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Origin and evolution of the anuran postnasal wall and adjacent parts of the palatoquadrate

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In early anuran larvae the posterior wall of the nasal capsule is not developed. The olfactory nerves are exposed dorsally. Later paired, transversely located elements roof these nerves. They fuse and, later, produce, by downward growth, the walls of the olfactory canals. Laterally, the first functional partition between the future nasal capsule and orbit is the commissura quadratocranialis anterior. The ophthalmicus nerve runs across the dorsal surface of the commissura. In the course of further development, a new element (called the lamina orbitonasalis), arises anterolaterally to the commissura; consequently, the above mentioned nerve is enclosed in a canal between the lamina orbitonasalis and the braincase. Meanwhile, the commissura becomes detached from the braincase and fixed to the lamina. Later another element, the epipraemandibulare, arises anterodorsally to the lamina; it encloses a branch of the ophthalmicus nerve in a canal. On the lateral end of the lamina orbitonasalis a further element arises: the processus maxillaris posterior. As the commissura later becomes detached even from the lamina, the processus ultimately represents the only connection of the palatoquadrate with the postnasal wall. Thus the postnasal wall, and adjacent parts of the palatoquadrate are of complex origin, though in adults they are a single unit. Comparison with those labyrinthodonts in which corresponding data are available reveals that the structure of their postnasal wall corresponds to certain larval stages of anurans. Thus the structure in adult anurans represents an evolutionary addition lacking in labyrinthodonts. For this reason, in the search for anuran ancestors one may compare adult labyrinthodonts not only with adult but also larval anurans.

KEY WORDS: Amphibia, Anura, Labyrinthodontia, skull, ontogeny, evolution.

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INTRODUCTION

Anuran phylogenetic continuity with Palaeozoic amphibians is not satisfactorily explained. Some features of the anuran skull seem to be found in the juvenile representatives of the family Dissorophidae (Bolt 1979). Comparison with fossils is important because they represent direct evidence of past evolutionary processes but, as the cartilaginous structures are lost, they are of limited use. Moreover, only adults and subadults are usually used for comparison. However, these are often specialized to such an extent that original features present in ancestors are already lost or obscured by morphological characters acquired in postmetamorphic stages. In contrast, tadpoles retain some ancestral characters, and therefore determination of evolutionary sequences and phylogenetic relationships from the development of primitive contemporary forms can add important data for evaluation. For this purpose it is necessary to distinguish those features of the larvae inherited from ancestors, from larval adaptations. This is comparatively easy if we follow characters throughout development (Fig. 1). As larval and adult adaptations are acquired independent from each other (in accordance with water and terrestri-

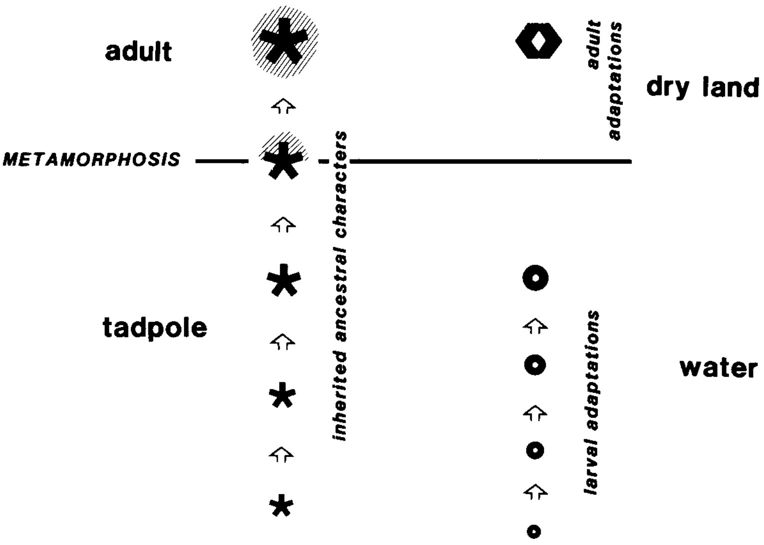


Fig. 1. — Scheme to show the continuity of ancestral characters throughout anuran metamorphosis, contrasting with developmental discontinuity of adaptive characters. Only the former should be used in evolutionary studies.

al ways of life), larval adaptations do not persist in adults, and adult specializations cannot be manifested in the tadpole's structure. Hence, those structures are important which can be followed in continuity throughout development. It may be supposed that these characters can also indicate relationships with ancestral forms (cf. HANKEN 1986).

The anuran ethmoid is remarkable in that whereas it is comparatively uniform in adults, larvae of various taxa display differences. Although embryonic material is basically similar (i.e., mandibular section of the neural crest; TOERIEN & ROSSOUW 1977, SADAGHIANI & THIEBAUD 1987), the structure of the larval ethmoidal endocranium differs considerably (Fig. 2). For instance, most larvae in which development is sufficiently investigated have the ethmoidal endocranium composed of two cornua trabecularum and various number of free, or articulated cartilaginous elements. Pipidae, on the other hand, lack trabecular horns, but have an ethmoid plate, and lack free elements. It is difficult to consider the structures homologous because whereas in tadpoles with trabecular horns the septum nasi arises from new material between them, and the horns are incorporated into the adult nasal structures, in pipids the whole ethmoid plate disappears and the adult nasal structures are new (ROČEK 1989, ROČEK & VESELÝ 1989).

Because of the developmental variation of the ethmoidal endocranium contrasting with its relative uniformity in adults, the question arises to what degree the developmental features reflect past evolutionary processes. This can be tested exclusively by paleontological evidence. For this reason the postnasal wall and adjacent parts of the palatoquadrate were chosen because these structures are well documented on fossils (the postnasal wall is for the most part ossified, and the cartilaginous parts may be reconstructed from the imprints on the inner surface of the exocranial bones). Besides, nerves piercing the wall enable comparison of its homologous parts. Two methodological approaches were used: first, developmental

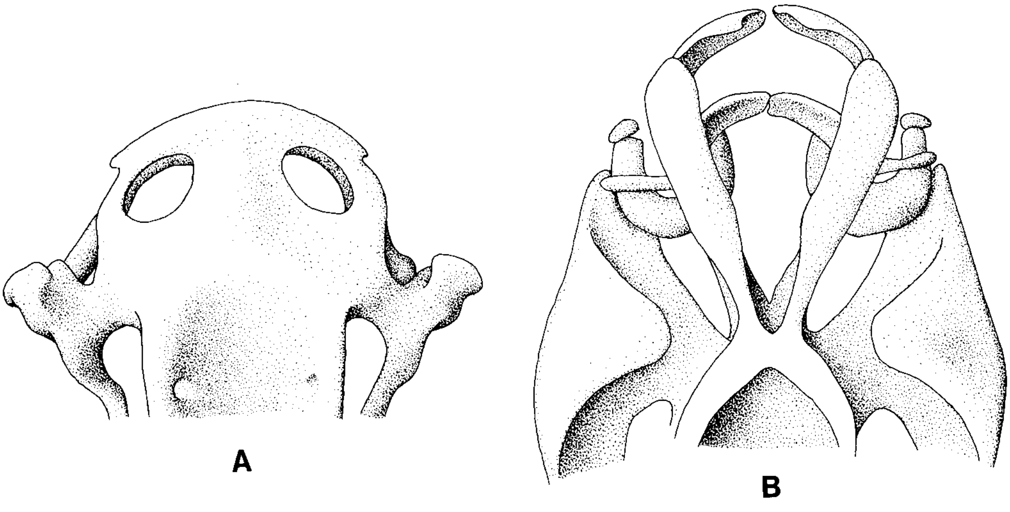


Fig. 2. — Larval ethmoidal endocrania in Pipidae (A) represented by *Pipa carvalhoi* (stage 52) and anurans with cornua trabecularum (B) represented by *Pelobates fuscus* (stage 55-57).

features found in Recent anurans were compared with data on labyrinthodonts, and comparison of adult anurans and adult labyrinthodonts served as the starting point. When homologous features were found, anuran and labyrinthodont larval development were compared, permitting the developmental shift to reconstruct evolutionary sequence.

MATERIAL AND METHODS

The description of development in the Anura is summarized from accounts of various Recent taxa, including those considered archaic (*Ascaphus, Leiopelma, Pelobates, Discoglossus, Pipa*), or sufficiently well investigated (*Rana*).

Except for *Leiopelma*, most data on these genera were gained from sectioned larvae in the Department of Paleontology, Academy of Sciences, Prague. Relevant information on labyrinthodonts was summarized from three-dimensionally preserved representatives of the Dvinosauridae, Melosauridae, Benthosuchidae and Capitosauridae, in the Paleontological Institute of the Russian Academy of Sciences, Moscow. Comparison with osteolepiforms was based on the wax-model of the endocranium of the Devonian fish *Eusthenopteron* from the Swedish Museum of Natural History, Stockholm.

DEVELOPMENT OF THE POSTNASAL WALL IN RECENT ANURA

In early development the nasal capsule including the posterior wall does not appear. In pipids (which have no cornua trabecularum but possess an ethmoid plate), the olfactory nerves lie on the dorsal surface of the plate (pers. observ., KOTTHAUS 1933). Hence, there is no partition between the ethmoid plate and future braincase cavity. This partition arises later, from a distinct mesenchymous and later cartilaginous layer covering the olfactory nerves dorsally (Figs 3A, 4). The walls of the olfactory canals grow downwards from this layer, reaching ultimately the planum praecerebrale. These vertical partitions are called "pilae ethmoidales" by DE BEER (1937).

In early developmental stages of non-pipids (anurans with the cornua trabecularum) the olfactory nerves pass uncovered anteriorwards (see also GAUPP 1893: figs 6-7), similar to pipids. A more developed stage was documented by PLASOTA (1974: figs 17-19) who recorded that *Pelobates* has paired cartilaginous elements bounding the olfactory nerves from above. He termed them C1 and Cp, and correctly distinguished them from the columnae ethmoidales (GAUPP 1893) which are only ventral extensions of these elements (cf. BORN 1876). In the earliest recognizable stages of *Ascaphus* and *Leiopelma*, the partition between the future nasal capsule and the braincase cavity, including the olfactory canals, already exists (pers. observ., VAN EEDEN 1951: fig. 2; STEPHENSON 1951. The latter author speaks about pila ethmoidalis that bounds the olfactory canal from above, but this statement apparently refers to the structure in other anurans). Because in *Ascaphus* and *Leiopelma* stages detailing earlier development are not yet sufficiently chondrified, nothing can be said about the process of formation of their olfactory canals. It should be noted that in both genera these canals are directed laterally so that the future median section of the postnasal wall is paired, and on either side changes its position from one originally confluent with the braincase sidewall, into the secondary, adult transverse position. The above mentioned early larval position probably indicates the primitive state and not a derived condition associated with the downward bending of the trabecular horns, because in those anurans that have trabecular horns the olfactory sacs are located laterally from the telencephalon (e.g. early *Breviceps*; see SWANEPOEL 1970).

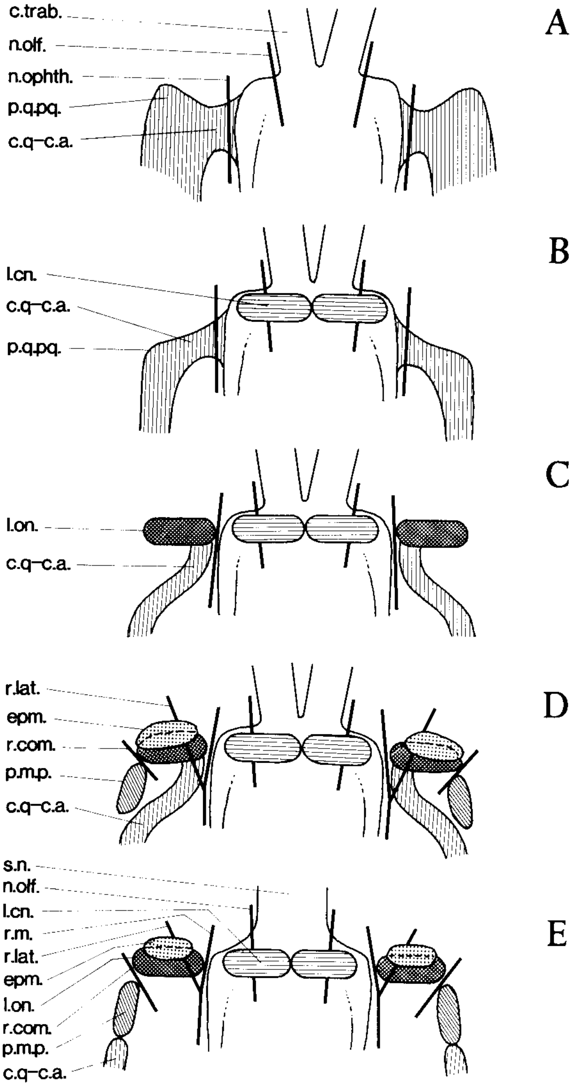


Fig. 3. — Diagrams of the main ontogenetic stages (A to E) representing the development of the anuran postnasal wall. Abbreviations: *c.q-c.a.*, commissura quadratocranialis anterior; *c.trab.*, cornu trabeculae; *epm.*, epipraemandibulare; *l.cn.*, lamina cerebronasalis; *l.on.*, lamina orbitonasalis; *n.olf.*, nervus olfactorius; *n.ophth.*, nervus ophthalmicus; *p.m.p.*, processus maxillaris posterior; *p.q.pq.*, pars quadrata palatoquadrati; *r.com.*, ramus communicans between the r. maxillaris V and r. palatinus VII; *r.lat.*, ramus lateralis narium proprius; *r.m.*, ramus medialis nervi ophthalmici; *s.n.*, septum nasi.

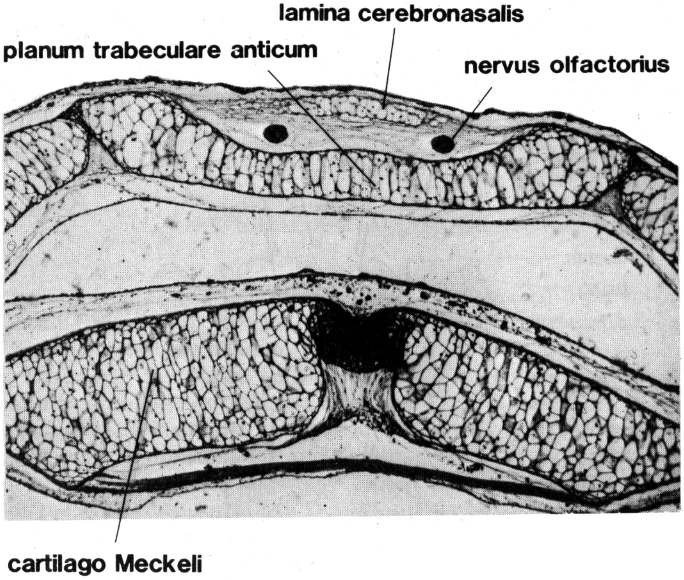


Fig. 4. — *Pelobates fuscus*, NIEUWKOOP & FABER (1967) stage 55-57. Transversal section through the median part of the endocranium, at the level of the future olfactory canals. The lamina cerebronasalis, though already unpaired, does not reach yet the braincase walls.

Despite of rather fragmentary knowledge of *Ascaphus* and *Leiopelma* one can suppose that the median portion of the postnasal wall in anurans arises only partly from the ventral portion that originally forms the anteriormost section of the braincase floor (= the planum trabeculare anticum sensu GAUPP 1893), adjacent to the bases of the cornua trabecularum or the posterior part of the ethmoid plate. Later, a dorsal portion is added, originally paired and later fused, which produces walls of the olfactory canals by the downward growth. This structure may be termed the lamina cerebronasalis, to emphasize its separate origin, similar to the lamina orbitonasalis (see below).

The development of the lateral part of the postnasal wall is more complicated. In the early developmental stages, the commissura quadratocranialis anterior serves exclusively as a functional partition between the future nasal capsule and the orbital area (Fig. 3B). On the dorsal surface of the commissura, the nervus ophthalmicus runs anteriorly. Only later new material is added, anterolaterally to the commissura. This results in enclosing the nerve in a slot and later in a canal between the braincase wall and this new cartilage (see also SWANEPOEL 1970). The latter is generally termed the lamina orbitonasalis (see Table 1 for synonyms), and the passage the canalis orbitonasalis. The commissura quadratocranialis anterior does not contribute to the formation of the canal because in the meantime it detaches from the braincase wall (see also PUSEY 1943), and its anterior end is shifted onto the posterior surface of the lamina orbitonasalis (Fig. 3C; see also REINBACH 1951) or terminates freely (VAN EEDEN 1951: figs 15-16; PLASOTA 1974), or has other relations to the lamina orbitonasalis (VAN SETERS 1922: fig. 8). Consequently,

Table 1.

List of anatomical terms used in the present paper, with their synonyms.

Present paper	Synonyms
Lamina cerebronasalis	"Ethmoidalplatte" (in *Rana*; Gaupp 1893: 313)
	"Präcerebralplatte" (in Anura; Gaupp 1906: 729)
	"bars of cartilage joining the dorsal ends of the preoptic roots of the orbital cartilages and the pilae ethmoidales" (de Beer 1937: 201)
	"sphenoseptal commissure" (de Beer 1937: 201)
	pila ethmoidalis (in *Leiopelma*; Stephenson 1951: 212)
	tectum anterius (in *Xenopus*; Sedra & Michael 1957: 14, figs 3, 7)
	"ethmoidal plate" (in *Rana*; de Jongh 1968: 8, pls VI-VII)
	C1, Cp (in *Pelobates*; Plasota 1974: 113, figs 17-19)
Downward outgrowths of lamina cerebronasalis	columnae ethmoidales (in *Rana*; Gaupp 1893: 313, fig. 12)
	pilae ethmoidales (in *Rana*; de Beer 1937: 201)
	pila praecerebralis (in *Calyptocephalus*; Reinbach 1939: 254-255)
	"lateral tectal processes" (in *Palaeoherpeton*; Panchen 1970: 17)
Planum praecerebrale	"Internasalplatte" (in *Rana*; Stöhr 1882: 85)
	"vordere Trabecularplatte" (in *Rana*; Gaupp 1893: 289)
	septum praecerebrale (Stadtmüller 1936: 550)
	"intertrabecular plate" (in *Rana*; de Beer 1937: 201)
	"ethmoid plate" (in *Rana*; de Beer 1937: 201)
	planum trabeculare anticum (in *Rana*; Plasota 1974: 103, fig. 4)
Lamina orbitonasalis	"Antorbitalfortsatz" (in *Rana*; Gaupp 1893: 415, 430)
	planum antorbitale (in Anura; Gaupp 1906: 729)
	processus antorbitalis (in *Alytes*; Van Seters 1922: 457, 462, fig. 8)
	planum antorbitale (in Amphibia; Stadtmüller 1936: 549)
	processus antorbitalis (in Urodela; Stadtmüller 1936: 549)
	planum antorbitale primarium (in *Calyptocephalus*; Reinbach 1939: 255)
	"larvales Planum antorbitale" (in Anura; Reinbach 1951: 113)
	processus antorbitalis (in *Pipa pipa*; Roček & Veselý 1989: 303, fig. 1B-C)
Lateral section of postnasal wall in adult	pars plana (in *Rana*; Gaupp 1893: 415)
	"postnasal wall" (in *Rana*; Jarvik 1942: 315)
	"definit. Planum antorbitale" (in Anura; Reinbach 1951: 113)
	lamina orbitonasalis (in *Breviceps*; Swanepoel 1970: 86)
Epipraemandibulare	adrostral (in *Pelobates*; Dugès 1835: 86, fig. 71; Born 1876: 599; Schulze 1892: 7)
	"?second pair of suprarostrals" (in *Megophrys montana*; de Beer 937: 213)
	planum triangulare (in adult *Breviceps*; Swanepoel 1970: 49, 108)
	"bulge" (in adult *Ascaphus*; Jurgens 1971: figs 1A, 2A)
	"anterior process on postnasal wall" (in adult *Barbourula, Hypopachus, Hyla*; Jurgens 1971: figs 4A, 5, 10-11, 13-14)
	"x" (in *Pelobates*; Plasota 1974: 113, figs 18-23)

(*continued*)

Table 1 (*continued*)

Present paper	Synonyms
Epipraemandibulare	"processus antorbitaire" (in *Discoglossus*; Kraemer 1974: fig. 10)
	processus antorbitalis (in adult *Pelobates*; Roček 1981: 51)
	processus maxillaris anterior (in adult *Pipa pipa*; Roček & Veselý 989: 303)
Commissura quadrato-cranialis anterior (Gaupp 1893: 292)	"ethmovomerine cartilage" (in *Rana*; Huxley 1858: 423)
	"Pterygopalatfortsatz" (in *Rana*; Stöhr 1882)
	"vordere suspensorio-trabeculare Verbindung" (Stadtmüller 1936: 570)
	"anterior basal process" (in *Ascaphus*; Pusey 1943: 156)
	"antorbital plate" (in *Discoglossus*; Toerien & Rossouw 1977: fig. 1d)
	lamina orbitonasalis (in Amphibia; Toerien & Rossouw 1977: 373)
Ramus communicans between the r. maxillaris V and r. palatinus VII	ramus communicans cum nervo palatino des Nervus maxillaris (in *Rana*; Gaupp 1893: 298; 1899: 137; in *Calyptocephalus*; Reinbach 1939: 268-269)
	r. postchoanalis (in *Breviceps*; Swanepoel 1970: 49, 86)
non	ramus praechoanalis nervi maxillaris (in *Calyptocephalus*; Reinbach 1939: figs 3-4)
non	ramus palatonasalis des Nervus maxillaris (in *Calyptocephalus*; Reinbach 1939: 271)

the course of the canalis orbitonasalis may be used as an indicator of medial extent of the lamina orbitonasalis (Fig. 5, Stadtmüller 1936, de Beer 1937).

The lateral limit of the lamina may be ascertained by the course of the ramus communicans between the ramus maxillaris V and the ramus palatinus VII (Fig. 3D). In the majority of species it is enclosed into a canal which marks the border between the lamina orbitonasalis and the processus maxillaris posterior (e.g. van Eeden 1951).

The ophthalmicus nerve splits into a medial branch (the ramus medialis nervi ophthalmici) directed toward the anterior aperture of the canalis olfactorius, and a lateral one (the ramus lateralis narium proprius) crossing the dorsal surface of the lamina orbitonasalis. This latter nerve is enclosed in a canal by a distinct ovoid or rod-like cartilage (epipraemandibulare sensu Roček 1981) which is closely associated with the posterolateral portion of the cartilago labialis superior in non-pipid anurans. This was reported by Dugès (1835: fig. 71), Born (1876), Schulze (1892), and Nikitin (1986: fig. 1A) who termed it adrostrals, Plasota (1974) who designated it by "x" on his figs 18-23, and Roček (1981) who called it epipraemandibular on his figs 14-15, 18, 22. The "second pair of suprarostrals" of de Beer (1937) are probably homologous. Although not mentioned by other authors, the characteristic morphology of the area in various adult anurans (termed "bulge" or "anterior process on postnasal wall" by Jurgens 1971: figs 1A, 2A, 4A, 5, 10-11, 13-14, and the "processus antorbitaire" by Kraemer 1974: fig. 10) indicates a distinct origin of this part of the postnasal wall and the lamina orbitonasalis. It may be connected to the planum terminale (Jurgens 1971: fig. 7). Swanepoel (1970) suggested that the planum triangulare in an adult develops independently of the medial part of the postnasal wall (= lamina orbitonasalis). It may be assumed, from the comparison

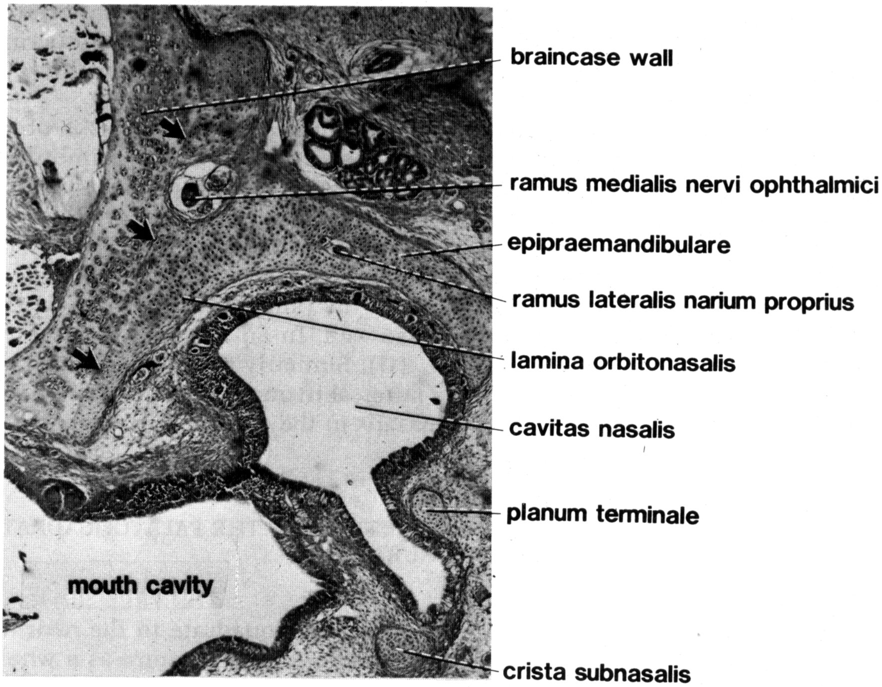


Fig. 5. — *Ascaphus truei*, Nieuwkoop & Faber (1967) stage 64. Transversal section through the right nasal capsule in posterior view, at the level of the posterior orifice of the canalis orbitonasalis. Arrows mark the line of coalescence between the braincase wall and the lamina orbitonasalis. Similar line between the latter structure and the epipraemandibulare is already indistinct.

of the condition in *Breviceps* (Swanepoel 1970) with that in *Pelobates* (Roček 1981: fig. 22) that the early embryonic planum triangulare might be homologous with the epipraemandibular.

On the other hand, in those anurans that have no cornua trabecularum (pipids) there is another structure instead of a free rod-like cartilage adjoining later in development the anterodorsal surface of the orbitonasal lamina and enclosing thus the ramus lateralis narium proprius into a canal. This is, contrary to the condition described above, not pre-existing as a separate element, but adjoins to the orbitonasal lamina as new cartilaginous material, enclosing ultimately the ramus lateralis narium proprius, as in the case above. This results in formation of an anteriorly directed process too, termed (incorrectly) the processus maxillaris anterior by Roček & Veselý (1989: fig. 1D-H). It is, however, homologous with that designated as "bulge" and "anterior process on postnasal wall" by Jurgens.

In summary the lateral part of the postnasal wall in adult anurans has a composite origin. It consists of the lamina orbitonasalis that extends from the canalis orbitonasalis located medially, to the foramen (or level) of the ramus communicans between the ramus maxillaris V and the ramus palatinus VII, laterally. Anterodorsally the postnasal wall is completed by a process given different names by various authors; its limits are marked by the position of the canalis pro ramus lateralis narium proprius (cf. Jurgens 1971). It is clear from this summary that the terms "postnasal wall" and the "lamina orbitonasalis" do not designate the same structures. It also should be emphasized that the commissura quadratocranialis anterior does not contribute to the structure of the adult postnasal wall (cf., however, REINBACH 1951).

As for the processus maxillaris anterior, nothing suggests that it is of separate origin similar to the processus maxillaris posterior, and of the primordium of the process roofing the canal for the ramus lateralis narium proprius (the latter occurring in pipids). Instead its existence is associated with the attachment of some muscles or, as can be explained on the basis of the condition in labyrinthodonts (see below), may be considered a vestige of the lamina nariochoanalis.

It is also worth of note that the course of the ramus medialis may be shifted medially, so it seemingly enters the braincase wall. In *Pipa*, it may even enter the braincase cavity ROČEK & VESELÝ 1989, fig. 1G). Similarly the lateral branch of the ophthalmicus nerve may be shifted. This latter shift may indicate positional and proportional changes of the lamina orbitonasalis in the course of development.

DEVELOPMENT OF THE ANTERIOR CONNECTIONS OF THE PALATOQUADRATE IN RECENT ANURA (Fig. 6)

To understand properly the fixation of the palatoquadrate to the neurocranium it is convenient first to outline the development of this structure as a whole. As the homology of the palatoquadrate proper and of its posterior connections is beyond the scope of this paper, the former will be only mentioned and the latter (= connections with the braincase and otic capsule) avoided.

Rana is conventionally regarded as an anuran that is sufficiently well studied to document developmental processes. However, some developmental stages preceding those considered the earliest ones in *Rana* (GAUPP 1906) are preserved in the ontogeny of *Ascaphus*, so the following account is based mainly on the latter form (cf. also VAN EEDEN 1951) although data from other anurans were included.

In the earliest stages recorded in *Ascaphus* (PUSEY 1943: figs 15, 17, 19; VAN EEDEN 1951: figs 2, 6-7) the palatoquadrate body is attached ventrally to the cranial side-wall along the former trabecula cranii. This attachment extends from the posterior margin of the choana (foris sensu BJERRING 1989: fig. 6) to a position closely in front of the anterior wall of the otic capsule. The nervus ophthalmicus (*seu* profundus) is enclosed in a canal that follows the line of attachment. The canal arose earlier in ontogeny by fusion of the palatoquadrate body with the trabecula. The palatoquadrate has a nearly vertical position in its anterior part, and proceeding backwards it gradually slants sidewards. Its pars quadrata (marking the position of the future jaw joint) is situated closely behind the level of the anteriormost extent of the palatoquadrate. It is possible that KRAEMER (1974: fig. 1) in his stage 27 of *Discoglossus* (characterized by commencing chondrification of the trabeculae) recorded an earlier stage with the palatoquadrate not yet entirely coalesced with the trabecula, and hence still free in its posterior portion. This suggests that the fusion of these two structures in ontogeny proceeds in anteroposterior direction, exactly as in *Ascaphus* (VAN EEDEN 1951; see also GAUPP 1906 and RAMASWAMI 1938; the latter author recorded the palatoquadrate still free posteriorly in large larvae of *Philautus variabilis*). The palatoquadrate may be distinguished from the trabeculae (SWANEPOEL 1970).

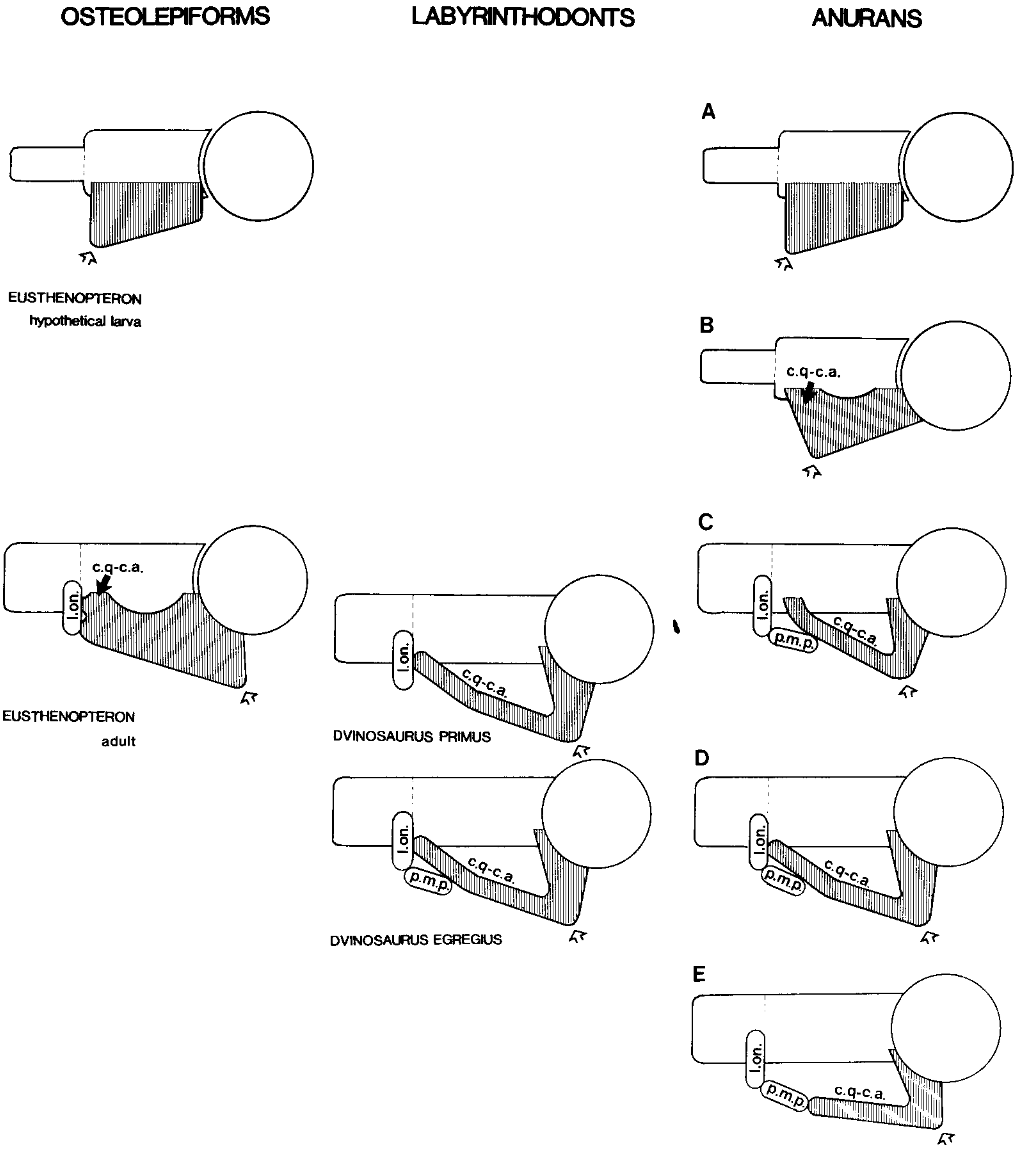


Fig. 6. — Diagrams representing development of the palatoquadrate and its anterior connections in anurans, from early larva (A) till adult (E), compared with labyrinthodonts (earlier developmental stage deduced from the condition in fetalized brachyopoid *Dvinosaurus primus*), and with hypothesized development in osteolepiform fishes exemplified by *Eusthenopteron*. Abbreviations: *c.q-c.a.*, commissura quadratocranialis anterior; *l.on.*, lamina orbitonasalis; *p.m.p.*, processus maxillaris posterior. Palatoquadrate incl. the commissura quadratocranialis anterior hatched. Position of the jaw joint is marked by arrows.

In the course of subsequent development (VAN EEDEN 1951) the palatoquadrate becomes detached from the braincase in its mid-section, by the enchondral destruction starting from the canal for the ophthalmicus nerve. Consequently, the subocular vacuity develops. However, the destruction does not reach the anterior limit of the palatoquadrate. Here the palatoquadrate remains fused with the trabecula. The connection is called the commissura quadratocranialis anterior. This stage is documented by GAUPP (1893), DE JONGH (1968: pl. V), PLASOTA (1974) for *Rana*, KRAEMER (1974: figs 2-3) for *Discoglossus*, VAN SETERS (1922: fig. 1) for *Alytes*, PLASOTA (1974: fig. 20) and ROČEK (1981: figs 14-15) for *Pelobates*.

Later, the palatoquadrate is a subject of two simultaneous processes. First, its originally horizontal subocular bar is relatively shortened and rotated posteroventrally, attaining the ultimately vertical position. Second, this shift of the pars quadrata beneath the otic capsule is accompanied by the increase in length of the originally anterior connection of the palatoquadrate with the braincase walls (ROČEK 1981: figs 22, 24; WASSERSUG & HOFF 1982 and references therein). Consequently, the horizontal subocular bar of adult anurans may be considered homologous with the commissura quadratocranialis anterior (e.g. VAN EEDEN 1951, SWANEPOEL 1970), called the processus pterygoideus palatoquadrati.

At the level where the commissura is curved anteromedially, a strip of mesenchyme arises, directed anteriorly to the most anterolateral corner of the nasal capsule. Although later chondrified, it is distinguishable from the nasal capsule and from the commissura (GAUPP 1893: figs 24-26; VAN EEDEN 1951: figs 15-17; SWANEPOEL 1970). This bar is the processus maxillaris posterior. Only in the course of subsequent development it fuses with the nasal capsule anteriorly, and with the anterior portion of the commissura. Where both structures contact, passes the ramus communicans (termed the ramus postchoanalis by SWANEPOEL 1970) between the ramus maxillaris V and the ramus palatinus VII. Later, when both structures (lamina orbitonasalis and processus maxillaris posterior) coalesce this nerve is enclosed in a foramen or lies in a groove. In post-metamorphic anurans, or in those in advanced stages of metamorphosis, it runs free and only its course indicates the former line of coalescence between the mentioned structures (in *Ascaphus*, VAN EEDEN 1951: figs 15-17), or through a foramen (in *Caudiverbera*, former *Calyptocephalus*, REINBACH 1939: fig. 10; in *Xenopus*, SEDRA & MICHAEL 1957: fig. 27). REINBACH (1939) distinguished two nerves in this area, namely the "ramus communicans cum nervo palatino des Nervus maxillaris", passing through the slot between the commissura quadratocranialis anterior and the processus maxillaris posterior, and what he termed the "ramus praechoanalis nervi maxillaris" or the "ramus palatonasalis des Nervus maxillaris" (see Table 1). Whereas the first nerve runs over the medial surface of the former processus maxillaris posterior in the adult (because the commissura quadratocranialis anterior was destroyed), the second runs through a canal. As the condition in this respect seems to be highly variable (the second nerve may be lacking on one side of a single specimen; REINBACH 1939) it is difficult to determine which branch is homologous with that usually designated as "the ramus communicans" in other anurans.

In *Ascaphus* the proximal part of the commissura is destroyed, so that its connection with the braincase wall is interrupted (VAN EEDEN 1951). This proceeds simultaneously with the appearance of the lamina orbitonasalis. In *Rana* (DE BEER 1937, PLASOTA 1974) and *Discoglossus* the commissura later loses its contact with the braincase wall. This is because first the commissura becomes attached to the already existing postnasal wall forming thus, together with the processus maxillaris posterior, a foramen (DE JONGH 1968: pls XIII-XV; SWANEPOEL 1970; KRAEMER 1974: figs 8-9), and because later this contact with the nasal capsule is interrupted (DE BEER 1937: pl. 75, fig. 3; DE JONGH 1968; SWANEPOEL 1970; KRAEMER 1974). The detachment of the braincase wall and the anterior part of the palatoquadrate is a common feature of anuran development (JURGENS 1971; PLASOTA 1974: fig. 24; however, DE BEER 1937 maintained that the pterygoid process of the palatoquadrate in anurans may fuse with the ethmoid capsule, and REINBACH 1951 considered that the adult postnasal wall included the commissura quadratocranialis anterior). Data from other species suggest that the figure drawn by ROČEK (1981: fig. 22) giving an impression that the commissura is incorporated into the postnasal wall in the adult *Pelobates*, is incorrect. It is probable that the part of the subocular bar which in *Caudiverbera* is medial to the canal for the ramus communicans between the ramus maxillaris V and the ramus palatinus VII is a remnant of the commissura quadratocranialis anterior.

After the destruction of the proximal portion of the commissura, the subocular bar connecting the pars quadrata palatoquadrati with the nasal capsule consists of the residual commissura posteriorly and the processus maxillaris posterior anteriorly. Hence, an original medial connection of the anterior section of the palatoquadrate was functionally substituted by the lateral one, present in adult anurans. Only in *Hymenochirus* (PATERSON 1945: figs 1-2) the adult subocular bar is incomplete, probably due to the lack of fusion of the processus maxillaris posterior with the residual commissura.

THE DEVELOPMENT OF THE POSTNASAL WALL IN LABYRINTHODONTS AND CROSSOPTERYGIANS, AND ITS COMPARISON WITH ANURANS

There is limited evidence how the postnasal wall developed in labyrinthodonts. The most valuable data are those by PANCHEN (1964: fig. 9a-b). In a specimen of *Palaeoherpeton* (Anthracosauria) PANCHEN found signs of the downward growth of the lateral walls of the olfactory canals, from the braincase roof. The specimen, whose downward extensions of the braincase roof at the level of the postnasal wall do not coalesce with the ventral part of the sphenethmoid, recalls the anuran condition described above. It seems that, despite the fact that in some labyrinthodonts there are two additional canals, medial to those for the olfactory nerves (claimed to have transmitted the vomeronasal nerves; PANCHEN 1964: fig. 8; 1970), the origin of the median portion of their postnasal wall is similar to anurans.

The lateral portion of the labyrinthodont postnasal wall is poorly documented because it was not ossified. In *Palaeoherpeton* it can be restored from the impressions on the inner surface of the dermal skull roof and from the course of the ramus medialis nervi ophthalmici whose canal is preserved in part on the lateral surface of the sphenethmoid. The lateralmost extension of the postnasal wall can be restored exclusively from the imprints on the inner surface of the dermal bones. In *Dvinosaurus primus* (Brachyopoidea), considered to be a paedomorphic form, there is an impression of the semilunar convexity which has no connection with the commissura quadratocranialis anterior via the processus maxillaris posterior, as is the case with *Dvinosaurus egregius*. It is supposed by SHISHKIN 1973: figs 47-48, 73) that the processus maxillaris posterior was not developed. This semilunar lateral extension is called by SHISHKIN the "pars postchoanalis". In *Benthosuchus*, there is a horizontal, thin extension of the roof of this postchoanal part that in older individuals even contacts the commissura quadratocranialis anterior in its short extent. This extension occupies the same space as the processus maxillaris posterior but is always continuous with the posterior wall of the postnasal wall. The processus maxillaris anterior, if present in labyrinthodonts (SÄVE-SÖDERBERGH 1936: text-fig. 8), seems to be a vestige of the lamina nariochoanalis.

In adult osteolepiforms, exemplified by *Eusthenopteron* (JARVIK 1942: figs 49-51; 1980) the postnasal wall is large. It is pierced by several foramina, the most conspicuous being the fenestra endonarina posterior (sensu JARVIK 1942, 1980) or the canal for the lateral branch of the profundus nerve (sensu BJERRING 1989: fig. 2B), located in the lower part of the postnasal wall. Two other foramina are important for the comparison with anurans, the orifice of the orbitonasal canal (*seu* profundus canal, *seu* the canal for the ramus ophthalmicus profundus). This canal enters the nasal cavity dorsolateral to the orifice of the olfactory canal. The second is the canal for the ramus lateralis narium proprius (*seu* ramus ophthalmicus lateralis) located almost at the same vertical plane as the former.

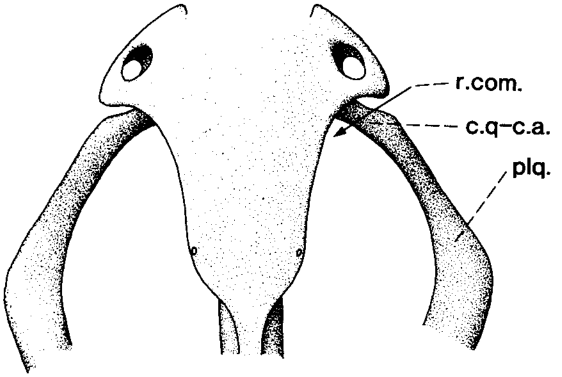
Homology of the dorsal portion of the postnasal wall roofing the olfactory canal in anurans and labyrinthodonts seems to be beyond doubt. A similar supposition may be made in the case of the lateral portion of the postnasal wall, though the development of that area adjacent to the canal for the ramus lateralis is not evidenced by fossils.

On the other hand, comparison between anurans and osteolepiforms is difficult (BJERRING 1989: fig. 2B; JARVIK 1942). The most important is the position of the foramina for the canals transmitting nerves. In *Eusthenopteron* they are almost vertical: explained by the fact that the nervus ophthalmicus splits shortly before entering the postnasal wall. From the larval anuran condition it can be deduced that the portion of the postnasal wall in osteolepiforms (between the olfactory ridge and the canalis orbitonasalis) belongs to the braincase wall.

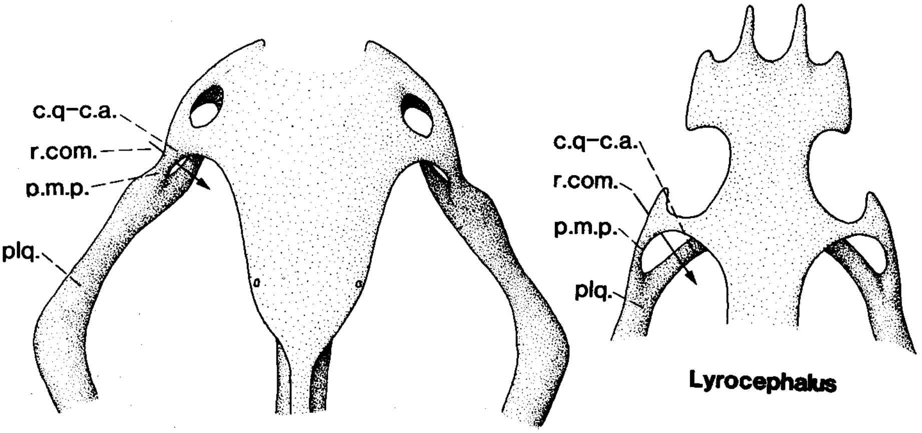
It also follows from comparison with larval anurans that the part of the postnasal wall between the foramina should be considered homologous with the lamina orbitonasalis (see Fig. 6). Noteworthy is the position of the canalis for the ramus lateralis which in *Eusthenopteron* is located close to the dorsolateral border of the postnasal wall, roofed by small but distinct processus supraorbitalis only, whereas in anurans this canal is roofed by more or less massive bulge of cartilage.

To summarize comparison of *Eusthenopteron* to anurans, the posterior wall of the nasal capsule of *Eusthenopteron* comprises more structural elements than anurans. The proportional changes in the skull that occurred during the transition from fishes to amphibians caused the ventral portion of the postnasal wall including the fenestra endonarina posterior to become in anurans part of the floor of the nasal capsule. The position of the canals transmitting the nervus ophthalmicus branches suggests that the substantial part of the postnasal wall in fishes and amphibians could have arisen from the same elements. However, the structure of the wall in *Eusthenopteron* can be regarded specialized to such a degree that the structure of the wall in amphibians could be easier derived from larval osteolepiforms than from adults (cf. JARVIK 1942: figs 65, 67). This is, however, impossible to confirm, as larval osteolepiforms have not been found.

Concerning the anterior palatoquadrate connections, in labyrinthodonts (whose sphenethmoid involved only mid-section of the postnasal wall with the adjacent internasal structures) the only way how to reconstruct these connections is to deduce from impressions on the inner surface of the covering dermal bones. This is why data on the endocranial structures in fossil amphibians are scarce. Despite these limits, SÄVE-SÖDERBERGH (1936: figs 8, 14) found imprints of two connections of the palatoquadrate with the nasal capsule in *Lyrocephalus* (Trematosauridae). He considered them (Fig. 7) homologous with the commissura quadratocranialis anterior (the medial one), and the processus maxillaris posterior (the lateral one). WATSON (1940: fig. 23) interpreted similar imprints in *Branchiosaurus*, and followed SÄVE-SÖDERBERGH's interpretation. A similar condition was found by SHISHKIN (1973: figs 49, 73) in three species of *Dvinosaurus* (Dvinosauridae) (Fig. 7), and called them the commissura quadrato-ethmoidalis medialis and lateralis, respectively.



Dvinosaurus primus



Lyrocephalus

Dvinosaurus egregius

Fig. 7. — Reconstruction of the anterior palatoquadrate connections in some labyrinthodonts. *Dvinosaurus* after SHISHKIN 1973: figs 47 and 49, *Lyrocephalus* based on SÄVE-SÖDERBERGH 1936: text-fig. 8. Abbreviations: *c.q-c.a.*, commissura quadratocranialis anterior (= commissura quadratoethmoidalis medialis sensu SHISHKIN); *plq.*, palatoquadratum; *p.m.p.*, processus maxillaris posterior (= commisura quadratoethmoidalis lateralis sensu SHISHKIN); *r.com.*, ramus communicans between the r. maxillaris V and r. palatinus VII.

It seems that nothing contradicts the SÄVE-SÖDERBERGH's interpretation. Moreover, it is supported by the fact that in paedomorphic forms (such as *Dvinosaurus primus*) the lateral commissure is not closed, resembling the condition in larval anurans before the appearance of the processus maxillaris posterior. In *Benthosuchus* there is only a medial commissure, however, in larger (and presumably older) individuals the lateral, postchoanal part almost contacts the palatoquadrate (both structures are detached only by a narrow slot that was most probably filled with dorsal outgrowth of the palate). Thus the condition in younger and older *Benthosuchus* individuals rather resembles that in *Dvinosaurus primus* and *D. egregius*, respectively. That the medial commissure precedes in ontogeny the lateral is, besides topographic relations, the most important fact favouring the homology of the medial commissure in anurans and labyrinthodonts. Only PUSEY (1943) denied this homology, on the basis of his assumption that the commissura quadratocranialis anterior develops from the posterior basal process. However, in the light of SHISHKIN's findings PUSEY's interpretation of the posterior maxillary process as the anterior maxillary process, seems untenable (see also VAN EEDEN 1951).

If tracing the anterior connections of the palatoquadrate is extended to osteolepiform fishes considered remote anuran ancestors, the information is far more complete because of a higher degree of endocranial ossification. The palatoquadrate in *Eusthenopteron*, the best known osteolepiform, is a single element (JARVIK 1942; 1954: fig. 23B; 1980: fig. 109 and BJERRING 1977: fig. 26) thickened in its anterior (the pars autopalatina) and posterior (the pars pterygoquadrata) portions. Both were connected by a thin layer of bone called the commissural lamina (sensu JARVIK), or the vinculum (sensu BJERRING). The vinculum varied considerably in its extent. This suggests that in younger specimens (JARVIK 1954: fig. 23B; BJERRING 1977: fig. 26) it was completed by cartilage, whereas in adults (JARVIK 1972: fig. 26A; 1980: fig. 109) it was completely ossified. The pars autopalatina was connected to the ethmoidal endocranium by two commissures (JARVIK 1954, 1980), the anteromedial ethmoidal articulation (= rostropalatine articulation in actinopterygians) and the posterolateral ethmoidal articulation (= ethmopalatine articulation in actinopterygians). A third connection of the anterior part of the palatoquadrate complex does not include the pars autopalatina; it is established between the dorsomedial process of the commissural lamina and the crista suspendens of the interorbital wall.

The question now arises which of these connections is homologous with those described in anurans and labyrinthodonts. JARVIK (1942: 521) considered the connection between the commissura quadratocranialis anterior and the endocranial braincase of anuran larvae corresponding to the above first and third connections. VAN EEDEN (1951) maintained that the commissura quadratocranialis anterior in larval anurans must be homologous with the connection between the palatoquadrate and the crista suspendens. He based his assumption on his own statement that "the anuran connections concern only the dorsomedial surface of the processus pterygoideus". JARVIK (1954) suggested that the pars autopalatina is homologous with the subocular bar (= the processus pterygoideus palatoquadrati) of adult anurans, and agreed that the suborbital ledge that is intimately paralleled by the crista suspendens, is a homologue of the trabecula. The homology between the suborbital ledge and the trabecula was confirmed by BJERRING (1977). Hence the fact that in early anuran larvae the commissura quadratocranialis anterior intimately adjoins that part of the braincase wall, which is derived from the trabecula, similarly to osteolepiforms where the homologue of the trabecula (= the suborbital ledge with the crista suspendens) is in direct contact with the anteromedial portion of the palatoquadrate, supports VAN EEDEN's view. Accordingly, the anuran commissura quadratocranialis anterior may be considered homologous neither with the anteromedial (= rostropalatine) nor with the posterolateral (= ethmopalatine) ethmoidal articulations because both join the lamina orbitonasalis arising later in ontogeny. The commissura quadratocranialis anterior joins the orbitonasal lamina only secondarily, after its detachment from the trabecular portion of the braincase wall.

The homology of the processus maxillaris posterior was dealt with above, together with the elements associated with the adult postnasal wall.

If the evolution of the anterior connections of the palatoquadrate should now be hypothesized, early *Ascaphus* (and in lesser extent also *Discoglossus*) with its comparatively robust palatoquadrate adjoining the braincase wall along its entire length, may be considered an embryonic specialization shared presumably also by early developmental stages of osteolepiforms, with unossified endocranial structures. It may be supposed that in both anurans and osteolepiforms this was accompanied by the anterior position of the quadrato-mandibular joint. The known *Eusthenopteron* represents later developmental stages. As seen in Fig. 6, adult *Eusthenopteron* corresponds approximately to that stage of labyrinthodonts represented by paedomorphic forms (*Dvinosaurus primus*). It may be noted that in living anurans this stage cannot be recorded because when the lamina orbitonasalis appears, the commissura quadratocranialis anterior is already detached from the braincase wall, being either attached to the nasal capsule directly or via the processus maxillaris posterior.

It follows from the comparison given on Fig. 6 that both articulations of the palatoquadrate with the nasal capsule in *Eusthenopteron* may be considered a specialization acquired by osteolepiforms but shared by neither labyrinthodonts nor anurans. From the Fig. 6 it is also easy to understand why the postnasal wall and adjacent parts of the palatoquadrate in adult anurans cannot be compared reasonably with both adult labyrinthodonts and adult osteolepiforms, for they are more derived.

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