55. Frontoparietal of *Pelobates cf. syriacus balcanicus* (AF 10/64 PAN Krakow); Pliocene, Rebielice Krolewskie, Poland.

b) The *processus posterior superior* is represented by the indistinct convexity of the posterior margin of the *facies dorsalis*.
c) The squamoso-frontoparietal contact is in a shorter suture than is the case in the nominate form. Posteriorwards the suture opens as the margins of the respective bones diverge. However, this contact need not be constantly present. There even exist such individuals which possess this suture asymmetrically (BASOĞLU and ZALOĞLU 1964, fig. 26).

The frontoparietal from the Pliocene of the locality Rebielice Krolewskie in Poland (fig. 55), which is assigned by MLYNARSKI (1977: 16, 25) to *Pelobates syriacus balcanicus* has its left *processus lateralis superior* formed in such a way that it is beyond any doubt that it took part in a squamoso-frontoparietal suture (the right processus is reduced, not broken away, judging by the nature of the sculpture). This would really suggest a relationship to *Pelobates syriacus balcanicus*. On the other hand, the distinctly convex central part of the *facies dorsalis*, which is separated from the elevated margins of the latter by a lengthened depression running parallel with these margins, suggests some relationship to *Pelobates fuscus*. Consequently it is possible to consider this frontoparietal as belonging to a form which might be transitional by its anatomy between *Pelobates syriacus balcanicus* and *Pelobates fuscus*.

The maxilla

a) That part of the margin between the *lamina anterior* and the anterior end of the *crista dentalis* is deeply concave.

b) The *processus frontalis* is comparatively distinct due to the large extent of its unsculptured part which takes part in the formation of the groove for the *ductus nasolacrimalis*.

The vomer

a) The flattened part of the bone located medially from the *torus dentigerus* is poorly developed.

The parasphenoid

a) In contrast to the nominate form, the *processus posterior* is only poorly developed.

b) The *pars medialis* reaches far beyond the level of the postnasal walls.

In other characters which have been listed in connection with *Pelobates syriacus syriacus, Pelobates syriacus balcanicus* is identical with *Pelobates fuscus*.

4.3.10 *Pelobates syriacus boettgeri* Mertens, 1923

(MERTENS, 1923, fig. 2; BASOĞLU and ZALOĞLU, 1964, figs 22—25)

For synonymy see MERTENS (1923: 122), GORHAM (1966: 25); cf. BASOĞLU and ZALOĞLU (1964: 237).

Geological age: Recent

Only those characters are given in which this subspecies differs from the nominate form as it does from *Pelobates fuscus* (see also MERTENS, 1923: 122).

The sphenethmoid

a) On the ventral surface there is a rather depressed field in which the anterior end of *pars medialis parasphenoidei* fits.

b) That part of the *solum nasi* adjacent to the postnasal wall gradually becomes wider laterally, which is why it also borders the *fenestra endochoanalis* posterolaterally.

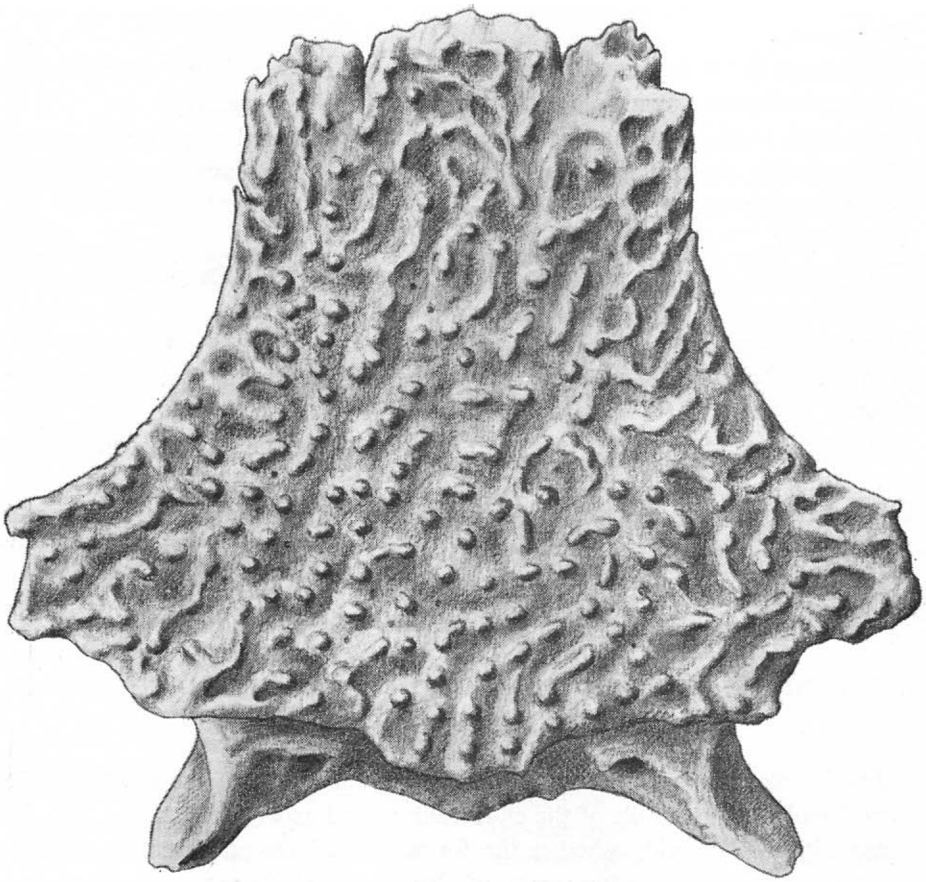


Fig. 56. Frontoparieta of *Pelobates syriacus boettgeri* (DP FNSP 3677).

The prooticooccipital

a) The *crista frontoparietalis* is well developed, but not to such an extent as the *crista frontoparietal isposterior*. The latter is of the same course as is in the nominate form.
b) From the *crista frontoparietalis posterior,* a similarly well developed ridge runs towards the lateral margin of the *foramen magnum.* This condition resembles that in *Pelobates cultripes.*
c) Due to the presence of a well developed pterooccipital fissure the margin of the prooticooccipital has a deep but narrow incisure.

The praemaxilla

a) The tooth positions count is 19.
b) The tooth row reaches up to the median symphysis.
c) In contrast to the nominate form, *pars dentalis* is similarly formed as that in *Pelobates fuscus*.

The nasal

a) In contrast to the nominate form, the *processus anterior* is not pointed, but is represented instead by a wide and comparatively long outgrowth.
b) In contrast to the nominate form, there is a well developed *processus parachoanalis*; due to this, the course of the margin of the *fenestra exonarina* is similar to that in *Pelobates fuscus*.

The vomer

a) The *processus choanalis anterior* is slender and pointed, the *processus anterior* is rounded.

The pterygoid

a) The ossified part of the *pars quadrata palatoquadrati* tends to fuse with the pterygoid.

In other cranial elements, this subspecies does not differ from those in the nominate form.

It is necessary to emphasize that the variation ranges of diagnostically important osteological characters considerably overlap in all subspecies of *Pelobates syriacus* (see Basoğlu and Zaloğlu, 1964; Mertens, 1932). Due to this the question arises whether or not it is justified to consider these forms subspecies.

5. OUTLINES OF THE PHYLOGENY AND SYSTEMATICS OF THE FAMILY PELOBATIDAE

Judging the above-mentioned diagnostic differences from the point of view of the assumed evolutionary trends of the endocranium and exocranium (see p. 75, 113), we may objectively decide whether the forms studied are advanced or archaic in some characters. The following survey of characters and the tab. 1 gives only those characters whose state could be ascertained in most forms studied. But it must be realized that to a considerable extent the tab. 1 schematizes the general picture, as there exist a number of transitional stages which have been evaluated as advanced or archaic according to the extent to which they approach the extremes considered. This means that in the tab. 1 the transitional stages are evaluated in the same way as the extreme variants. However, this distortion does not affect some quantitative features (e. g. character 8, see below) whose evaluation is unambiguous. For the above-mentioned reasons, the tab. 1 can serve only as a starting point for further considerations. The number of items in this table is not important, as it depends on the state of preservation of the fossil material.

State of characters

	archaic	advanced
1.	Sphenethmoid large; also the interior of *processus praenasalis medius* is ossified.	The interior of *processus praenasalis medius* inclusive of the parts adjoining the *tectum* and the *solum nasi* is not ossified.
2.	*Lamina supraorbitalis* large.	*Lamina supraorbitalis* reduced.
3.	Prooticooccipital forming one compact unit in adult.	Signs of division into *prooticum* and lateral occipital.
4.	Braincase rather high and narrow.	Braincase rather low and wide.
5.	*Fenestra frontoparietalis* is small in its extent, not extending to the level of postnasal walls.	*Fenestra frontoparietalis* extending anteriorly to the level of postnasal walls.
6.	Quadratojugal and quadrate separated from each other by a suture.	Quadratojugal and quadrate fused.
7.	*Processus posterior maxillae* short, quadratojugal relatively long.	*Processus posterior maxillae* long, substituting functionally a part of quadratojugal.
8.	Palatine is an independent element.	Palatine is ankylosed to maxilla.
9.	Frontoparietal embryonically developing from a larger number of elements than of paired frontal and paired parietal alone.	Frontoparietal is embryonically composed only of paired frontal and paired parietal.
10.	Vomers occupy a rather larger area of the palate.	The area occupied by vomers is reduced.
11.	*Lamella alaris squamosi* and some parts of frontoparietal cover otic capsules dorsally.	The mentioned parts of exocranium are reduced and hence they do no cover otic capsules dorsally.
12.	*Processus posterior parasphenoidei* is not developed.	*Processus posterior parasphenoidei* present.
13.	Teeth throughout the whole range of praemaxilla.	Teeth lacking at the medial section of praemaxilla.
14.	Praearticular arch-like.	Praearticular S-shaped.
15.	*Arteria occipitalis* passes through a narrow canal within frontoparietal.	*Arteria occipitalis* runs on the dorsal surface of frontoparietal.
16.	Sculpture present on the surface of exocranial bones.	Sculpture on the surface of exocranial bones absent.

In the tab. 1 the characters in which their states could not be recognized with certainty are denoted with a question-mark. The other characters given in the survey of diagnostic differences cannot be objectively interpreted as to their phylogenetic trends and - at the present state of knowledge - they can be regarded only as characters significant for diagnosis.

On the basis of tab. 1 it follows that:

a) All the forms studied, without exception, bear a more or less expressive sculpture on the surface of the nasals, frontoparietals, maxillae and squamosals. This character is usually considered to be important and typical of the family Pelobatidae so that

Tab. 1. *Survey of the investigated forms with assessment of the state of their characters*

	State of character																															
	archaic																advanced															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Eopelobates leptocolaptus		–			–	? –	? –	–		–			–	–		–				? –							–					
Hitherto undescribed form from the Cretaceous of Mongolia				–	–	? –	–							–	–	–									–		–	–				
Macropelobates osborni		–			–									–	–	–									–		–					
Eopelobates bayeri									–							–	–										–	–		–		
Pelobates fuscus fuscus	–		–	–					–			–			–	–		–			–	–	–	–		–	–		–	–		
Pelobates fuscus insubricus	–		–	–	–		–		–									–				–		–		–	–	? –		–		
Pelobates cultripes									–	–	–		–		–	–	–	–				–	–	–				–		–		
Pelobates varaldii				–	–				–	–	–		–		–	–	–	–	–			–	–	–				–		–		
Pelobates syriacus syriacus				–	–				–		–		–		–	–	–	–	–			–	–	–		–		–		–		
Pelobates syriacus balcanicus				–	–				–		–	–	–		–	–	–	–	–			–	–	–		–				–		
Pelobates syriacus boettgeri				–	–				–		–		–		–	–	–	–				–	–	–		–		–		–		

e. g. Noble (1924: 1) gave the very sculpture of the bones and the presence of teeth on the upper jaw as the only cranial characters in assigning *Macropelobates osborni* to Pelobatidae. Parker (1929: 280) considered the close relations between the genus *Eopelobates* and Pelobatidae on the basis of the sculpture on the exocranial bones. Also Špinar (1972: 192) mentioned this character among the diagnostic features of the family Pelobatidae; he gave the presence of a sculptured frontoparietal as a diagnostic character of the subfamily Pelobatinae (op. cit.: 195); similarly Estes (1970: 295) regarded this character*) as the only typical character of the subfamily Pelobatinae. But he also pointed out that the sculptured surface of the exocranial elements of the skull roof also occurs in some representatives of the families Hylidae, Leptodactylidae, Ranidae, Bufonidae, Rhacophoridae and Discoglossidae although he remarked that in most these forms sculpture could developed secondarily. Hence, the scultpure on the exocranial roof is not by itself a proof for assigning a specimen to pelobatids, and neither is it a proof that the forms studied belong to one sole group.

b) In all forms in which it was possible to study the posterior wall of the frontoparietal, the *arteria occipitalis* passes in a canal through this bone. In connection with what was said above (p. 111) on the evolutionary trend of this character it may be stated that the level of the course of this vessel may be considered as an indicator which points to the ancient nature of all these forms, but which gives no information on their mutual phylogenetic relations.

c) It seems that the mode of the embryonic development of the frontoparietal complex is a very important feature. In all recent representatives of the genus *Pelobates* this element consists not only of paired ossifications (i. e. of frontals and parietals) but also of an additional unpaired one which covers the *tectum synoticum*. The incorporation of this unpaired ossification is responsible for the fact that on a definitive frontoparietal (i. e. of adult) the median suture can never reach the posterior margin of this bone complex. The embryonic development of the frontoparietal of *Eopelobates bayeri* is of the same type, which fact may be stated not only according to adult specimen but also well-preserved tadpoles (fig. 50). In contrast, in the hitherto undescribed form from the Cretaceous of Mongolia the median suture reaches the posterior margin of the frontoparietal. In *Macropelobates osborni* no sign of median suture is discernible on the *facies dorsalis* except for the median notch on the posterior margin of the bone, which however is asymmetrical (see p. 122, fig. 48; Noble 1924, fig. 1 A). In a thorough examination of the *facies posterior*, it may be readily ascertained that this notch continues up to the posterior margin of the *facies ventralis*, and that in this view it appears beyond doubt as symmetrical. On the basis of this fact it may be maintained that the frontoparietal of this

---

*) His formulation (loc. cit.) that »dermal ossification well developed and fused to skull roof« gives the impression that the sculpture on the bone surface originated independently and only secondarily fused to the respective bones. However, the sculpture develops as folds of the ossifying primordium, and during the whole ontogeny is an integral part of the bone.

form was embryonically developed without the presence of the posterior unpaired element.

The presence of the posterior unpaired element within the frontoparietal cannot be regarded as a result of specialization which took place in a restricted number of forms, among others also in the genera *Pelobates* and *Eopelobates*. If we accepted this opinion then the above-mentioned unpaired element should be regarded as an evolutionarily new structure, because as early as in *Triadobatrachus* - which is nowadays considered a stage immediately preceding frogs - a median suture is clearly visible within the whole range of the frontoparietal. But if we suppose that ossification centres indicate originally independent exocranial elements, then we may infer that the evolution of frogs which possess an unpaired posterior element within their frontoparietals could not pass through a stage where this element is already lacking. Due to this, it is necessary to exclude not only the Mongolian forms studied from the circle of possible ancestors of the genera *Pelobates* and *Eopelobates* (which is supported also by palaeogeography, as Europe and Central Asia were separated from one another till the Lower Tertiary), but - within a broader context - also *Triadobatrachus*. This means that the forms whose frontoparietal arises through the incorporation of a posterior unpaired element had to arise quite independently from the main evolutionary line of frogs which supposedly passed through the *Triadobatrachus* stage.

When investigating from this point of view all the forms given under the generic name *Eopelobates*, we find that not only have the forms possessing the frontoparietal without a median suture on its posterior margin been assigned to this genus, but also those whose median suture is clearly visible within the whole range of the frontoparietal.

The genus *Eopelobates* has been established by PARKER (1929: 277) who in the diagnosis gave the following cranial characters: presence of teeth on the maxilla, sculpture on the frontoparietal, squamosal and maxilla, and an extensive contact between the squamosal and maxilla, which is located posterior to the orbit. It is clear that these features do not represent any difference in relation to the genus *Pelobates*. In the diagnosis revised by ESTES (1970: 296, 298) the following cranial characters are given: presence of sculpture, flat or convex cranial roof, and the presence of maxillar teeth. In ŠPINAR'S (1972: 196—197) diagnosis of this genus, sculpture and maxillar teeth are also given, but in contrast to PARKER and ESTES the absence of the squamosal-frontoparietal contact is added as well as three processes on the *ramus medialis* of sphenethmoid (i. e. in the terminology used in the present paper the ossified interior of the *processus praenasalis medius* and the anterolaterally projecting ossified parts of the *solum nasi*), and the long lateral processes of the parasphenoid. In addition, ŠPINAR mentioned that in tadpoles the frontoparietal is composed of two separated halves, but that in adults this is not the case (op. cit.: 196). The latter assertion is incomplete, as in those tadpoles where paraspheonid is dislocated, the posterior unpaired element is well discernible (ŠPINAR, 1972, tab.

171/2). In describing the skull of *Eopelobates,* PARKER (1929: 278—279) wrote that the frontoparietal there is clearly one sole element. ESTES (1970: 304) has found a groove between the two halves of the frontoparietal, but he was not sure whether this concerns a median suture; in addition he did not mention whether this suture is situated in the orbitotemporal or also the otic parts of the frontoparietal (op. cit.: 306): »There is a well defined groove between the frontoparietals, but a distinct suture cannot be seen«. But in spite of this doubt he drew the median suture in the figure showing the reconstructed skull (op. cit., fig. 8). According to the published pictures (PARKER, 1929, fig. 4; ESTES, 1970, figs 1, 8) the convexity of the posterior margin of *facies dorsalis* between both *processus paraoccipitales* is very conspicuous (more than in *E. bayeri*), which strikingly suggests the case in some representatives of the genus *Pelobates*. For this reason it might be assumed that in *Eopelobates anthracinus* the frontoparietal developed in the same way as that of *Eopelobates bayeri.*

As to the forms given under the designation *Eopelobates hinschei* (ESTES, 1970, fig. 10, where in tab. 1 synonymy is also given) still less information in this respect is available than is the case in *Eopelobates anthracinus.* KUHN'S data (KUHN being the first to describe these Geiseltal frogs) are not fully reliable. In defining the relationships of this form to *Eopelobates bayeri,* ESTES (1970: 306) indirectly indicated that its frontoparietal is paired »...both have rather elongate frontoparietals, though that of *Eopelobates bayeri* is fused«. The uncertainty concerning the systematic position of the forms which are termed *Eopelobates hinschei* is lasting and therefore this form is not considered below.

In contrast to *Eopelobates bayeri,* and most probably also to *Eopelobates anthracinus,* all American forms assigned to the genus *Eopelobates* have their frontoparietal distinctly divided longitudinally by the median suture. The frontoparietal of *Eopelobates grandis* (ZWEIFEL, 1956, figs 1, 2; ESTES, 1970, fig. 13 A) is sufficiently preserved (to an extent important from this point of view). ZWEIFEL'S (1956: 5; cf. ESTES 1970: 308) description of the skull is not quite accurate, and does not contain any note on the paired nature of the frontoparietal. However, ESTES (1970, fig. 13 A) in the reconstruction of this form indicated apparently without hesitation the median suture by the full line. *Eopelobates guthriei* (ESTES, 1970: 311, figs 13 B, 14) also has a frontoparietal distincly divided.

In the Asian form designated as *Eopelobates leptocolaptus* a frontoparietal is lacking, but many characters point to a close relationship to the form hitherto undescribed and collected on the same locality, whose frontoparietal is distinctly divided and is of the discoglossid type.

From the above statements the following conclusions may be drawn: (1) Representatives of the genus *Eopelobates* whose frontoparietals include also the posterior unpaired element occurred only in Europe, whereas forms which although also given under the name *Eopelobates* have a frontoparietal which does not include the mentioned element, and have also been found elsewhere (North America and Asia). (2) From what has been said in connection with the independent development of the »pelobatid type« of frontoparietal it is evident that the European representatives of the genera *Eopelobates* and *Pelobates* can have close relations neither to the forms described as American or Asian eopelobatids nor those belonging to the genus *Scaphiopus*.

If we turn once again to the published information on American eopelobatids we see that both differ from the European representatives in their comparatively short skull (ESTES 1970: 309) manifested by a short frontoparietal (ESTES op. cit.: 308). In redescribing *Eopelobates grandis* ESTES (op cit.: 308) gave some characters (the mode of connection between quadratojugal and maxilla, ethmoid) in which it resembles the representatives of the genus *Megophrys*, but he does not regard this fact as important and considers these differences to belong rather within the variation range of the genus *Eopelobates*. The original description by ZWEIFEL (1956: 5, figs 1, 2) contains some mistakes concerning particularly the relationship between the frontoparietal and the squamosal, and a misleading interpretation of the element located close to the *processus posterior maxillae*. Originally, ZWEIFEL interpreted this element as a *stapes* (this fact itself would have excluded the above-mentioned form from a relationship with *Pelobates)*, while ESTES (1970: 308) regarded it as a quadratojugal. The corectness of these interpretations could be definitely judged only on the basis of a study of the original material; however, even from the photograph (ZWEIFEL, 1956, fig. 1) it may be inferred that an element is involved which is very robust in relation to the *processus posterior maxillae* as well as to the *processus posterolateralis squamosi*, and that it may possibly represent a displaced fragment of a quite different origin. The dislocation of the right posterolateral part of the skull may suggest this. But this is only a speculative consideration provoked by the above-mentioned photograph.

In *Eopelobates guthriei*, the *columella* is well preserved (ESTES, 1970: 311, fig. 14 d) in contrast to the genus *Pelobates* where it is lacking, as well as to *Eopelobates bayeri* and *Eopelobates anthracinus* where it has not been found. *Eopelobates guthriei* does not possess a quadratojugal although the quadrate is preserved in its original position (ESTES, op. cit.: 311, 312). If the consideration by ESTES were correct (i. e. that the quadratojugal was broken away during the dislocation of the temporal area), then it could be correct only in the case that the quadratojugal and quadrate were not fused (in the opposite case where both these elements would be fused with each other, the quadrate would certainly be lacking too). Hence the interpretation that in *Eopelobates guthriei* the quadratojugal was originally lacking seems to be more natural. With regard to this, the absence of the quadratojugal and the presence of the *columella* may be regarded - besides the frontoparietal - as further characters which exclude this form from the circle of close relatives of the genera *Pelobates* and *Eopelobates*, and which rather indicate its relationship to the genus *Scaphiopus*. A similar case may be assumed in *Eopelobates grandis*.

Eopelobates anthracinus, *Eopelobates bayeri* and all representatives of the genus *Pelobates* therefore form a homogeneous group markedly differing especially by the origin of their frontoparietal from American eopelobatids and scaphiopodids.

Eopelobates anthracinus is known from the Lower Miocene (PARKER, 1929: 271) of the Federal Republic of Germany (Rott near Bonn) and the Oligomiocene of Czechoslovakia (Bechlejovice near Děčín, the Nástup mine near Kadaň and the Hrabák mine near Most; see ŠPINAR, 1972: 219). *Eopelobates bayeri* has been found in the Oligomiocene of Czechoslovakia (Bechlejovice near Děčín, the mines Hrabák, Merkur and Nástup near Kadaň, Děvínská Nová Ves near Bratislava; see ŠPINAR 1972: 216). The note on the Pliocene age of the eopelobatids of Czechoslovakia in the paper by SANCHÍZ and MLYNARSKI (1979: 164) is erroneous. Skeletal fragments of Pliocene age found in the Polish locality Waze near Częstochowa (MLYNARSKI, 1961: 261*); 1977: 25; SANCHÍZ and MLYNARSKI, 1979: 162—164), not determined as to species, have been referred also to the genus *Eopelobates.*

However, together with eopelobatids, also forms surviving up to the recent time occurred in Europe in the Tertiary. These are especially *Pelobates fuscus***) known from the Pliocene of Poland (Waze near Częstochowa; MLYNARSKI, 1961: 264—266; 1962: 182; Rebielice Krolewskie near Częstochowa; MLYNARSKI, 1962: 182; 1977: 15—16, tab. IV/1; Zalesaki near the first above-mentioned locality; MLYNARSKI, 1977: 19; Kozi Grebiet in the Swiętokrzyskie Gory Mts; MLYNARSKI, 1977: 21; see also fig. 51 in the present paper). A further form has been described from the Pliocene of Poland, which is regarded as related to *Pelobates syriacus balcanicus* (Rebielice Krolewskie; MLYNARSKI, 1977: 16, 25, pl. IV/2; see also fig. 55 and the note on p. 138 in the present paper). In addition, *Pelobates robustus* has been described from Romania, probably also of Pliocene age (BOLKAY, 1913: 219); this species was later reassigned to the genus *Miopelobates* (ESTES, 1970: 328). However, ŠPINAR (1979) considers now this genus to be synonym of *Latonia* referred to discoglossids***).

From the above statements it follows that the genera *Eopelobates* and *Pelobates* coexisted in the Tertiary. This fact together with some specializations in the anatomy of eopalobatids excludes the possibility that they could have been the ancestors of the representatives of the genus *Pelobates.* However, it is very probable that both genera had a common ancestor. ŠPINAR (1972: 226—227) sees an ancestor of eopelobatids in some representatives of the evolutionary line leading to recent pipids; this is probable, as pipids also possess an unpaired frontoparietal (TRUEB, 1973: 71; SOKOL, 1977; RAMASWAMI, 1956).

---

*) ESTES (1970: 309) expressed some doubts as to the corectness of this assignment, but SANCHÍZ and MLYNARSKI (1979) maintain the original view of MLYNARSKI.

**) The form considered by ŠPINAR (1976, pl. II/1) »*Pelobates fuscus fossilis*« of the Miocene of Valeč (West Bohemia) probably does not belong to the fossil material found in this locality; perhaps it is of Subrecent age.

***) According to Dr J. C. RAGE (oral communication) there are undoubtedly some pelobatids also in the material from the Eocene and Oligocene of Quercy, France. This material was not yet published.

Pelobates decheni TROSCHEL, 1861 has been recently rediscovered by Dr W. BŐHME in the palaeontological collections of the Fridrich Wilhelm University in Bonn. According to present autor it is a very archaic pelobatid (the extensive squamoso-frontoparietal contact, the robust and sculptured quadratojugal). The specimen is an object of the further study.

As to the mutual relationships within the genus *Pelobates*, only recent forms may serve as a basis for this study. But the fossil forms give valuable information of a zoogeographical character. In all the *Pelobates* species except *Pelobates fuscus* the exocranial cover of the otic capsules is more or less developed. As it has been pointed out above, a more expanded exocranial cover indicates a more archaic state. From this point of view *Pelobates cultripes* would be the most archaic because its otic capsules were bridged broadly and completely by the squamosal and frontoparietal. Boas (1914: 255, 256)*) has expressed the same opinion. Estes (1970: 298) believed that the exocranial cover of otic capsules is a secondary state, as in *Eopelobates* and *Macropelobates* this cover is lacking. In the light of the above-mentioned views on the origin of the genera *Eopelobates* and *Pelobates* (as well as the quite

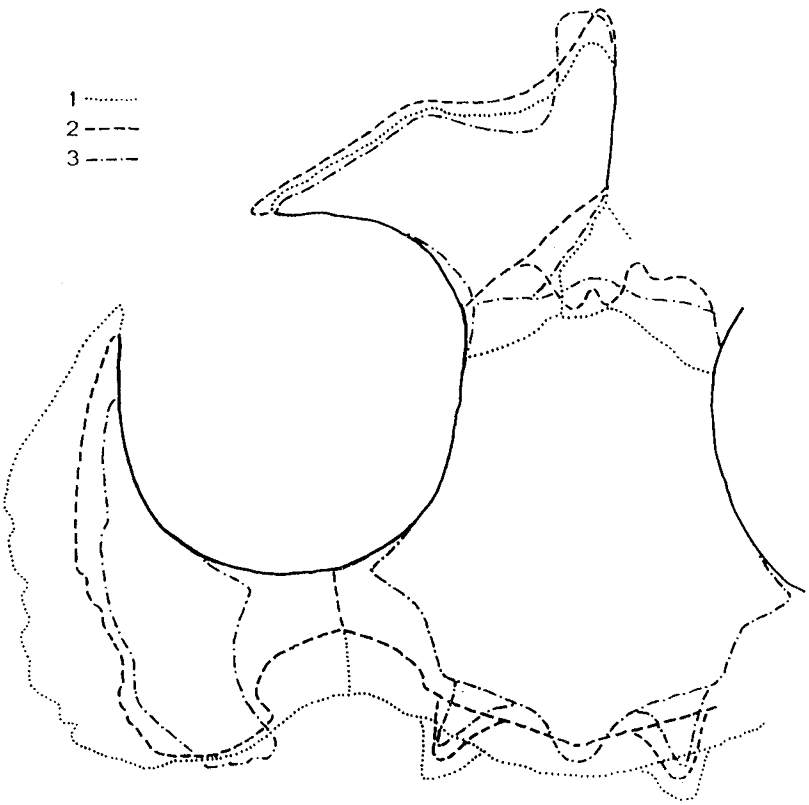


Fig. 57. Sketch to show proportionality and shape differences of the left nasal, frontoparietal and left *lamella alaris squamosi*. 1 - *Pelobates cultripes*; 2 - *Pelobates syriacus syriacus*; 3 - *Pelobates fuscus fuscus*. All bones are drawn in perpendicular view.

---

*) Gislén (1936: 121) also agreed with the assumption that *Pelobates cultripes* represents an archaic form, but Mertens (1925: 125—126) is of an opposite opinion, maintaining that this species is the most progressive form.

separate position of the genus *Macropelobates*) there is no hindrance to regarding the condition of *Pelobates cultripes* as a really archaic one. This opinion is also supported by the occurrence (although not general) of teeth on the parasphenoid of this species (BOULENGER, 1890: 664—665; 1897: 205) which fact may also be taken for an archaic character (cf. ESTES, 1970: 326). From this original state forms evolved in which the exocranial cover of the otic capsules was partly reduced, i. e. *Pelobates varaldii* and *Pelobates syriacus*. Reduction of the exocranial cover is most advanced in *Pelobates fuscus* where the squamosal and frontoparietal already stand apart, and the posterior osseous margin of the orbit is replaced by the ligament. A transitional state of this reduction is represented by *Pelobates syriacus balcanicus* in which the squamoso-frontoparietal suture may not occur in all speciemens (GISLÉN, 1936: 121; BASOĞLU and ZALOĞLU, 1964, fig. 26). In the Pliocene, this form extended much farther to the north, and lived together with *Pelobates fuscus* in the area of Central Europe. Its recent distribution is restricted to the area of the Balkan peninsula south of the Carpathians*).

There is a problem which can hardly be solved only on the basis of anatomy: whether this gradual reduction of the exocranial cover really took place in the above indicated succession from *Pelobates cultripes* to *Pelobates fuscus* (as GISLÉN believed; 1936: 125, 126) or whether on the one hand *Pelobates varaldii* and *Pelobates syriacus* developed from *Pelobates cultripes* (with the reduction attaining its maximum in the state of *Pelobates syriacus balcanicus*) and, on the other hand, *Pelobates fuscus*. The mechanism of these changes, i. e. the temporal muscles becoming more robust, could have acted parallel in several evolutionary lines. But the fact is evident that the ancestor of all the representatives of the genus *Pelobates* must have been a form in which a higher or at least equal degree of development of the exocranial cover of the otic capsules as that in *Pelobates cultripes* could be assumed. If this ancestor belonged to the circle of forms which were also ancestral to the genus *Eopelobates*, the above-mentioned reduction could have taken place independently and at different rates in various evolutionary lines (rapidly during the origin of the genus *Eopelobates*, and slowly during the origin of the genus *Pelobates*).

Let us return now to the basic character according to which frogs may be divided into two well distinguishable groups. But first it is necessary to emphasize that this character must be defined as the mode of embryonic development of the frontoparietal, which leaves a trace on the frontoparietal of adults, manifested by the presence or absence of the median suture in its posterior part. It should not be defined in such a way that the frontoparietal is unpaired, because an unpaired frontoparietal may also develop through the fusion of originally paired ossifications. The mode of embryonic development of the frontoparietal in the genera *Pelobates*,

---

*) Pasteur's opinion (1958) that the form now regarded as *Pelobates syriacus boettgeri* should represent an independent genus *Pseudopelobates* is based on an underestimation of intraspecific variability (cf. KLUGE, 1966: 7).

Eopelobates and further forms (Palaeobatrachidae?, Pipidae?, Rhinophrynidae?) cannot be derived from the forms which lack the unpaired median element within the frontoparietal. Neither is acceptable the opposite assumption that frogs having a paired frontoparietal could have originated from frog-ancestors with »pelobatid« type of the frontoparietal. The fact that *Triadobatrachus* does not yet represent a quite definitive frog and that it already possesses a frontoparietal throughout divided by a median suture only suggests that the separation of both lineages must have taken place as early as at an evolutionary level still lower than that of frogs. As both these groups of frogs represent independent evolutionary lines, it is necessary to express this fact also from the point of view of systematics.

In the first place it should be stressed that *Triadobatrachus* might represent a very early evolutionary stage in one evolutionary line only. Both these fundamental evolutionary lines may be purposefully designated as Archaeosalientia and Neosalientia, which might be considered separate orders. In this case, *Triadobatrachus* represents an evolutionary stage on the line of Neosalientia. Its essential anatomical differences in relation to the other groups of this lineage can be expressed by assigning *Triadobatrachus* to the independent suborder Proanura. The proposed system which clearly reflects the phylogenetic relations is as follows:

Class: AMPHIBIA LINNAEUS, 1758
  Order: Archaeosalientia n. ordo
  Order: Neosalientia n. ordo
    Suborder: + Proanura ROMER, 1945
    Suborder: Anura GIEBEL, 1845

Archaeosalientia - The frontoparietal complex embryonically developing with the participation of an unpaired median element adjoining the *tectum synoticum*; on a definitive frontoparietal in the adult the median suture never reaches the posterior margin of this bone complex.

Neosalientia - The frontoparietal is either a paired or an unpaired bone. In either case, the median unpaired element adjoining the *tectum synoticum* is lacking in the whole course of ontogeny. Hence, if median suture is present on a definitive frontoparietal, it reaches up to the posterior margin of the bone.

According to this concept, all frogs which belong to the newly established order Archaeosalientia are excluded from the group Anura which is regarded here as a suborder.

It should be noted that another concept may also be proposed which can hypothetically explain the differences in the composition of the frog frontoparietal by iterative evolution, which is the subsequent splitting of the side branches with similar characteristics from one main stock. According to this concept, *Triadobatrachus* may be regarded as the representative of one of the most ancient side branches which lost the posterior unpaired median element and which died out without any descendants.

The ancient discoglossids could be considered as a similar case. However, their descendants could survive till the recent time. Pelobatids and other related groups which still possess the element in question could also survive till the Recent as the only representatives of the main evolutionary line. However, palaeogeographic conditions strongly disfavour this concept and hence it must be refused.

If we return now to the first concept, the question arises which groups may be included into Archaeosalientia. Besides *Pelobatidae*, probably also Palaeobatrachidae, Pipidae and Rhinophrynidae may be concerned. In the tadpoles of palaeobatrachids, the frontoparietal in the stages preserved is already fused and unpaired, but in some rather old specimens a very fine edge is perceptible which according to Špinar (1972: 51) might represent a median suture. However, this may also be interpreted such that in these cases an imprint of the margin of the *pars medialis parasphenoidei* caused this condition (Špinar, oral communication), and thus the frontoparietal might be of »pelobatid« type. In the tadpoles of *Pipa carvalhoi* which are at stage 58 the frontoparietal does not show any traces of median suture (Sokol, 1977: 360; see also Trueb, 1973, fig. 2-2b). In contrast, in the tadpoles of *Xenopus tropicalis* a paired nature of the frontoparietal may be observed (Sokol, 1977, fig. 20), although it is not clear whether a median element above the posterior part of the *fenestra frontoparietalis* may or may not additionaly form. Thus it is necessary to exclude from the family Pelobatidae the genera *Macropelobates* and *Scaphiopus* as well as the Asian and American forms hitherto described under the generic name *Eopelobates*. The relationships of the last named forms should be reconsidered, although it is already clear now that they display characters which would permit them to be regarded as related to the genus *Scaphiopus* or *Megophrys*. Noble's (1924: 10) idea that *Macropelobates* could represent an ancestor of Europen pelobatids is not realistic, particularly because *Macropelobates* lived at the time when undoubtedly pelobatids already occurred in Europe. Asia cannot be considered to be the centre of origin of pelobatids also for the reason that within the pre-Oligocene time Europe was separated from this assumed centre of their origin by a vast zone of sea (see also Gislén, 1936: 121).

The independent position of the genus *Scaphiopus* and related forms must be stressed more markedly by re-attributing to them the rank of the family Scaphiopodidae which was established by Cope (1865). The following survey of the differences is given here in order to illustrate that the different nature of the families Pelobatidae and Scaphiopodidae is not manifested only by the different embryonic development of the frontoparietal.

Scaphiopodidae differ from the family Pelobatidae in the following characters (see also Zweifel, 1956, pl. 1).

The sphenethmoid

a) In the area of the *laminae supraorbitales* there are massive processes directed dorsolaterally, separated by a deep notch from the dorsolateral margins of the braincase in the orbitotemporal region.

b) The level of the ossified part of the postnasal walls exceeds laterally only slightly the level of the *laminae supraorbitales*; this means that the postnasal walls are ossified to a lesser extent than those in pelobatids.

c) The ossified part of the *solum* which borders posteromedially the *fenestra endochoanalis* projects into the nasal cavity, forming a sharply prominent elevation (»the skeletal support of the *eminentia olfactoria*« according to Jurgens 1971, figs 7 A, 8, 9 B, C; »solar ossification of the *eminentia*« according to RAMASWAMI, 1956, fig. 4) which the vomer adjoins laterally. In pelobatids the margin of the *fenestra endochoanalis* is only slightly thickened, and the attachment of vomer is quite different.

d) The ossified part of the *tectum nasi* passes into the ossified interior of the *processus praenasalis medius* through a conspicuous break which is responsible for the fact that the *pars facialis praemaxillae* is at right angle to the nasal (see ZWEIFEL, 1956, fig. 22, 23).

e) In all the species of the subgenus *Spea*, the sphenethmoid is fairly exposed, as the nasals and the frontoparietals are considerably reduced (see ZWEIFEL, 1956, fig. 23).

f) The sphenethmoid is fairly flattened (see RAMASWAMI, 1956, figs 7, 7 A, 8).

g) The *fenestra endochoanalis* is completely closed laterally (in the area where in pelobatids only the *spina parachoanalis anterior* and *posterior* are situated - see JURGENS 1971, figs 7, 8).

The prooticooccipital

a) On the dorsal side of the otic capsule the lateral occipital is separated from the *prooticum* by a stripe of cartilage which extends from the *tectum synoticum* to the *prominentia ducti semicircularis posterioris*. This cartilaginous stripe is continued by a much narrower stripe of cartilage forming the roof of the *canalis semicircularis anterior*.

b) The *canalis semicircularis anterior* is manifested on the anterodorsal part of the surface of the otic capsule as a prominent ridge.

c) The *crista frontoparietalis* is lacking.

d) The ventral margin of the *fenestra ovalis* has a deep notch which nearly reaches medially the cartilaginous part of the floor of the braincase in the otic region. This is always larger than that in pelobatids.

e) The *crista parotica* does not form an overhanging cover above the *fossa fenestrae ovalis*; in a dorsal view, the otic capsulae are slender.

f) The *condyli occipitales* are very prominent, so that in a ventral view a deep notch (*fossa condyloidea*) is visible in the place of the *foramen jugulare*; due to this, this opening is directed ventrolaterally and not laterally.

The praemaxilla

a) The *pars facialis* projects dorsally, not posterodorsally, from the *pars dentalis*.

b) The *lamina horizontalis* (which in most species is identical to the posterior margin of the *pars dentalis*) projects laterally into a sharp and comparatively long process, which in pelobatids is never developed.

c) In some genera the *pars palatina* is lacking throughout, but in pelobatids it is always present.

d) The base of the *pars facialis* is distinctly shifted nearer to the medial margin of the *pars dentalis*.

The nasal

a) In all the species of the subgenus *Spea* nasals are reduced, so that they do not adjoin one another in the median suture; in *Scaphiopus intermontanus* and *Scaphiopus hammondi* they do not even meet the frontoparietals (see Zweifel, 1956, figs 23 A, C).

b) In all the species of the subgenus *Spea* the dorsal surface is not sculptured.

The frontoparietal

a) In all the species of the subgenus *Spea* the frontoparietals are not sculptured, and between them a variously sized fontanelle may open (but this does not hold in general, neither within one species; the specimen's age doubtlessly plays a certain role here).

b) The posterior unpaired element does not participate in the structure of the frontoparietal, so that the median suture is always clearly visible (fig. 58).

The maxilla

a) In all the species of the subgenus *Spea,* the *processus zygomatico-maxillaris* and the *processus posterior* are reduced, so that the squamosal does not reach the maxilla at all (see Zweifel, 1956, fig. 23).

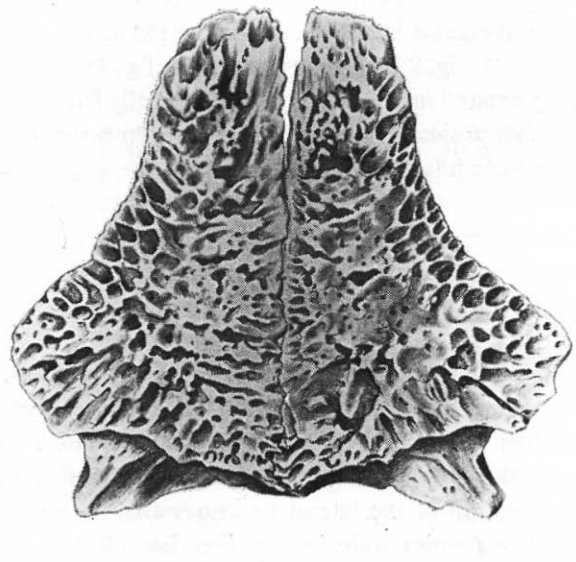


Fig. 58. Frontoparietal of *Scaphiopus couchi* (DP FNSP 1420).

b) In all the species of the subgenus *Scaphiopus,* the *processus posterior* is reduced.

c) The *processus palatinus* is not developed, as the palatine is fused with the vomer (fig. 59 c-g).

The quadratojugal

a) This is lacking throughout.

The squamosal

a) In all the species of the subgenus *Spea,* the *lamella alaris* is reduced so that it is represented only by a very small non-sculptured widening of the dorsal end of the *processus posterolateralis* (see ZWEIFEL, 1956, fig. 23); in the species of the subgenus *Scaphiopus* the *lamella alaris* is also reduced but not to such an extent.

b) The dorsal surface of the *ramus paroticus* projects into a massive ridge which begins on the *processus posterodorsalis* (if it is present) or at a corresponding place of the margin of the *lamella alaris.*

c) The *processus posterolateralis* is very long, so that in lateral view it reaches considerably below the level of the ventral margin of the maxilla (see ZWEIFEL, 1956, figs 22, 23),

The vomer (fig. 59 c-g)

a) The *processus anterior* and the *processus choanalis anterior* are not developed; in their place the vomer projects into a widened and flat lamella.

b) The palatine is ankylosed to the *processus choanalis posterior*; ZWEIFEL (1956: 28) interprets this erroneously as a reduction of the palatine and its replacement by the process of the vomer.

c) The *torus dentigerus* is shifted up to the level of the *fenestra exochoanalis* or up to the level of its posterior margin. In pelobatids it lies in front of the level of the anterior margin (fig. 59 a, b; see also ZWEIFEL, 1956, fig. 24).

d) The vomer is fairly high and laterally adjoins the thickened margin of the *solum nasi* (see JURGENS, 1971, fig. 9 B; RAMASWAMI, 1936, fig. 4).

e) The vomer tends to expand into the area posteromedially from the *torus dentigerus.* In some cases, its flat projection arisen in this way almost meets the point of the parasphenoid. In pelobatids, the vomers and parasphenoid are widely separated.

The palatine

a) It is ankylosed to the *processus choanalis posterior vomeri* (fig. 59 c-g).

b) It is situated obliquely in relation to the postnasal wal.

c) It is separated from the maxilla by a suture.

The parasphenoid

a) In *Scaphiopus holbrooki,* a rhomboid field exists on the ventral surface between both *processus laterales,* which is bounded by very marked (up to overhanging) concavely bent edges. Anteriorly, these edges do not unite into one sole ridge (the keel begins in the area between them but not adjoining them). The edges extending in the direction of the lateral processes also do not join one another, and unite forming one point only in the direction of the *processus posterior.* A similar field, although not so conspicous, exists in *Scaphiopus hammondi,*

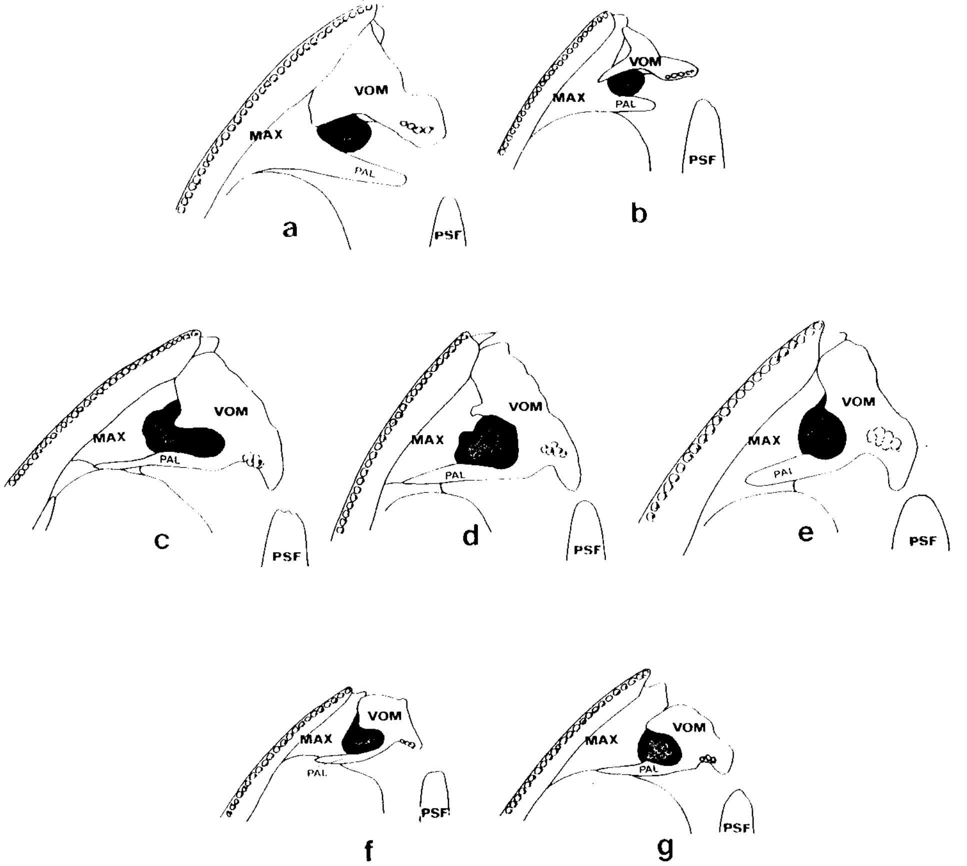


Fig. 59. Right praeorbital part of the palate in ventral view. a - *Pelobates cultripes* (DP FNSP 10002); b - *Pelobates fuscus* (DP FNSP 6339); c - *Scaphiopus couchi* (DP FNSP 6408); d - *Scaphiopus hurteri* (DP FNSP 6374); e - *Scaphiopus holbrooki* (DP FNSP 6472); f - *Scaphiopus bombifrons* (DP FNSP 6334); g - *Scaphiopus hammondi* (DP FNSP 6412). MAX - maxilla; PAL - palatine; PSF - parasphenoid; VOM - vomer.

S. couchi and *S. hurteri*. In *S. bombifrons* such a field is only poorly developed.

b) The *processus posterior* is very conspicuous in some cases, so that it reaches up to the ventral margin of the *foramen magnum*.

The pterygoid

a) In the species of the subgenus *Spea*, the *ramus interior* joins the *prooticum* by a very small part of its surface.

b) In these species no long suture is developed in the place of the contact with the *processus laterales parasphenoidei*.

c) Both these above-mentioned facts lead to the conclusion that in these species the pterygoid may be movable in relation to the *prooticum*.

d) In these forms, the central part of the pterygoid is very reduced. In pelobatids this element is generally more robust.

The columella

a) It is well developed.

The operculum

a) It is ossified.

There is no doubt that at least some of these characters represent differences so significant that the view that scaphiopodids should be considered an independent family is quite justified. The respective characters are especially the following: the *eminentia olfactoria,* prooticooccipitals almost completely divided into the *prooticum* and *occipitale laterale,* the absence of quadratojugal, the reduction of squamosal, the different morphologies of the maxilla and vomer, the fusion of the vomer with palatine, the *columella* not reduced, and the ossification of the *operculum.* The external morphological similarities of the forms assigned to the subgenus *Scaphiopus* with pelobatids may be explained such that they are ecological vicariants of pelobatids on the American continent. In other words, these similarities could have resulted from adaptation to the same mode of live. The idea of a quite independent evolution of both above-mentioned families shows clearly the forced character of some attempts to reconstruct the mutual phylogenetic relationships between scaphiopodids and pelobatids within one sole family, and explains the enormous variation range of the forms formerly assigned to Pelobatidae (e.g. KLUGE, 1966). This led to a quite erroneous interpretation of some phenomena, such as the »reduction of palatine« in *Scaphiopus* (ZWEIFEL, 1956: 38, fig. 24; KLUGE, 1966: 13, 14). If we compare scaphiopodids with the Cretaceous forms found in the Gobi desert, it becomes clear that there are many anatomical connections between them which suggests that it is possible to seek the ancestors of scaphiopodids (and probably also megophrynids) among these Asian forms.

6. SUMMARY

(1) From the point of view of the relative speed of structural changes on whose basis the endocranium arises in its final appearance in the adult it may be stated that it is the otic and occipital regions (except for the occipital condyls originating in the final stages of metamorphosis in connection with the movable cranio-vertebral junction) which are the first to achieve their final shape and, soon after, the orbitotemporal region. These parts of the neural endocranium are developed (except for some details of the arrangement of the surface) as early as in the tadpole before metamorphosis. However, the *fissura prootica* persists till the final stages of metamorphosis. The fundamental reconstruction of the ethmoidal region takes place simultaneously with the conversion of the visceral endocranium as late as during the metamorphosis proper. The metamorphosis of the endocranium reverberates still in adult specimens by achieving the final form of the hyoid.

(2) During the metamorphosis of a tadpole into an adult frog the anterior parts of the *cornua trabeculae* become resorbed as well as a substantial part of the *processus ascendens palatoquadrati, processus muscularis palatoquadrati,* ceratopraemandibular cartilage and the posthyoid branchial arches. But also further elements of the endocranium, e.g. the *cartilago labialis superior et inferior* and palatoquadrate undergo together with their remodellation also intensive regressive changes.

(3) During the metamorphosis of a tadpole into an adult frog, the following new structures arise which in a tadpole were not yet developed: the medial part of the *septum nasi* in its section behind the level of the *fenestra nasobasalis,* complete *septum nasi* in its section in front of the *fenestra nasobasalis,* the *processus praenasalis medius,* lateral margins of *solum nasi,* anterior part of *tectum nasi,* all the remaining parts of the *divisio praenasalis communis,* the *laminae superior et inferior cristae intermediae, paries nasi, cartilago obliqua, cartilago alaris, cartilago praenasalis superior, cartilago subethmoidalis, processus anterolateralis et posterolateralis hyodei.*

(4) On the basis of a study of the changes occurring on the endocranium of *Pelobates fuscus* during the final stages of larval development, it is possible to state homologies between the following endocranial structures of a tadpole and those of an adult frog: the *fissura prootica* of a tadpole corresponds to the *recessus prooticus* and *foramen prooticum* of an adult, and its previous course is indicated by the posterior margin of the prootic fontanelle; the posterior part of the *cornua trabeculae* are homologous with the lateroventral parts of the *septum nasi* and the adjacent portions of the *solum nasi* in its section behind the level of the *fenestra nasobasalis*; the *cartilago labialis superior* is a homologue of the *cartilago praenasalis inferior*; the *commissura quadrato-cranialis anterior* is homologous with the *pars palatina palatoquadrati* and also participates in the formation of the postnasal wall; the palatoquadrate of a tadpole is homologous with the *pars quadrata palatoquadrati* of an adult specimen; Meckel's element is a homologue of a similar structure in an adult frog; the epipraemandibular cartilage corresponds to the *processus antorbitalis* (its part directed anteriorly); both copulae, the ceratohyals and hypobranchial plates are homologues of the respective parts of the hyoid.

(5) On the basis of a study of tadpoles and adults of *Pelobates fuscus* it is possible to state the following homologies between the endocranial structures of frogs and those of osteolepiform fishes: the *trabeculae cranii* are holomogues of the suborbital ledge (however, in an adult frog, a similar holomogue appearing as an independent morphological structure is lacking); in spite of some doubts due to the different positions of the opening for *nervus trigeminus,* the prootic fissure in a tadpole (and the *recessus prooticus* together with the *foramen prooticum* of an adult frog) may be regarded as a homologue of an intracranial juncture apparatus. The *crista prootica* is homologous with the horizontal ledge dorsally overlapping the *canalis jugularis*; the *operculum* is homologous with the cartilage which in *Eusthenopteron* fits in a similar opening in the otic capsule and therefore represents a derivate of the neural endocranium; the *fossa condyloidea* is holomogous with the *fissura*

occipitalis lateralis; the *prominentia ducti semicircularis posterioris* is a homologue of the postotic process in fishes. The suprapterygoid articulation in *Eusthenopteron* corresponds to the attachment of the *processus ascendens palatoquadrati* of a tadpole (in an adult frog the *processus ascendens* is reduced), the anteromedial ethmoidal articulation is homologous with the *commissura quadrato-cranialis anterior*; the paratemporal articulation corresponds to the area where the *processus ascendens palatoquadrati* of a tadpole joins the anterolateral part of the otic capsule (in an adult frog the *processus pseudobasalis* is developed in this place). The palatoquadrate of *Eusthenopteron* as a whole is homologous with that of an adult frog; however, it is only partly homologous with the structure also designated as palatoquadrate in tadpole. The *pars autopalatina palatoquadrati* of osteolepiform fishes is homologous with the anterior part of the *processus antorbitalis* of an adult frog. The epibranchials in a tadpole are represented by the *commissurae terminales*, and pharyngobranchials are the small (and sometimes absent) processes of these commissures. The ceratobranchials of osteolepiform fishes correspond to the major parts of the posthyoid branchial arches of tadpoles (inclusive of *commissurae hypobranchiales*); the hypobranchial plate of a tadpole (in adult frogs the lateral part of the *corpus hyoidei, manubrium* and *processus posteromedialis hyoidei*) represents fused hypobranchials. *Copula* 2 and *copula* 1 (in adult frogs the central part of the *corpus hyoidei*) are homologues of the *basibranchiale posterior* and *basibrachiale anterior*. Meckel's element agrees with the equally termed structure in fishes.

The »occiput« in *Eusthenopteron* is an analogue of the *processus posterior superior frontoparietalis* in frogs; in tadpoles a similar structure is not developed. The *fossa bridgei* of *Eusthenopteron* is represented in tadpoles only by an inconspicuous depression of the posterodorsal surface of the otic capsule; in adult frogs the squamosal and frontoparietal also participate in the formation of this depression so that it may be regarded only as a partial homologue of the *fossa bridgei*.

(6) In comparing the endocrania of osteolepiform fishes with those in frogs, the following main changes appearing during the origin of frogs may be stated: a reduction of the visceral skeleton and a modification of its parts into a hyoid and *plectrum* (in *Pelobates* the *plectrum* is developed only in the form of a non-functional vestige), a reduction of the walls of the neural endocranium manifested by the origin of fontanelles and openings, a lower degree of ossification, a dorsoventral flattening of the skull (in connection with this, changes in the position of the palatoquadrate and the orbit), an antero-posterior shortening of the posterior regions of the neural endocranium, the origin of a bicondyl cranio-vertebral junction, the disappearance of the intracranial juncture apparatus, a reduction of the notochord, a reduction of the size of the *lamina supraorbitalis*, the simplification of the surface structure of the otic region, a shift of the *fenestra ovalis* from a lateral into a posterolateral position, the complication of the surface structure in the ethmoidal region, changes in the attachment of the palatoquadrate to the neural endocranium, changes in the proportions of the palatoquadrate, the development of the *foramen jugulare*

from the originally separated openings for *nervus IX* and *nervus X*, a relative lowering and widening of the braincase, the development of the dorsal opening into the braincase, a dorsal shift of the *arteria occipitalis* (from the level of the endocranium into the level of the exocranium).

(7) On the basis of the changes which occurred during the evolution of frogs from their osteolepiform ancestors (through the anatomical stage corresponding to some type of stegocephalian) it is possible to define the following evolutionary trends on the endocranium of frogs: the tendency to a more subtle structure of the neural endocranium, a regressive development of the ossified parts manifested by their size reduction and desintegration into smaller units, a reduction of the *lamina supraorbitalis,* a reduction of the palatoquadrate, a reduction of the roof of the braincase, a lowering and widening of the braincase, a shift of the course of the *arteria occipitalis* to the level of the exocranial cover of the braincase, a shift of morphological changes into earlier stages of ontogeny.

(8) The ossification of the exocranium begins in the frontoparietal and parasphenoid regions; on the other hand, the quadratojugal is one of the last ossifying exocranial elements. The unpaired frontoparietal develops from a paired ossification above the orbitotemporal region and anteromedial part of the otic region, from an unpaired median ossification above the *tectum synoticum,* from a paired ossification above the medial parts of the otic capsulae, and from a less conspicuous and variable ossification above the anterior part of the orbitotemporal region. The squamosal originates through a fusion of the ossification above the *crista parotica* with the ossification laterally adjoining the palatoquadrate.

(9) On the basis of the topographical relations to the endocranium, the individual elements of the exocranium were homologized with the following dermal bones of osteolepiform fishes: the praemaxilla is a homologue of the nasorostropraemaxillare of *Eusthenopteron* which, in addition, was adjoined by a further one from the series of free nasals. The nasal of frogs is homologous with the complex originated through the fusion of the *tectale anterior* with the posterior elements of the series of nasals. The frontoparietal of *Pelobates* (but not of those frogs where this bone develops without participation of unpaired median element!) is a homologue of the paired frontal, parietal, medial extrascapular, the paired supratemporal and probably also the medial postrostral. The *processus paraoccipitales* are probably homologues of lateral extrascapulars. The septomaxilla is a homologue of the proc. dermintermedius of the *rostrale laterale*; the maxilla, quadratojugal and vomer are homologues of the equally termed bones of fishes. The palatine corresponds to a part of dermopalatine. The squamosal is homologous with the complex arisen by fusion of the praeoperculum and squamosal, the parasphenoid corresponds to the complex arisen by fusion of the parasphenoid of *Eusthenopteron* with the dental plates which ventrally and ventrolaterally adjoin the otic capsules. The pterygoid is the homologue of the entopterygoid of fishes. The dentary is either homologous with the equally termed element of fishes, or represents a complex formed

by fusing of the dentary and two most anterior infradentaries. The praearticular is a complex which developed from the praearticular and two posterior infradentaries. The *os parahyoideum* may be homologized only very approximately with the remainders of dermal ossifications covering the respective parts of the visceral arches.

(10) By comparing the exocranium of osteolepiform fishes with homologous elements in *Pelobates,* the following main changes may be stated, which took place on the exocranium during the origin of frogs: the fusion of originally independent dermal bones, or their reduction or disappearance in the areas of the *pars palatina* and *pars quadrata palatoquadrati,* and also in the regions of the nasal capsule, the cranial roof and the lower jaw. The entopterygoid ceased to be an element exclusively associated with the palatoquadrate and has become a bone which considerably participated in the attachment of the lateral part of the skull to the neurocranium. The orbit fairly widened, and in connection with this the bones of the circumorbital ring disappeared throughout. For the same reason, a reduction of the palate occurred, where the dermopalatine was reduced and the ectopterygoid disappeared throughout. The regressive development of the exocranium was also manifested by the exposure of the endocranium particularly in the ethmoidal region, furthemore on the lower jaw and in the region of the dorsal cover of the otic capsules. The parasphenoid expanded into the otic region. The *arteria occipitalis* shifted farther dorsally, so that only in some groups of frogs (e.g. Pipidae) it still retains a connection with the endocranium. In most frogs it already runs through a canal in the frontoparietal (e. g. in Pelobatidae and Discoglossidae) or even on the surface of this bone (Ranidae and Bufonidae). The maxilla expands at the expense of the praemaxilla and quadratojugal.

(11) On the basis of the above changes which occurred during the phylogeny of frogs from their osteolepiform ancestors (through an anatomical stage corresponding to some types of stegocephalians), it is possible to define these main evolutionary trends on the exocranium of frogs as follows: The »centralization« of the exocranium manifested by a fusion of the originally independent elements; a reduction of praemaxilla and quadratojugal in connection with the increase of maxilla; a reduction of the exocranial cover of the endocranium (particularly in the ethmoidal region and on the dorsal side of the otic capsules); an increase of the existing openings in the endocranium; an increase of the contact surface of the pterygoid with the otic capsule; an expansion of the parasphenoid into the occipital region; a shift of the *arteria occipitalis* to the dorsal surface of the skull; a shift in the formation of the ossification centres of the dermal bones into earlier stages of ontogeny; a reduction of the *os parahyoideum*; a reduction of the dentition, the disappearance of the sculpture on the dorsal surface of dermal bones; the appearance of the S-shaped curvature of the praearticular.

(12) Participation of median element in the embryonic development of the frontoparietal complex of *Pelobates,* which is supposedly the phylogenetic remnant of the originally independent dermal bone excludes the possibility that this exocranial

complex could develop from the stage where these median vestige is already lacking throughout (*Triadobatrachus*, ancient discoglossids and generally all the groups of frogs whose frontoparietal is developed without the participation of unpaired median element). This different mode of embryogeny of the frontoparietal suggests that the respective frogs must have evolved independently of the line running through the stage anatomically represented by *Triadobatrachus*, and through ancient discoglossids.

(13) This concept of the basic phylogeny of frogs is expressed by the modified macrosystematic division of this group. The evolutionary line where within the frontoparietal complex a median element is still preserved, is classified as the order Archaeosalientia; the line where this element is already reduced and the frontoparietal is composed exclusively of paired ossifications is classified as the order Neosalientia. *Triadobatrachus* represents the evolutionary stage in the line of Neosalientia and its archaic anatomical nature may be expressed by its assignment to the independent suborder Proanura. All the other groups of frogs whose frontoparietal is composed exclusively of paired elements are assigned to the suborder Anura.

(14) If one regards the mode of embryogeny of frontoparietal as the main diagnostic and phylogenetically significant character of the family Pelobatidae, then it is necessary to exclude from it *Eopelobates leptocolaptus* BORSUK-BIALYNICKA, 1978, *Eopelobates grandis* ZWEIFEL, 1956, *Eopelobates guthriei* ESTES, 1970, *Macropelobates osborni* NOBLE, 1924, and all Asian and North American forms hitherto assigned here, which however differ in the type of frontoparietal structure.

(15) Then, all fossil and recent representatives of the genus *Pelobates* and the remaining representatives of the genus *Eopelobates* are assigned without any problem to the newly defined family Pelobatidae which is now a group reduced as for number of species, but which has been more naturally defined. Pipidae and Palaeobatrachidae also are probably representatives of the evolutionary line of Archaeosalientia, but they clearly differ from the family Pelobatidae.

(16) The independent taxonomic position of the forms which up to the present time have been assigned to the non-homogenous complex *Scaphiopus-Spea*, should be emphasized by re-attributing it the rank of the family Scaphiopodidae.

(17) The genera *Pelobates* and *Eopelobates* occurred simultaneously in the Tertiary of Europe, and probably evolved from a common ancestor. Within the genus *Pelobates* the most archaic form is represented by *Pelobates cultripes*, while the most advanced is *Pelobates fuscus*.

(18) The form designated as *Eopelobates leptocolaptus* as well as the Cretaceous frogs found recently in Mongolia undoubtedly display the characters of discoglossids. The origin of scaphiopodids and probably also megophrynids should be sought among these Central Asian forms.

7. REFERENCES

Basoğlu, M. and S. Zaloğlu, 1964: Morphological and osteological studies in Pelobates syriacus from Izmir region, Western Anatolia. *Senckenb. biol.* 45: 233—242

Bayer, F., 1884: O kostře žab z čeledi pelobatid. *Pojednáni král. čes. spol. nauk, tř. mat. přír.* 6 (12): 1—24

Bjerring, H. C., 1977: A Contribution to Structural Analysis of the Head of Craniate Animals. *Zool. Scr.* 6: 127—183

Bjerring, H. C., 1979: Quondam Gill-Covers. *Zool. Scr.* 8: 235—240

Boas, J. E. V., 1914: Die Schläfenüberdachung und das Palatoquadratum in ihrem Verhältnis zum übrigen Schädel bei den Dipnoern und den terrestren Wirbeltieren. *Morph. Jahrb.* 49: 229—307

Boettger, O., 1889: Ein neuer Pelobates aus Syrien. *Zool. Anz.* 12: 144—147

Bolkay, S. J., 1913: Additions to the fossil Herpetology of Hungary from the Pannonian and Praeglacial Periods. *Mitt. Jahrb. Ung. Geol. Anst. Budapest* 21: 217—230

Bolkay, S. J., 1919: Osnove uporedne osteologije anurskih batrahija. *Glasnik Zamaljskog Muzeja Bosni i Hercegovini* (1919): 277—357

Born, G., 1876: Ueber die Nasenhöhlen und den Thränennasengang der Amphibien. *Morph. Jahrb.* 2: 577—646

Borsuk-Bialynicka, M., 1978: Eopelobates leptocolaptus sp. n. - The first Upper Cretaceous pelobatid frog from Asia. *Pal. Pol.* 38: 57—63

Boulenger, G. A., 1890: On the presence of Pterygoid Teeth in a Tailless Batrachian (Pelobates cultripes), with Remarks on the Localization of Teeth on the Palate in Batrachians and Reptiles. *Proc. Zool. Soc. London* (1890): 664—666

Boulenger, G. A., 1897: The tailless Batrachians of Europe. Part I. London

Bruno, S., E. Burattini and A. Casale, 1974: Il rospo bruno del Cornalia. *Atti del IV Simposio Nazionale sulla Conservazione della Nature* vol. II: 33—56

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

Cope, E. D., 1865: Sketch of the Primary Groups of Batrachia Salientia. *Nat. Hist. Review* (1865): 97—120

De Beer, G. R., 1926: Studies on the vertebrate head. 2. The orbitotemporal region of the skull. *Quart. J. microsc. Sci.* 70: 263—370

De Jongh, H. J., 1968: Functional Morphology of the jaw apparatus of larval and metamorphosing Rana temporaria L. *Netherl. J. Zool.* 18: 1—103

Duellman, W. E., 1975: On the classification of frogs. *Occ. Papers Mus. Nat. Hist. Univ. Kansas* 42: 1—14

Eaton, T. H., 1939: Development of the frontoparietal bones in frogs. *Copeia* (1939) 2: 95—97

Eaton, T. H., 1942: Are »frontoparietal« bones in frogs actually frontals? *J. Wash. Acad. Sci.* 32: 151—153

Estes, R., 1970: New Fossil Pelobatid Frogs and a Review of the genus Eopelobates. *Bull. Mus. Comp. Zool.* 139: 293—340

Estes, R. and O. Reig, 1973: The early fossil records of frogs: a review of the evidence. In: Vial, J. L. (ed.): Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 11—63

Fuchs, H., 1929: Über das Os parahyoideum der anuren Amphibien und der Crossopterygier; nebst Bemerkungen über phylogenetische Wanderung der Haut- und Deckknochen. *Morph. Jahrb.* 63: 408—453

Gaupp, E., 1896: Anatomie des Frosches. I. Lehre vom Skelett und vom Muskelsystem. Braunschweig

Gaupp, E., 1905: Die Entwicklung des Kopfskeletts. Hartwig's Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere, 3 (2). Jena

Geiger, W., 1956: Quantitative Untersuchungen über das Gehirn der Knochenfische mit besonderer Berücksichtigung seines relativen Wachstums. *Acta anat.* 26: 121—163

Gislén, T., 1936: On the History of Evolution and Distribution of the European Pelobatids. *Zoogeographica* 3: 119—131

Gorham, S. W., 1966: Liste der rezenten Amphibien und Reptilien. *Das Tierreich* 85: 1—222

Griffiths, I., 1954a: On the nature of the fronto-parietal in Amphibia, Salientia. *Proc. Zool. Soc. London* 123: 781—792

Griffiths, I., 1954b: On the »otic element« in Amphibia Salientia. *Proc. Zool. Soc. London* 124: 35—50

Jarvik, E., 1942: On the structure of the snout of Crossopterygians and lower Gnathostomes in general. *Zool. Bidr. Uppsala* 21: 237—675

Jarvik, E., 1952: On the fish-like tail in the ichthyostegid Stegocephalians. *Medd. Gronland* 114 (12): 1—90

Jarvik, E., 1954: On the visceral skeleton in Eusthenopteron with a discussion of the parasphenoid and palatoquadratum in fishes. *Kungl. Svenska Vetenskapsakad. Handl.* 5: 5—104

Jarvik, E., 1967: The homologies of frontal and parietal bones in fishes and tetrapods. *Colloques int. Cent. natn. Rech. Scient.* 163: 181—213

Jarvik, E., 1968: Aspects of vertebrate phylogeny. In: Ørvig, T. (ed.): Current Problems of Lower Vertebrate Phylogeny: 497—527

Jarvik, E., 1972: Middle and Upper Devonian Porolepiformes from east Greenland with special reference to Glyptolepis groenlandica n. sp. *Medd. Gronland* 187 (2): 1—307

Jarvik, E., 1975: On the saccus endolymphaticus and adjacent structures in Osteolepiformes, anurans and urodeles. Colloques int. *Cent. natn. Rech. Scient.* 218: 191—211

Jarvik, E., 1980: Basic Structure and Evolution of Vertebrates I, II. London

Jollie, M., 1968: Chordate Morphology. Reinhold Book Corp.

Jurgens, J. D., 1971: The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. *Ann. Univ. Stell.* 46, ser. A: 1—137

Kingsbury, B. F. and H. D. Reed, 1909: Columella auris in Amphibia. *J. Morphol.* 20: 549

Kluge, A. G , 1966: A new pelobatine frog from the Lower Miocene of South Dacota with discussion of the evolution of the Scaphiopus-Spea complex. *Los Angeles County Mus. Contr. Sci* 113: 1—26

Kothe, K., 1910: Entwicklungsgeschichtliche Untersuchungen über das Zungenbein und die Ohrknöchelchen der Anuren. *Arch. Naturgesch.* 76: 29—64

Lebedkina, N. S., 1968: The development of bones in the skull roof of Amphibia. In: Ørvig, T. (ed.): Current Problems of Lower Vertebrate Phylogeny: 317—329

Lebedkina, N. S., 1979: Evoljucija tscherepa amfibij. Moscow

Luther, A., 1914: Über die vom N. trigeminus versorgte Muskulatur der Amphibien. *Acta Soc. Sci. Fenn.* 44, 7: 1—90

Lynch, J. D., 1973: The transition from archaic to advanced frogs. In: Vial, J. L. (ed.): Evolutionary Biology of the anurans: contemporary research on major problems. Missouri Press. Columbia: 133—182

Marcus, H., 1935: Zur Entwicklung der Stapesplatte bei Hypogeophis. *Anat. Anz.* 80: 142—146

Mertens, R., 1923: Beiträge zur Kenntnis der Gattung Pelobates Wagler. *Senckenbergiana* 5: 118—128

Miles, R. S., 1971: Palaeozoic Fishes. London

Mlynarski, M., 1961: Plazy (Amphibia) z pliocenu Polski. *Acta Palaeont. Pol.* 6: 261—282

Mlynarski, M., 1962: Notes on the Amphibian and Reptilian Fauna of the Polish Pliocene and Early Pleistocene. *Acta Zool. Crac.* 7: 177—194

Mlynarski, M., 1977: New Notes on the Amphibian and Reptilian Fauna of the Polish Pliocene and Pleistocene. *Acta Zool. Crac.* 22: 13—36

Nieuwkoop, P. D. and J. Faber., 1967: Normal table of Xenopus laevis (Daudin). Amsterdam

Noble, G. K., 1924: A new Spadefoot Toad from the Oligocene of Mongolia with a summary of the evolution of the Pelobatidae. *Amer. Mus. Novit.* 132: 1—15

Orska, J., 1976: Szkielet. In: Szarski, H. (ed.): Anatomia porownawcza kregowcow. Warszawa

Parker, H. W., 1929: Two Fossil Frogs from the Lower Miocene of Europe. *Ann. Mag. Nat. Hist.* 4: 270—281

Parrington, F. R., 1949: A theory of the relations of lateral lines to dermal bones. *Proc. Zool. Soc. London* 119: 65—78

Piveteau, J., 1937: Paléontologie de Madagascar. XXIII. Un Amphibien du Trias Inférieur. *Ann. Paléontol.* 26: 135—177

Plasota, K., 1974: The development of the chondrocranium (neurocranium, and the mandibular and hyoid arches) in Rana temporaria L. and Pelobates fuscus (Laur.). *Zool. Pol.* 24: 99—168

Pusey, H. K., 1938: Structural changes in the anuran mandibular arch during metamorphosis, with reference to Rana temporaria. *Quart. J. micr. Sci.* 80: 479

Ramaswami, L. S., 1935: The Cranial Morphology of some examples of Pelobatidae (Anura). *Anat. Anz.* 81: 65—96

Ramaswami, L. S., 1956: »Frontoparietal« bone in Anura (Amphibia). *Curr. Sci.* 25: 19—21

Reig, O. A , 1958: Proposiciones para una neuva macrosistematica de los anuros (Nota preliminar). *Physis* 21: 109—118

Pasteur, G., 1958: Sur les tendences évolutives et la phylogenie des Pelobates (Batraciens Anoures) actuels. *C. R. Séanc. Acad. Sci. Paris* 247: 1037—1039

Reinbach, W., 1939a: Untersuchungen über die Entwicklung des Kopfskeletts von Calyptocephalus Gayi. *Jena Z. Naturw.* 72: 211—362

Reinbach, W., 1939b: Über das Os supratemporale von Pelobates fuscus. *Morph. Jahrb.* 84: 169—186

Ridewood, W. G., 1897: On the Structure and Development of the Hypobranchial Skeleton of the Parsley-Frog (Pelodytes punctatus). *Proc. Zool. Soc. London* (1897): 577—594

Sanchíz, F. B. and M. Mlynarski, 1979: Remarks on the Fossil Anurans from the Polish Neogene. *Acta Zool. Cracov.* 24: 153—174

Säve-Sőderbergh, G., 1932: Preliminary Note on Devonian Stegocephalians from East Greenland. *Medd. Grønland* 94: 1—107

Säve-Sőderbergh, G., 1936: On the morphology of Triassic Stegocephalians from Spitsbergen, and the interpretation of the endocranium in the Labyrinthodontia. *Kungl. Svenska Vetenskapsakad. Handl.*, ser. 3, 16: 1—181

Säve-Sőderbergh, G., 1937: On the dermal skull of Lyrocephalus, Aphaneramma, and Benthosaurus, Labyrinthodonts from the Triassic of Spitsbergen and N. Russia. *Bull. Geol. Inst. Upsala* 27: 189—208

Säve-Sőderbergh, G., 1944: New data on the endocranium of Triassic Labyrinthodontia. *Ark. Zool.* 36; A, (9): 1—9

Sedra, S. N , 1949: On the Homology of certain elements in the Skull of Bufo regularis Reuss (Salientia). *Proc. Zool. Soc. London* 119: 633—641

Sedra, S. N., 1950: The metamorphosis of the jaws and their muscles in the toad Bufo regularis Reuss, correlated with the changes in the animal's feedings habits. *Proc. Zool. Soc. London* 120: 405

Sedra, S. N. and M. I. Michael, 1959: The ontogenesis of the sound conducting apparatus of the Egyptian toad, Bufo regularis Reuss, with a review of this apparatus in Salientia. *J. Morphol.* 104: 359—375

Sewertzow, A. N., 1891: Ueber einige Eigenthümlichkeiten in der Entwickelung und im Bau des Schädels von Pelobates fuscus. *Bull. Soc. Imp. Nat. Moscou*, N. Sér. V: 143—160

Severtzov, A. S., 1970: The evolution of the hyobranchial apparatus in the larvae of Amphibia *Smith. Herpet. Inform. Services Shis* 21: 1—8

Schulze, F. E., 1892: Über die inneren Kiemen der Batrachier-larven II. *Abh. Akad. Wiss. Berlin* (1892): 1—66

Sokol, O. M., 1977: The Free Swimming Pipa Larvae, with a Review of Pipid Larvae and Pipid Phylogeny (Anura: Pipidae). *J. Morphol.* 154: 357—426

Stadtmüller, F., 1936: Kranium und Visceralskelett der Stegocephalen und Amphibien. In: Bolk, L , Göppert, E., Kallius, E. and Lubosch, W. (ed.): Handbuch der vergleichenden Anatomie der Wirbeltiere: 501—698

Szarski, H., 1962: The Origin of the Amphibia. *Quart. Rev. Biol.* 37: 189—241

Shishkin, M. A., 1973: Morfologija drevnych zemnovodnych i problemy evoljucii nizschich tetrapod. Moscow

Špinar, Z. V., 1952: Eopelobates bayeri nová žába z českých třetihor. *Sborn. ÚÚG* 19: 457—488

Špinar, Z. V., 1972: Tertiary Frogs from Central Europe. Prague

Špinar, Z. V., 1976: Endolymphatic sacs and dorsal endocranial pattern: Their significance for systematics and phylogeny of frogs. *Věst. ÚÚG* 51: 286—290

Špinar, Z. V., 1979: Latonia kolebabi Špinar, 1976 (Amphibia) and remarks on the »genus Miopelobates«. *Paleontologická konference* '77 - Universita Karlova Praha: 289—303

Trewavas, E., 1933: The hyoid and Larynx of the Anura. *Phil. Trans. Soc. London* Ser. B 222: 401—527

Trueb, L., 1973: Bones, Frogs, and Evolution. In: Vial, J. L. (ed.): Evolutionary Biology of the Anurans: contemporary research on major problems: 65—132

Van Eeden, J. A., 1951: The development of the chondrocranium of Ascaphus truei Stejneger with special reference to the relations of the palatoquadrate to the neurocranium. *Acta Zool.* 32: 42—124

Watson, D. M. S., 1940: The Origin of Frogs. *Trans. R. Soc. Edinburgh* 60: 195—231

Zweifel, R. G., 1956: Two Pelobatid Frogs from the Tertiary of North America and Their Relationships to Fossil and Recent Forms. *Amer. Mus. Novit.* 1762: 1—45

Author's address: Dr. Zbyněk Roček, CSc.
Katedra paleontologie UK
Albertov 6
128 43 Praha 2
Czechoslovakia

Contents

ACTA UNIVERSITATIS CAROLINAE - BIOLOGICA
Vol. 1980 Nos 1—2

Univerzita Karlova, Praha 1981

Prorektor-editor: prof. RNDr. Václav Prosser, CSc.
Odpovědný redaktor: doc. RNDr. J. V. Černý, CSc.
Vedoucí univerzitní edice: PhDr. Zdeňka Vávrová-Rejšková
Vytiskly Moravské tiskařské závody n. p., Olomouc, závod 10

Náklad 800 výtisků
Cena brožovaného výtisku 20 Kčs