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Ethmoidal endocranium in primitive Triassic amphibians

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With 7 figures

Kurzfassung: Dreidimensional erhaltene und chemisch präparierte Schädel sowie Schädelabdrücke von Vertretern der Familien Benthosuchidae, Melosauridae und Capitosauridae haben Informationen über das ethmoidale Endokranium geliefert, das heißt über die ursprünglich nur verknorpelten nasalen Schädelstrukturen. Diese Arbeit zeigt, daß das ethmoidale Endokranium ursprünglich eine dorsoventral komprimierte Platte war, durchbohrt von einem breiten und schräg verlaufenden Kanal, der vorne mit der äußeren Dorsalfläche der Fenestra endonarina, hinten mit der Öffnung der Fenestra endochoanalis (*seu* foris) in Verbindung stand. Der Kanal war sehr kurz und enthielt das olfaktorische Organ. Das ethmoidale Endokranium war mit dem Palatoquadratum durch die Commissura quadratocranialis anterior verbunden. Es gab keine laterale ethmoidale Kommissur, doch konnte bei älteren Individuen der vordere Abschnitt des Palatoquadratums auch den postchoanalen Teil des nasalen Endokranialskelettes berühren.

Abstract: Three-dimensionally preserved and chemically prepared skulls and natural casts of representatives of the families Benthosuchidae, Melosauridae, and Capitosauridae yield data on the structure of the ethmoidal endocranium, i.e. of those nasal cranial structures that consisted originally of cartilage. This study demonstrates that the ethmoidal endocranium was principally a dorsoventrally compressed plate, pierced by a broad and oblique canal which communicated anteriorly with the outer dorsal surface by the fenestra endonarina and posteriorly with the mouth cavity by the fenestra endochoanalis (*seu* foris). The canal was very short, and housed the olfactory organ. The ethmoidal endocranium was connected with the palatoquadrate by the commissura quadratocranialis anterior; there was no lateral ethmoidal commissure, however, in older individuals the anterior section of the palatoquadrate might also contact the postchoanal part of the nasal endocranial skeleton.

Introduction

Information on the skull of early amphibians is based mainly on exocranial (= membrane or dermal) bones; these arise by endesmal ossification (directly from mesenchyme) in the dermis and consequently they are located on the skull surface. Only a minor part of amphibian skull is formed by endocranial (= endochondral) bones; these arise by ossification of cartilaginous primordia and usually are located below the dermal bones (hence "endocranial"). However, bones are not the only structural elements of the skull; the endocranium of amphibians consists primarily of cartilage. The endocranium of crossopterygian fishes (which are considered amphibian ancestors) was fully ossified, but it remains cartilaginous in amphibians due to progressive blocking of the ossification process. During fossilization, the cartilage is lost (unless calcified) and this is the main reason why comparison of the endocrania in these two groups is rather difficult. However, even cartilaginous (and thus

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temporary from the point of view of fossilization) structures may leave their traces on the inner surface of the dermal bones and this allows us to reconstruct, with a reasonable degree of accuracy, their shape. Natural endocasts, though unfortunately rarely preserved, provide additional valuable information. Reconstructions based upon these two sources of information enables us to follow evolutionary transformations of the endocranium.

Only few data on the ethmoidal endocranium in primitive tetrapods are available (Bystrov & Efremov 1940, Säve-Söderbergh 1936, Shishkin 1973, Wilson 1941, see Roček 1990 for a review). Some of them are inaccurate or fairly hypothetical, compared to the condition in anurans. This is why numerous three-dimensionally preserved specimens of the Benthosuchidae (see Getmanov 1989) and to a lesser extent also of Melosauridae and Capitosauridae, deposited in the Paleontological Institute of the USSR Academy of Sciences, have offered an excellent opportunity to complete hitherto known data.

Description

Family Melosauridae
Melosaurus vetustus Konzhukova 1955

Material: PIN N4273/1; PIN 520/1.

The specimen PIN N4273/1 (Fig. 1) is a part of the palate that includes the fenestrae endochoanales and the most anterior part of the palatine. Its surface can be investigated both from inner (dorsal) and outer (ventral) sides.

In general, as can be judged from the inner surface of the mentioned bones, the posterior section of the ventral surface of the ethmoidal endocranium is similar to that in Benthosuchidae (see below). There is a distinct groove along the medial margin of the fenestra endochoanalis, most probably for the arteria maxillaris and accompanying nerve.

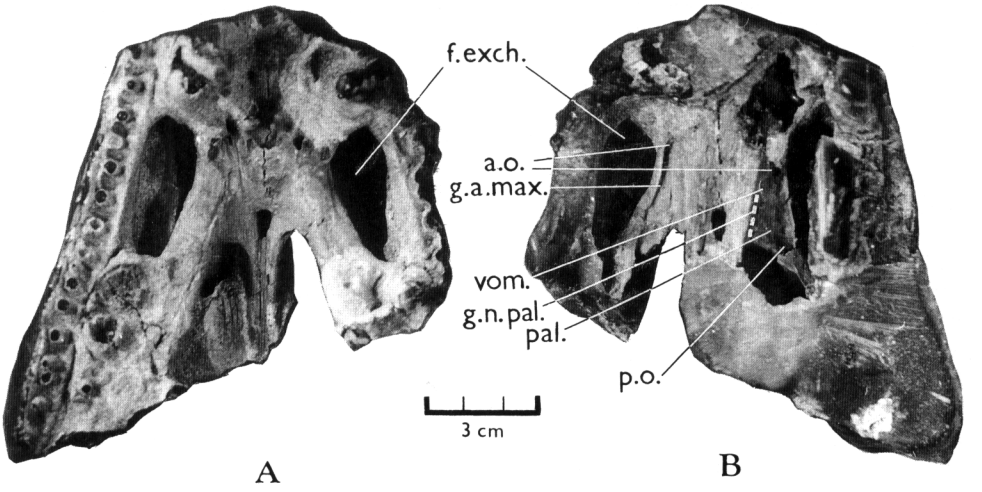

Fig. 1. *Melosaurus vetustus* Konzhukova 1955. PIN N4273/1. Ventral (A) and dorsal (B) views of the palatal bones. Abbreviations: a.o. – groove for arteria maxillaris entering anteriorly vomer; f. exch. – fenestra exochoanalis; g.a. max. – groove for arteria maxillaris; g.n.pal. – groove for nervus palatinus; pal.-palatine; p.o. – groove for arteria maxillaris entering posteriorly palatine; vom. – vomer.

Anteriorly, the groove becomes a canal piercing the vomer; the orifice of the canal is situated posterior to the level of the anterior limit of both fenestrae (this may be rather asymmetrical as can be seen from Fig. 1). In contrast to *Benthosuchus*, the groove becomes a canal also posteriorly, within the palatine. The same condition can be seen on specimen PIN 520/1.

The median part of the ventral surface is thin; this area is marked laterally by distinct ridges that diverge slightly anteriorly. As the adjacent section of the posterior margin of the vomer is rounded and rather concave (which is seen clearly in posterior view) one can judge that there was a canal running along the mentioned ridge, formed by endocranial cartilage dorsally, and by inner surface of the vomer ventrally. Presumably it served for the palatine nerve and accompanying vessel.

There is a distinct foramen within the median intervomerine suture. It is difficult to say to what extent structures that passed through this foramen were visible on the endocranium.

Family Benthosuchidae
Benthosuchus korobkovi (IVAKHNENKO 1972)

Material: PIN 3200/4, PIN 3200/167, PIN 3200/179, PIN 3200/181, PIN 3200/189, PIN 3200/207, PIN 3200/238, PIN 3200/240.

General shape of the ethmoidal endocranium may be seen in Figs. 2, 3 and 4. These reconstructions are based mainly on the exposed natural casts (PIN 3200/240 and PIN 3200/4) and on the morphology of the inner surface of the ethmoidal exocranial skeleton.

The dorsal surface is smooth and flat. Between the fenestrae endonarinae and slightly posterior to them is a shallow depression which is seemingly deeper because of elevated medial margins of these openings. The fenestrae are directed dorsolaterally; consequently the lateral margin of the complete naris is formed by the praemaxillary and maxillary. On the dorsal surface of the cast PIN 3200/240 one can see traces of the suture indicating the anterior margin of the lacrimal and of the median suture separating both nasals. Curiously, the median nasal suture is interrupted in the centre of the above mentioned shallow depression by tiny ridges that form a rhomboid with additional ridges extending laterally. No corresponding sutures were reported between adjacent dermal bones, but BYSTROV (1935), BYSTROV & EFREMOV (1949: Fig. 56), and GETMANOV (1989: 81) mentioned the presence of some additional median ossifications. On the inner surface of the lacrimal and frontal there is an impression with the distinct posterolateral margin; it no doubt indicates the extent of the lamina supraorbitalis.

On the ventral surface of the endocranium there is a well defined depression with a flat bottom which is exposed through the anterior palatal fenestra of the exocranium. Posterolaterally there are the fenestrae endochoanales (fores sensu BJERRING 1989). In contrast to the fenestra endonarina, the fenestra endochoanalis is bordered laterally by cartilage. The extent of the nasal capsule connecting both apertures is marked on the ventral surface of the cast by a distinct convexity. In the midline there is a slight imprint of the parasphenoid. Its anterior tip exceeds the level of the anterior margins of both fores, however, it does not reach the fossa apicalis.

If the position of both fenestrae of the nasal capsule are compared on the exoskeleton, then the anterior margin of the fenestra exochoanalis reaches the level of the posterior margin of the fenestra exonarina. However, if a similar comparison is carried out on the endoskeleton (as shown by natural casts), then both apertures are well separated (compare Figs. 2 and 3). This naturally means that endoskeletal fenestrae are smaller than exoskeletal ones. In some specimens (e.g. PIN 3200/207) there is a distinct outgrowth on the inner

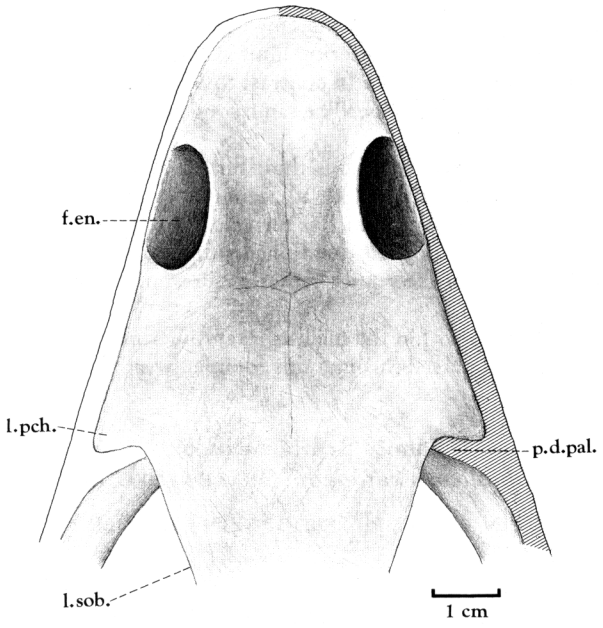

Fig. 2. *Benthosuchus korobkovi* IVAKHNENKO 1972. Reconstruction of the ethmoidal endocranium in dorsal view. Based mainly on specimens PIN 3200/167, PIN 3200/177, PIN 3200/207, and PIN 3200/240. Abbreviations: f.en. – fenestra endonarina; l.pch. – lamina postchoanalis; l.sob. – lamina supraorbitalis; p.d.pal. – processus dorsalis palatini. Hatched is the horizontal section through the exocranium.

surface of the dermal bones, making a sharp lateral indentation of the endocranium just at the level of the posterior margin of the fenestra endonarina. In other specimens the lateral endocranial outlines are almost straight. The mentioned inner dermal outgrowth may be interpreted as the septomaxillary. It can also be seen in the dorsal view of the fenestra endonarina. The outgrowth formed by the septomaxillary may continue medially in some specimens (e.g. PIN 3200/167) as a rounded ridge on the inner surface of the vomer, thus causing a corresponding imprint on the ventral surface of the endocranium (similar to *Thoosuchus;* see Fig. 7).

The posterolateral wall of the nasal capsule is rounded, however, the roof of the capsule considerably exceeds its level as a horizontal plate, that is pointed in dorsal view. It may be termed the lamina postchoanalis. At the border between this plate and the vertical wall there is a distinct horizontal groove which housed a corresponding horizontal ridge on the maxillary. In some specimens (e.g. PIN 3200/179) this ridge is so prominent that it is manifested on the inner surface of the posterolateral wall of the capsule when seen through the fenestra endochoanalis.

The palatoquadrate is connected with the ventral part of the postnasal wall by means of the commissura quadratocranialis anterior. The space between the lateral part of the postnasal wall and the anterior part of the palatoquadrate is occupied by vertical ridge produced by the palatine (proc. dorsalis palatini; GETMANOV 1989: Fig. 16). This process continues posteromedially as a gradually lowering ridge that adjoins synchondrotically the lacrimal, and marks the posterolateral outlines of the lamina supraorbitalis. It is termed the spina (torus) sublacrimalis (GETMANOV 1989: Fig. 16).

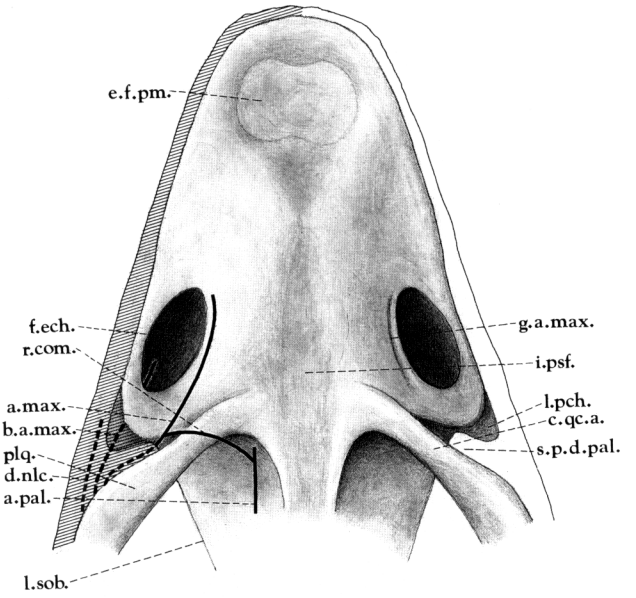

Fig. 3. *Benthosuchus korobkovi* IVAKHNENKO 1972. Reconstruction of the ethmoidal endocranium in ventral view. Based on the same specimens as in Fig. 2. Abbreviations: a.max. – arteria maxillaris; a.pal. – arteria palatina; b.a.max. – branch of arteria maxillaris; c.qc.a. – commissura quadratocranialis anterior; d.ncl. – ductus nasolacrimalis; e.f.pm. – surface exposed through fenestra praemaxillaris; f.ech. – fenestra endochoanalis; g.a.max. – groove of arteria maxillaris; i.psf. – imprint of parasphenoid; plq. – palatoquadratum; r.com. – ramus communicans between arteria maxillaris and arteria palatina; s.p.d.pal. – space for processus dorsalis palatini. Other explanations and scale as in Fig. 2.

The processus dorsalis palatini is pierced by at least three larger canals and, as can be seen in specimen PIN 3200/207, by several smaller ones that undoubtedly served for tiny branches of larger vessels housed in the former three canals. The posterior orifice of the medial canal (see Fig. 3) is located between the maxilla and palatoquadrate and is directed towards the medial ridge of the processus dorsalis palatini. If the anterior part of the canal could be extended it would reach a distinct groove that follows the medial margin of the fenestra endochoanalis. A similar groove is on the adjacent surface of the vomer. Both grooves together form a canal entering the vomer at the level of the anterior margin of the fenestra endochoanalis. This canal probably housed the arteria maxillaris. In some specimens, e.g. PIN 3200/167, there are two parallel canals entering the vomer, and two parallel grooves following the medial margin of the fenestra endochoanalis; this suggests that the vessel was accompanied by a corresponding nerve, although each ran separately.

The posterior orifice of the middle of the three canals that appear on the posterior surface of the processus dorsalis palatini is close to the medial one. The canal is directed toward the nasal capsule and probably housed another branch of the arteria maxillaris (called the ramus infraorbitalis by SHISHKIN 1973: Fig. 60b). The arteria palatina entered the vomer close to the palatine/vomer suture (see PIN 3200/207), beyond the posterior margin of the commissura quadratocranialis anterior; consequently, it had no contact with the ventral surface of the ethmoidal endocranium.

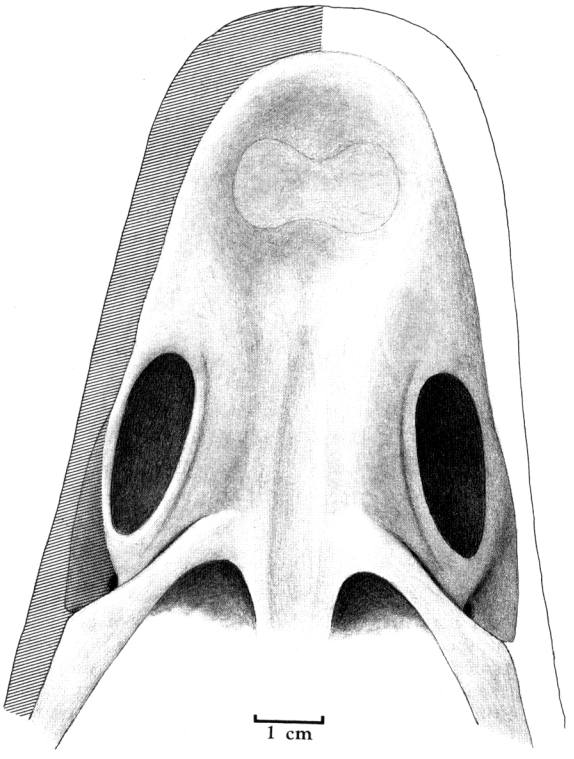

Fig. 4. *Benthosuchus korobkovi* IVAKHNENKO 1972. Reconstruction of the ethmoidal endocranium in the specimen PIN 3200/4 in ventral view. Exocranium hatched.

The most lateral and the largest canal does not pierce the processus dorsalis palatini but enters the maxillary, close to its suture with the lacrimal. It probably served for the ductus nasolacrimalis (GETMANOV 1989: 48).

Although no imprints of any vessel can be observed on the dorsal surface of the cast (PIN 3200/240), an aperture on the inner surface of the anterior part of each nasal suggests that vessels were present. Most probably they carried branches of the arteria ophthalmica.

The posterolateral part of the nasal capsule that was described above as the lamina postchoanalis can in some specimens (e.g. PIN 3200/4 which is natural cast; see Fig. 4) contact the palatoquadrate, even if it does not fuse with it. The processus dorsalis palatini was either separated from the maxillary or connected with it by a thin, vertical lamina which is thickened only in its medial part as a column. As this specimen is much larger than e.g. PIN 3200/240 (Fig. 3), one can speculate that this is an older individual. It is possible that in still older individuals the lamina postchoanalis can fuse with the anterior section of the palatoquadrate, and the processus dorsalis palatini can be preserved as a thin column, separated entirely from the maxillary. It is noteworthy that with the exception of the fenestra endochoanalis which is rather enlarged, the other features remain similar to those in presumably younger individuals.

In a manner analogous to that of *Benthosuchus sushkini* (Fig. 5), the ethmoidal endocranium is thin; only in ventral view can one distinguish the extent of the nasal capsules after indistinct elevations. Anteriorly, the endocranium follows the shape of the skull and as can be observed (e.g. PIN 3200/238) the premaxillary is very thin.

Benthosuchus sushkini (EFREMOV 1929)

Material: PIN 2/2243, PIN 3/2245, PIN 11/2252, PIN 19/2252, PIN 14/2252, PIN 2424.

The morphology of the ethmoidal endocranium is very similar to that in *B. korobkovi*. In specimen PIN 14/2252 which is the anterior half of the skull one can observe that the ethmoidal plate was very compressed. Its anterior edge was covered only by a thin premaxilla. Thus, this specimen shows that the anterior margin of the ethmoidal plate was archlike in dorsal view, paralleling the outline of the skull. Proportions of the ethmoidal plate in lateral view can be seen in Fig. 5. In the cross-section, the plate was rather compressed along its midline. Specimen PIN 3/2243 (ROČEK 1990: Figs. 5, 6) is a natural cast that indicates the original extent of cartilage and shows laterally thickened parts that probably reflect communication between both nasal openings. There is no lateral wall of the fenestra endonarina, its bottom is horizontal up to its lateral margin (this margin is rather convex in dorsal view, as shown by specimen PIN 2424). In the case of the fenestra endochoanalis (seu foris sensu BJERRING 1989), however, a horizontal groove on the inner surface of the maxilla indicates that this fenestra was bordered laterally by cartilage.

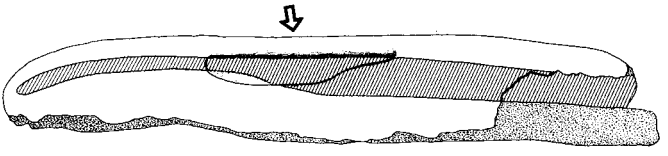

Fig. 5. *Benthosuchus sushkini* (EFREMOV, 1929). Diagrammatic section through the specimen PIN 9-19/2252 to show the ethmoidal endocranium (hatched) in lateral view. The position of the fenestra endonarina marked by arrow. Scale as in Fig. 2.

Benthosuchus uralensis (OCHEV 1958)

Material: PIN 4167/1.

The ethmoidal region of this specimen (which is the holotype) is composed partly of a natural cast and partly of the fragment of the palatal bones that can be investigated from the inner side. In contrast to the other two species of *Benthosuchus*, *B. uralensis* has a paired fenestra praemaxillaris. The ethmoidal plate was extremely compressed anteriorly and reached almost the anterior end of the skull (the praemaxilla was thin here). There is a distinct horizontal groove on the inner surface of the maxilla within the extent of the fenestra endochoanalis, suggesting that there was a cartilaginous lateral wall of the fenestra present. A distinct groove for the arteria maxillaris enters a canal at the level of the anterior limit of the fenestra; posteriorly the groove becomes shallower and finally disappears without entering into the palatine (similarly as in *Melosaurus vetustus* KONZHUKOVA; compare Fig. 1). The inner surface of the vomer is clearly depressed within the extent of the fenestra endonarina.

Thoosuchus jakovlevi (Riabinin 1927)

Material: PIN 3200/93, PIN 3200/127, PIN 3200/197, PIN 3200/199, PIN 3200/208, PIN 3200/239.

The snout in *Thoosuchus* can be restored from several specimens that are preserved partly as fragments of the exocranium and partly as natural casts. In contrast to *Benthosuchus,* both nasal openings in *Thoosuchus* are widely separated implying that the nasal capsule is comparatively longer than in the representatives of the former genus. It can not be excluded, however, that this feature is an age dependent character. In other words, both fenestrae could be closer to one another in younger individuals, but more distant in older ones. This hypothesis might be supported by the condition in other amphibians, e.g. in anurans, and by the fact that in specimen PIN 3200/239 which can be considered to be fully grown there is a separate ossification on the inner surface of exocranial bones that are adjacent to that part of the endocranium which is situated between both fenestrae. This ossification is no doubt the septomaxilla. It produced a distinct indentation on the ventrolateral surface of the ethmoid plate (see Fig. 7). According to Getmanov (1989: 51) the septomaxilla is present in all specimens of *Thoosuchus;* however, its medial outgrowth called the processus dermintermedius is developed to various degrees so that in some individuals it produced an impression in the ventrolateral surface of the ethmoid plate, in others it did not. As the extent of endesmal ossification might indicate relative age, one can conclude that the mentioned character might be age dependent. Variation of the same character in *Benthosuchus* (Getmanov 1989: 12) can be explained similarly.

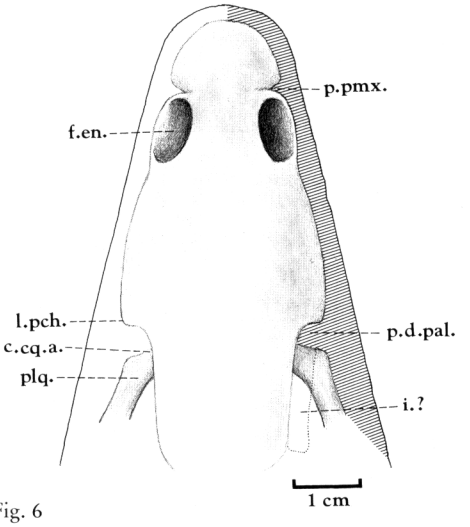

Fig. 6

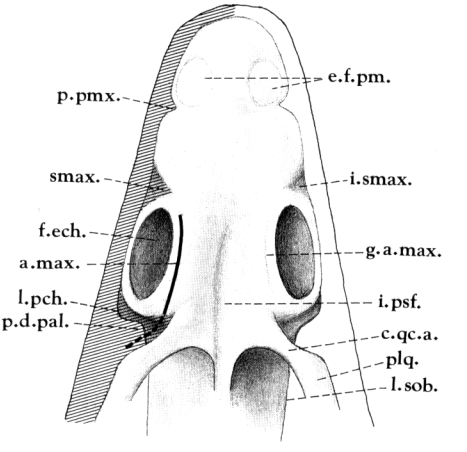

Fig. 7

Fig. 6. *Thoosuchus jakovlevi* (Riabinin 1927). Reconstruction of the ethmoidal endocranium in dorsal view. Based mainly on the specimens PIN 3200/93, PIN 3200/208, and PIN 3200/239. Abbreviations:i? – area of distinctly limited imprint on the inner surface of the lacrimal; p.pmx. – processus praemaxillaris. Other abbreviations as in Figs. 2 and 3.

Fig. 7. *Thoosuchus jakovlevi* (Riabinin 1927). Reconstruction of the ethmoidal endocranium in ventral view. Based on the same specimens as in Fig. 6. Abbreviations: i.smax. – imprint of septomaxilla; p.pmx. – processus praemaxillaris; smax. – septomaxilla. Other abbreviations as in Figs. 2 and 3. Scale as in Fig. 6.

There is another, much deeper indentation in the lateral margin of the ethmoid plate, just anterior to the fenestra endonarina. This can be seen clearly in specimen PIN 3200/93 in which the tip of snout is broken off at the level of the anterior limit of the fenestra endonarina, and can be verified on specimen PIN 3200/239 which is a natural cast. In both of these specimens the anterior margin of the fenestrae endonarinae was probably bordered by exocranial bone, namely by the connection between the pars facialis and lamina horizontalis praemaxillae. This connection is called the processus praemaxillaris on Figs. 6 and 7.

The course of the lateral margin of the lamina supraorbitalis can be deduced from the imprint on the inner surface of the exocranial bones. However, in contrast to other benthosuchids, there is no single ridge directed toward the medial margin of the orbit and connected anteriorly with the processus dorsalis palatini (see GETMANOV 1989: Fig. 16). Instead, there is an imprint of a longitudinal and rectangular structure which was topographically associated with the above mentioned palatine process, but posteriorly was terminated abruptly (Fig. 6, i?). This imprint can be seen on specimen PIN 3200/208 which includes a natural cast of the whole anterior moiety of the cranial cavity. It can be supposed that the lamina supraorbitalis was developed medial to this structure and the structure itself might be interpreted, with some doubts, as a posterior prolongation of the processus dorsalis palatini (spina seu torus sublacrimalis sensu GETMANOV 1989: Fig. 16).

There is a pair of fenestrae praemaxillares which are widely separated medially. The ethmoidal plate was slender when viewed dorsally; however, in accordance with other benthosuchids it was compressed dorsoventrally.

Angusaurus succedaneus GETMANOV 1989

Material: PIN N 2428/1.

The specimen is the holotype, comprising the palate. The pair of fenestrae praemaxillares is widely separated medially, and the lateral margin of exposed surface of the ethmoidal plate reaches the level of the praemaxillary tooth row. The course of the arteria maxillaris is indicated by a groove on the inner surface of the vomer and palatine. Close to the anterior limit of the fenestra endochoanalis the groove entered the vomer. In all other observable features the ethmoidal endocranium corresponds to that in *Benthosuchus*.

Angusaurus tsylmensis NOVIKOV 1990

Material: PIN 4333/6.

The specimen is the holotype. The anterior part of the snout is broken off at the level of the middle of the fenestrae endonarinae. It can be deduced from this natural cross section that the ethmoidal plate was compressed dorsoventrally, and its dorsal surface was rather concave along the midline. The fenestra endochoanalis and fenestra endonarina were separated widely. This can be associated with elongation of the snout or may be an age dependent character (see discussion in *Thoosuchus*).

Family Capitosauridae
Wetlugasaurus angustifrons RIABININ 1930

Material: PIN 3200/237.

The broken surface of this specimen suggests that there was only a thin layer of cartilage between the lamina horizontalis maxillae and the dermal skull roof. As in *Benthosuchus* there is a horizontal groove on the inner surface of the maxilla along the lateral margin of the fenestra endochoanalis, suggesting that the cartilaginous lateral wall of the fenestra was present. On the inner surface of the roofing bones above this fenestra there is a distinct imprint of a nerve or vessel running anterolaterally. From all the material studied, this feature was found only in *Wetlugasaurus*. If compared with benthosuchids, the shape of snout in dorsal view is slightly wider. However, in all other characters the ethmoidal endocranium of *Wetlugasaurus* corresponds in general morphology with that of the above described representatives of the Benthosuchidae.

Discussion

In the representatives of the three families discussed, the ethmoidal endocranium consists of single horizontal plate, the anterior margin of which is arch-like, thus corresponding to the outlines of the snout. No horns or structures resembling prenasal cartilages of anurans (cf. BYSTROV & EFREMOV 1940: 49; SÄVE-SÖDERBERGH 1936: Fig. 8) were found. It is possible that the anterior margin of the plate was similar in *Dvinosaurus* (cf. SHISHKIN 1973: 114, figs. 47–50).

The plate (one may use the term "ethmoidal plate") is pierced by two fenestrae: the fenestra endonarina situated on the dorsolateral surface, and fenestra endochoanalis on the ventral surface. The position of the former fenestra is anterior to the level of the anterior margin of the latter. The distance between both fenestrae is greater in those individuals in which the septomaxilla is present. If presence of this bone is taken as a character indicating individual age one may conclude that both fenestrae are more distant in older individuals. Both fenestrae were connected by a short and broad canal housing the olfactory organ. The specimen of *Benthosuchus sushkini* (PIN 3/2243) which is a natural cast consisting of two-coloured matrix suggests that the cavity of the nasal capsule was filled before cartilage was destroyed, and only later the space left by the cartilage was filled with sediment (see also ROČEK 1990: 396, fig. 6). On the rough cross section at the level of the anterior half of the fenestra endochoanalis the brownish pattern indicates a broad septum nasi, and a thin solum and tectum nasi. The bottom of the anterior fenestrae is horizontal and comes out onto the lateral margin of the skull. In contrast, posterior fenestrae are rimmed laterally with vertical wall of the maxillae, on the inner surface of which there is a distinct horizontal groove. This suggests that these fenestrae were bounded laterally both by endocranial (cartilaginous) and exocranial (maxillary) walls (cf. BYSTROV & EFREMOV 1940: figs. 32, 33; SÄVE-SÖDERBERGH 1936: fig. 8).

The palatoquadrate is attached to the medial part of the postnasal wall by a slender commissura quadratocranialis anterior. It runs in the groove on the inner surface of the palatine, along the base of its processus dorsalis. Only in *Melosaurus* is there uncertainty with respect to the course of the processus dorsalis. In the Benthosuchidae and *Wetlugasaurus* the course of the arteria maxillaris is indicated clearly by the course of the groove running parallel to the inner margin of the fenestra endochoanalis. Posteriorly the canal for this vessel pierced the processus dorsalis palatini. In *Melosaurus,* however, it entered the palatine in its border along the fenestra endochoanalis. In this respect the condition in the mentioned form deviates from the general scheme.

There is a problem of the lateral ethmoidal commissure. In old individuals of *Benthosuchus korobkovi* (exemplified by specimen PIN 3200/4) the lamina postchoanalis comes into contact with the anterior section of the palatoquadrate. Consequently, the processus dorsalis palatini is reduced to a thin lamina, and only its medial part remains as a column pierced by a canal for the arteria maxillaris and accompanying nerve. One may suppose that further development would theoretically result in complete fusion of the lamina postchoanalis and palatoquadrate, and consequently in the disappearance of the former partition between them. The lateral connection that could arise in this way might be considered lateral ethmoidal commissure or, in a broader context, the processus maxillaris posterior.

To sum up the above descriptions, one may conclude that the ethmoidal endocranium is surprisingly uniform in the members of all three families. It would be interesting to know whether the same holds also for other labyrinthodont groups. One should therefore investigate all the material in which either casts are preserved or a reconstruction can be made on the basis of traces of the inner surface of the dermal bones.

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