Ethmoidal endocranial structures in primitive tetrapods: their bearing on the search for anuran ancestry

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Although ethmoidal endocrania of adult anurans display comparative uniformity, at least two structural schemes that cannot be derived one from another were found in tadpoles. The most common scheme, found in a majority of anurans including discoglossids, pelobatids and leiopelmatids (with certain modifications), is characterized by the trabecular horns that give part origin to the nasal structures in adults, and by several free, rod-like elements. In pipids, on the other hand, there is an internasal plate that does not persist in adults, and no free elements. Given that events of phylogenetic importance may be reflected in development, it would be informative to search for the origin of these two patterns of larval ethmoidal development. Therefore, a comparison was made with temnospondyls in which corresponding data were available. Additionally a redescription of the ethmoidal endocranium of *Benthosuchus sushkini* was made, from a natural endocast. Results of this comparison revealed that in labyrinthodont-grade tetrapods the ethmoidal endocranium is basically uniform, even in rather distantly related groups. Similarities may be found between their structural type and larval pipids, however, no structures were found that would recall the trabecular horns.

KEY WORDS:—Ethmoidal endocranium – temnospondyls – anuran larvae – anuran ancestry – evolution.

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INTRODUCTION

The ethmoidal region of the endocranium is among those skeletal components of amphibians that are least affected by adaptations to various modes of life. Consequently, the ethmoidal region of extant species may be a valuable source of
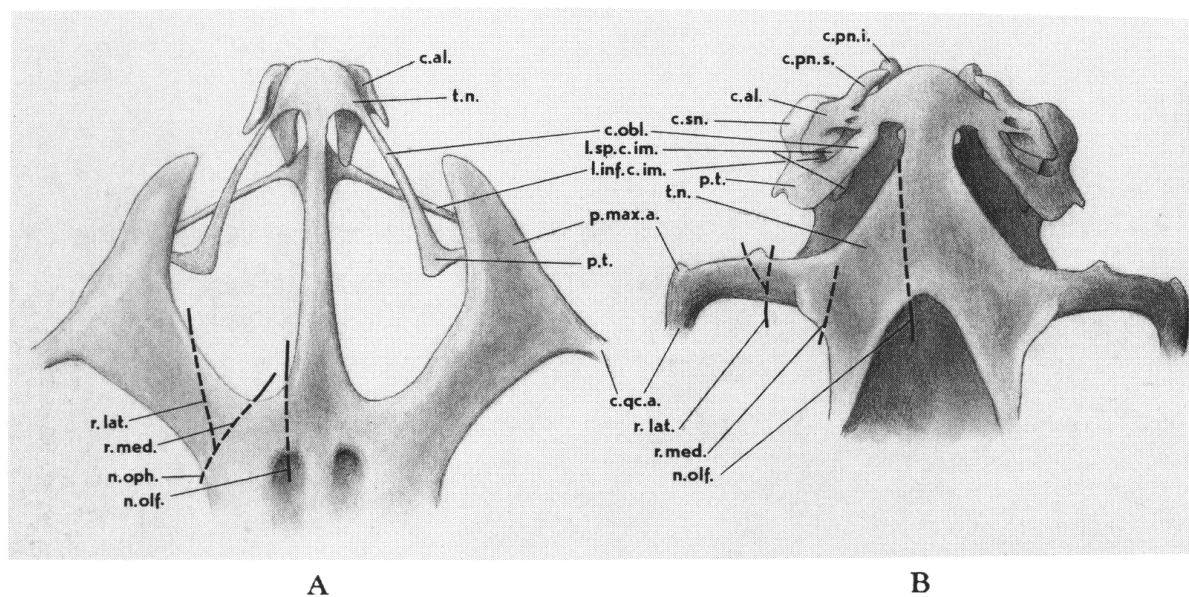
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Figure 1. Ethmoidal endocranial region in adult anurans (dorsal view). A, Pipidae (*Pipa pipa*). B, Anuran with trabecular horns (*Pelobates fuscus*). Based of wax models from the Department of Palaeontology, Charles University, Prague. Abbreviations: c.al.–cart. alaris; c.obl.–cart. obliqua; c.pn.i.–cart. praenasalis inferior; c.pn.s.–cart. praenasalis superior; c.qc.a.–commissura quadrato-cranialis anterior; c.sn.–crista subnasalis; l.inf.c.im.–lamina inferior cristae intermediae; n.olf.–nervus olfactorius; n.oph.–nervus ophthalmicus; p.t.–planum terminale; p.max.a.–processus maxillaris anterior; r.lat–ramus lateralis narium proprius; r.med–ramus medialis nervi ophthalmici; t.n.–tectum nasi.

information for the evaluation of this structure in ancestral forms because basic features may be inherited without major modifications.

The nasal region of the skull of adult anurans displays a basically uniform pattern (Fig. 1; see also Jurgens, 1971). Two nasal capsules are separated from one another by a vertical partition called the septum nasi; its upper and lower margins usually extend laterally to form the tectum and solum nasi, respectively. The postnasal wall separates the nasal capsules from the braincase and orbits. Anteriorly, the septum is usually confluent with the prenasal wall; the cartilago obliqua arises from the dorsal surface of the latter, crossing the nasal sac and terminating posteriorly in the planum terminale.

In the great majority of those anurans in which larval cranial development is known, the adult structural scheme described above arises from two anteriorly directed horns, the cornua trabecularum (Fig. 2B). They take their origin from the anterior part of the braincase floor, and articulate distally with the cart. labiales superiores that serve as larval upper jaws. The adult septum nasi arises from the cornue trabecularum and new material between them (see Roček, 1981: fig. 20); hence, larval structures are partly persistent in adults.

In pipid larvae, however, the situation is different (Fig. 2A; see also Kotthaus, 1933; Sedra & Michael, 1957; Roček & Veselý, 1989). There is only a single horizontal ethmoid plate, the main part of which is termed the planum internasale. The anterior edge of this plate is used as the larval upper jaw because upper labial cartilages are lacking, as are the cornua trabecularum. During the course of metamorphosis the plate disintegrates and disappears completely. Thus, all adult ethmoidal structures, including the septum nasi, arise from new material above the former ethmoid plate (Fig. 3), and no larval
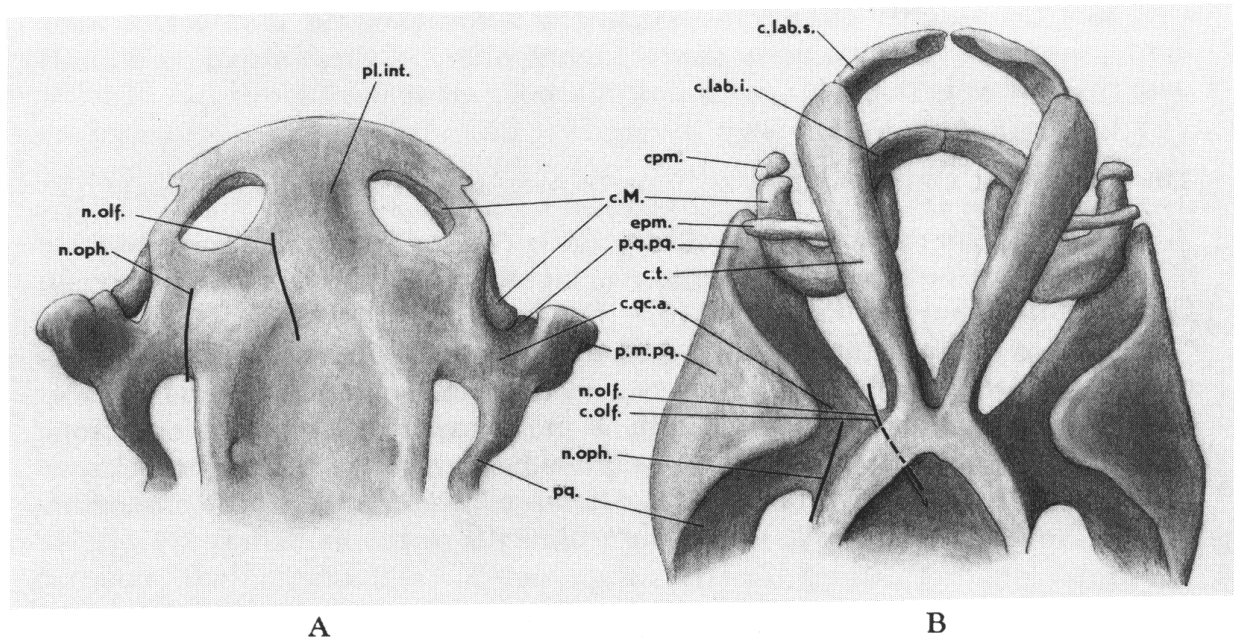
Figure 2. Two patterns of the ethmoidal endocranial region in larval anurans (dorsal view). A, Pipidae (*Pipa carvalhoi*, stage 54). B, Tadpole with trabecular horns (*Pelobates fuscus*, stages 55–57). Based on wax models from the Department of Palaeontology, Charles University, Prague. Stages after Nieuwkoop & Faber (1967). Abbreviations: c.lab.i.–cart. labialis inferior: c.lab.s.–cart. labialis superior (=suprarostrale); c.M.–cart. Meckeli; c.olf.–canalis nervi olfactorii; cpm.–ceratopraemandibulare; c.qc.a.–commissura quadrato-cranialis anterior; c.t.–cornu trabeculae; epm.–epipraemandibulare; n.olf.–nervus olfactorius; n.oph.–nervus ophthalmicus; p.m.pq.–proc. muscularis palatoquadrati; p.q.pq.–pars quadrata palatoquadrati; pl.int.–planum internasale; pq.–palatoquadratum.

structures are involved in the ethmoidal region of the endocranium in adults (Roček, 1989).

Considering these differences the question arises whether it would be possible to trace the origin of the anural larval ethmoidal structures. Given the accepted
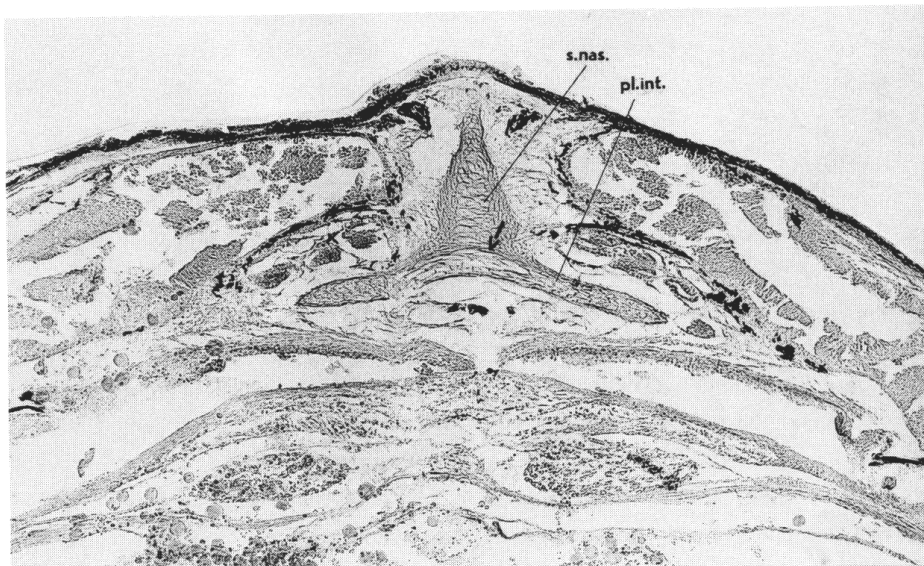

Figure 3. Cross-section through the ethmoidal region of larval *Pipa pipa* (stage 52). Note the septum nasi arising in the midline above the gradually disappearing planum internasale, with the distinct border between them. Abbreviations: pl.int.–planum internasale; s.nas.–septum nasi; the border between the two marked by an arrow.

view that the ancestry of anurans lies among temnospondyls, it would be both appropriate and informative to search for the origin of these disparate anuran patterns of larval ethmoidal development among these fossil forms.

THE ETHMOIDAL ENDOCRANIA IN TEMNOSPONDYLS AND ANTHRACOSAURS: A REVIEW

Compared with crossopterygian fishes, the endocranium of amphibians ossifies incompletely, as a result of progressive blocking of the ossification process. Consequently, substantial parts of the ethmoidal endocranium remain cartilaginous and are not preserved in fossils. The ossified part of the ethmoidal region forms the sphenethmoid; however, it represents only a minor part of the ethmoidal endocranium. The cartilaginous parts can be reconstructed only from imprints on the inner surface of the exocranial bones if these are present. Because such reconstructions have rarely been attempted, knowledge of the ethmoidal endocrania in temnospondyls and anthracosaurs is rather limited.

Temnospondyls

The interpretation of the ethmoidal region in *Edops* and *Eryops* seems to be ambiguous. In *Edops* (Fig. 4B; Romer & Witter, 1942: figs 2, 3, 8, 11), the sphenethmoid is diamond-shaped, and is pierced by two large divergent olfactory canals that open into receding grooves on the lateral surface of the bone, and by two short extra-braincase canals at its broadest portion. These lateral canals are presumed to transmit the ophthalmicus nerve. The
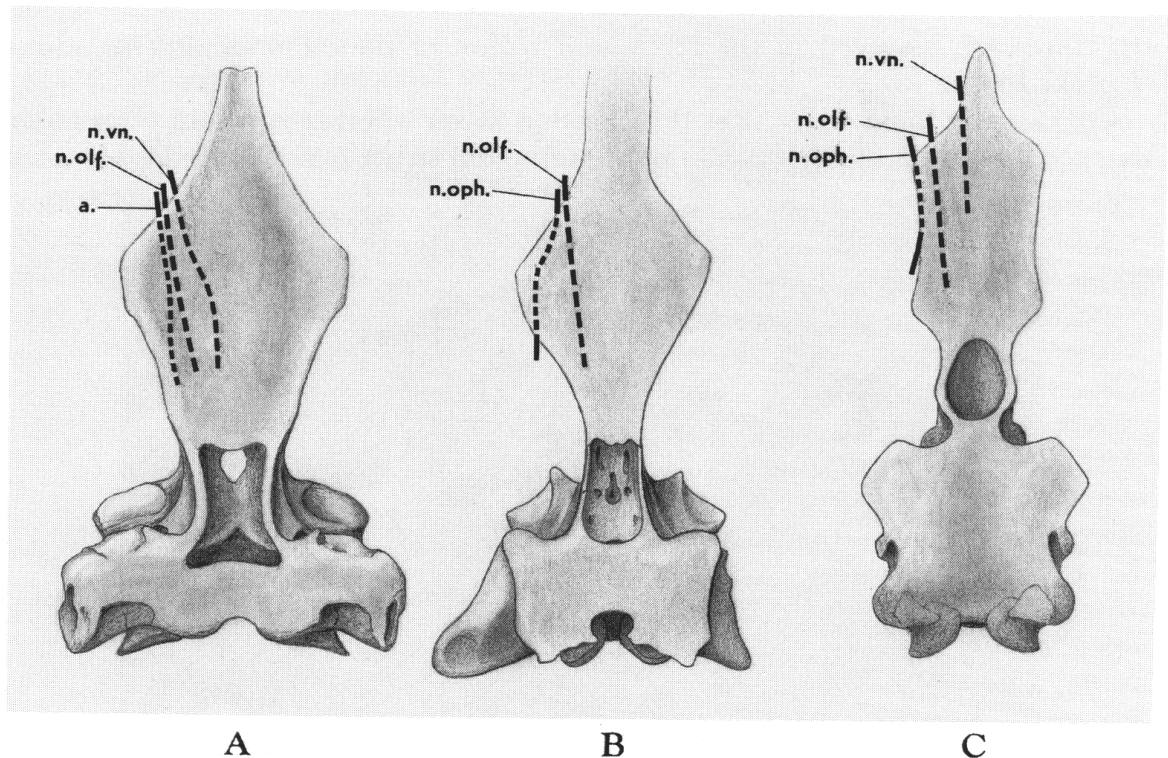

Figure 4. Restoration of braincase including the sphenethmoid in some labyrinthodonts (dorsal view). A, *Eryops megacephalus* (after Sawin, 1941: pl. 7). *Edops craigi* (based on Romer & Witter, 1942: figs 8, 9, 11). C, *Palaeoherpeton decorum* (based on Panchen, 1970: fig. 2). Abbreviations: a.–? blood vessel; n.olf.–nervus olfactorius; n.oph.–nervus ophthalmicus; n.vn–nervus vomeronasalis.

sphenethmoid in *Eryops* (Fig. 4A; Dempster, 1935: 177–178, figs 4, 5; Sawin, 1941: 432, fig. 5J–N, pls 2, 3, 7, 8) is similar in shape. According to Broom (1913: 587–588, fig. 16) and Dempster (1935: 178) it has two pairs of canals connecting the braincase and the nasal cavities. However, Sawin (1941: 432, fig. 5J, pl. 7B) maintained that *Eryops* had three, rather than two pairs of canals, and that all originate in the braincase. The most medial canal is supposed to have conducted the vomeronasal nerve (Dempster, 1935: 178) and if Sawin's above-mentioned statement is correct, the lateralmost canal would have transmitted a blood vessel (Sawin, 1941: 432, fig. 5J).

If only the isolated braincase is considered, then the morphology of the sphenethmoid in *Edops* could well correspond to that in anurans, and could be interpreted accordingly. This means that the anterior narrow part could be homologized with the septum nasi, and the lateral wings with ossified parts of the postnasal wall. Such an interpretation was proposed by Romer & Witter (1942: 941): "The brain case was obviously continued anteriorly and laterally in cartilage, the continuations of the curving lateral margins forming a planum antorbitale". Furthermore, the course of the n. olfactorius is similar to that in anurans, though in temnospondyls these canals are comparatively longer, due to the tropibasic configuration of the skull. In addition, the course of the ophthalmicus nerve in *Edops* would fit well into the variation range of anurans. However, the situation in *Eryops* is not quite clear. If the interpretation of Sawin is correct, then this form differs from anurans in having a separate canal for the vomeronasal nerve, and the lateral canal running from the braincase. The course of the latter is the reason why it cannot be considered as the canal for the ophthalmicus nerve; in anurans, this nerve only exceptionally enters the braincase cavity (e.g. temporarily during the development of *Pipa*). In any case, if this interpretation were accepted, it would be necessary to suppose that the position of the postnasal wall was immediately anterior to the orbit.

On the other hand, if a reconstruction of the skull as a whole is considered, then it should be stressed that the palatine/vomer contact in temnospondyls indicates the position of the anterior part of the palatoquadrate. The choana both in *Edops* and *Eryops* is situated immediately anterior to this area. These two observations suggest that the postnasal wall was situated here and not immediately anterior to the orbits (Shishkin, personal communication). If this interpretation is correct, then the lateral extensions of the sphenethmoid are of unknown function. The decisive observation that could confirm this interpretation would be the presence of a periosteal bone on the lateral surface of these extensions. It is difficult to decide, on the basis of published information, which of the two interpretations is correct.

In the Branchiosauridae which are supposed to be paedomorphic Dissorophoidea, the only information available concerns the relation between the most lateral part of the postnasal wall and the palatoquadrate (Boy, 1978: fig. 8a–c, personal communication). In the late larval stages the palatoquadrate does not reach the palatine, and runs medially to it in the groove on the dorsal surface of the pterygoid. Between this groove on the pterygoid and the narrow postchoanal depression on the dorsal surface of the palatine there is a well-defined dorsal ridge bordering the posterior margin of the latter bone. In still older larvae this ridge is more pronounced. In the course of metamorphosis, or shortly after its completion, this partition reached the margin of the orbit in the

area of the jugal/lacrimal suture. This condition is interpreted by Boy as evidence for the lack of contact between the palatoquadrate and the postnasal wall. However, if the postchoanal depression on the palatine held the most lateral of the postnasal wall or (possibly) the lateral ethmoidal commissure, then the dorsal ridge would be homologous with the similar structure described by Shishkin (1973: 57, 114, figs 30, 73a, b) as the crista ethmoidalis in *Dvinosaurus* and some other brachyopoids, and the groove on the pterygoid would have held the medial ethmoidal commissure (i.e. the commissura quadrato-cranialis anterior) connecting the palatoquadrate and the medial part of the postnasal wall.

In the Doleserpetontidae and Trematopsidae (Bolt, 1974a: 436, 454, 456, text-fig. 1; 1974b: 20) the area of contact between the palatoquadrate and the nasal capsule is similar to that described above. The ridge on the dorsal surface of the palatine (termed "laterally exposed portion of the palatine", or LEP by Bolt) could probably have served as a partition between the most lateral part of the postnasal wall and the medial commissure.

In the trematopsid specimen referred provisionally by Bolt to *Acheloma* sp., some data on the ethmoidal region were given that deserve attention (Bolt, 1974b: 19–21, fig. 3). Of particular note is the presence of the ventral ridge on the nasal and prefrontal, termed the nasal flange. Bolt (1974b: 21) suggested that the nasal capsules might have been confined only to the area lateral to the flanges.

In *Benthosuchus* (Bystrow & Efremov, 1940: 33–34, 49–50, figs 20, 21, 32, 33), an attempt was made to reconstruct the whole ethmoid region. Here, as in most temnospondyls in which the sphenethmoid is known, the latter extends over the posterior moiety of the orbitotemporal region. Hence, it seems to bear no direct relation to the nasal region. The reconstruction of the ethmoid region given by Bystrow & Efremov depicts the presence of a well-defined though low longitudinal ridge on the dorsal surface of the ethmoidal endocranium. However, neither the specimen from the Paleontological Institute of the USSR Academy of Science, Moscow, PIN 9/2243/3 nor other material that I investigated (Bystrow & Efremov, 1940: 7) bear anything that would permit such a reconstruction. It may also be noted that the location of the fenestra endonarina is not reconstructed correctly by Bystrow & Efremov; in fact it is located more anteriorly (see Fig. 6).

Specimen PIN 9/2243/3 (Figs 5, 6) consists of two parts. The ventral part comprises the tooth-bearing regions of the premaxillaries and the anterior section of the maxillaries, together with that part of the palate which is immediately in front of the fenestra endochoanalis. The dorsal part is a fragment of the natural cast that represents the ethmoidal endocranium including the posterior parts of both fenestrae endonarinae and reaching up to the anterior part of the right fenestra endochoanalis.

From the general shape of this cast, from its relations to the dermal bones, and from some other preserved features, the following facts may be inferred. The ethmoidal endocranium was considerably compressed dorso-ventrally. Its dorsal surface between both fenestrae endonarinae was flat, bearing only very low, indistinct, antero-posteriorly oriented ridges. The course of some of them is asymmetrical. They could be considered to be casts of grooves on the inner surface of the skull roof bones that originally transmitted blood vessels, or
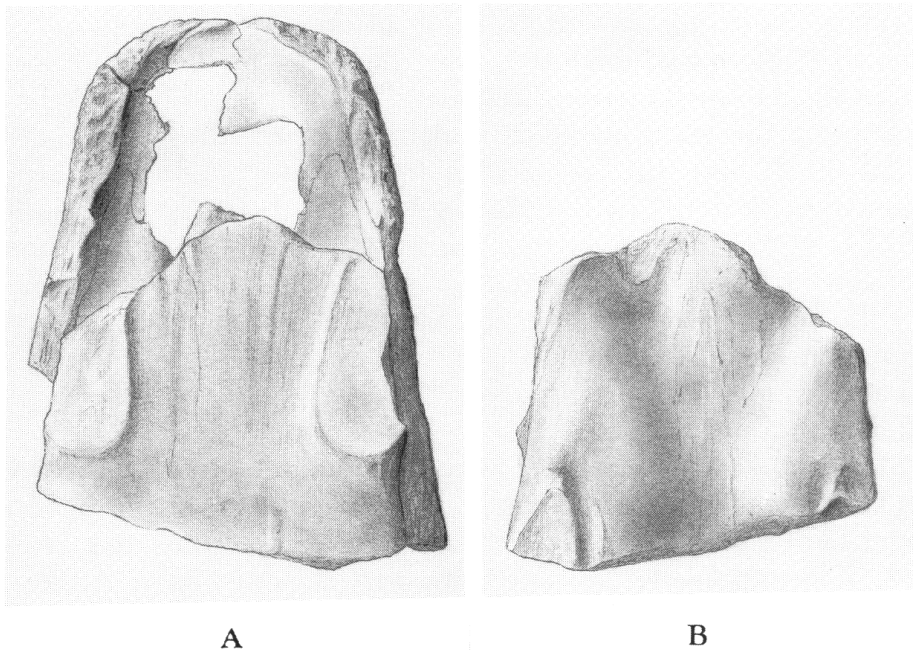
A   **B**

Figure 5. *Benthosuchus sushkini* (PIN 9/2243/3). A, Endocast of the part of the ethmoidal endocranium in dorsal view, together with its relations to the premaxillary and maxillary. B, Ventral view of the endocast. For explanation see Fig. 6.
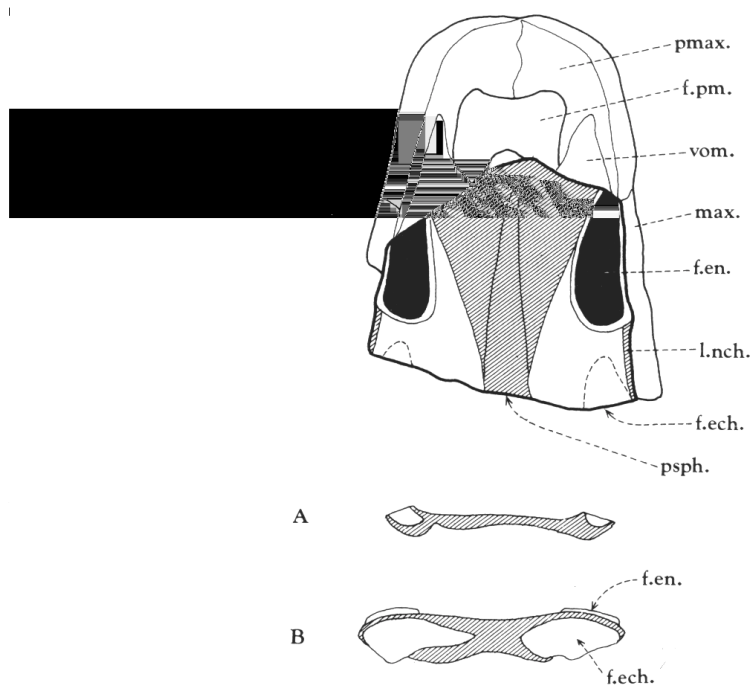
Figure 6. Partial reconstruction of the ethmoidal endocranium in *Benthosuchus sushkini*, in dorsal view. That part of the endocranium which separated both nasal capsules is hatched. Fenestrae endochoanales (on the ventral surface of the endocranium) are indicated by broken lines. A, B, Views of the crack surfaces (A shown as if in posterior view, in order to permit comparison between the two sections). Abbreviations; f.ech.–fenestra endochoanalis; f.en.–fenestra endonarina; f.pm.–fenestra praemaxillaris; l.nch.–lamina nariochoanalis; max.–maxilla; psph.–parasphenoid; p.max–praemaxilla; vom.–vomer.

possibly ridges indicating growth direction of these dermal bones. The ventral surface of this internarial region is also flat and further posteriorly rather depressed in the antero-posterior direction. This depression housed the anterior-most section of the parasphenoid, which occupied the space between the endocranial floor and the vomers. The medial margin of the fenestrae endochoanales is bordered by a distinct groove on the cast, which indicates the presence of a rounded ridge on the corresponding area of the vomers (torus parachoanalis *sensu* Bystrow & Efremov, 1940, fig. 17). The anterior extent of the fenestra endochoanalis almost reaches the level of the posterior limit of the fenestrae endonarinae. The lateral partition between both fenestrae is rather wide and according to its definition (Jarvik, 1942: 312; see also below) it may be termed the lamina nariochoanalis.

The anterior and posterior parts of the endocranial cast are broken to give rough transverse sections. The matrix on the surface of the cracks bears a pattern of dark and light colours. The dark colour on the posterior crack forms an "I" pattern. If it is supposed that this dark matrix indicates a space originally occupied by cartilage, then at the level of the choanae, the ethmoidal endocranium would contain two nasal capsules separated by a relatively thick septum and filled with a white matrix. It even seems that the roof of the capsules extended laterally up to the maxillary; consequently, the fenestra endochoanalis might have been surrounded by endocranial cartilage that took part also in the formation of its lateral margins. The anterior crack between both fenestrae endonarinae, on the other hand, displays almost exclusively dark matrix, and this part is even thinner in comparison with that in the interchoanal area. Only the lateral-most parts in the region of the fenestrae endonarinae are thickened and filled with matrix of light colour. This all indicates that in the region of the anterior part of the ethmoidal endocranium there was only a comparatively thin horizontal plate. Posteriorly, the connection between the fenestra endonarina and fenestra endochoanalis becomes more spacious, forming a simply-shaped capsule. The latter was separated from the corresponding hollow of the opposite side by a thick median partition. The shape and extent of the hollow connecting the fenestra endonarina and fenestra endochoanalis may be traced on the ventral surface of the endocranial cast as a distinct mound.

Imprints on the inner surface of the exocranial bones in the brachyopoids *Dvinosaurus, Tupilakosaurus* and *Batrachosuchoides* (Shishkin, 1973: 34, 57, 113–114, 116, figs 47–50) allowed reconstruction of cartilaginous ethmoidal structures with comparative accuracy. Dorsal and ventral surfaces of these structures are very similar to one another, though not identical. The main features of the ethmoidal regions of these temnospondyls are as follows (Fig. 7A): they are flat, rather short and broad; the fenestra endonarina is approximately coplanar with the fenestra endochoanalis; the dorsal surface of the ethmoidal endocranium is conspicuously large and flat; the nasal area was (probably—Shishkin, personal communication) completed by the lamina nariochoanalis; the pars postchoanalis (at least in *Dvinosaurus*) is composed of both roof and floor, the lateral diverticulum of the nasal sac being housed between them; the pars postchoanalis is parallel to the anterior section of the medial ethmoidal commissure (i.e. the commisura quadrato-cranialis anterior), enclosing a nerve between them both and fusing to various degrees with one another (the latter stage was found in old individuals of *Dvinosaurus egregius*). The nerve was originally interpreted by
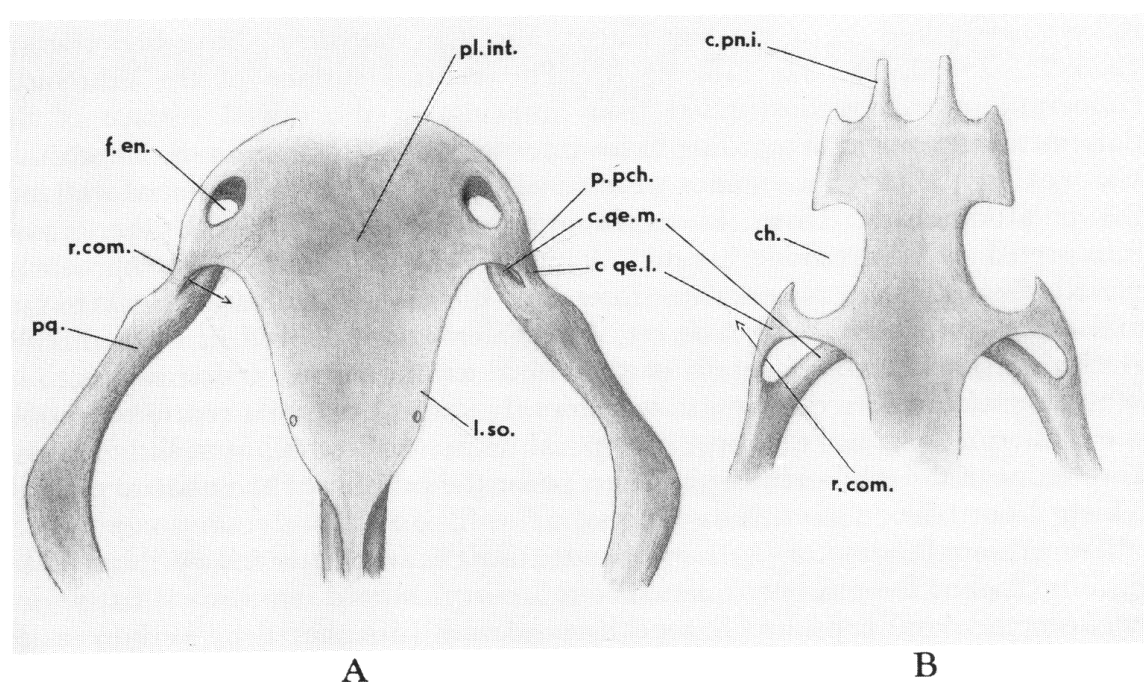
Figure 7. Reconstructions of the ethmoidal endocrania in some labyrinthodonts (dorsal aspect). A, *Dvinosaurus egregius* (after Shishkin, 1973: fig. 49). B, *Lyrocephaliscus euri* (based on Säve-Söderbergh, 1936: text-fig. 8). Abbreviations: c.pn.i.–supposed cart. praenasalis inferior; c.qe.l.–commissura quadratoethmoidalis lateralis (=proc. maxillaris posterior); c.qe.m.–commissura quadratoethmoidalis medialis (=commissura quadrato-cranialis anterior); ch.–space for choana; f.en.–fenestra endonarina; l.nch.–lamina nariochoanalis; l.so.–lamina supraorbitalis; pl.int.–planum internasale; p.pch.–pars postchoanalis; pq.–palatoquadrate; r.com.–canalis for the ramus communicans between the r. maxillaris V and the r. palatinus VII.

Shishkin (1973) as the postchoanal anastomosis between the V and VII cranial nerves, but later reinterpreted as that part of the maxillary nerve that followed the medial margin of the choana. The course of this nerve should be correctly depicted as passing underneath the pars postchoanalis but above the medial ethmoidal commissure (Shishkin, personal communication; cf. Shishkin, 1973: figs 47, 49).

The brachyopoids were paedomorphic. Their adults demonstrate some features typical for larval stages of other temnospondyls (Bystrow, 1938: 276–278, 282–285, 290; 1939: 126, 140; Shishkin, 1973: 146). On the basis of their structure one can even reconstruct the development of at least some parts of their ethmoidal endocrania. This is extremely useful because direct evidence detailing the development of the endocranium in these temnospondyls is lacking. On the basis of brachyopoid morphology, two processes of ethmoidal development can be followed. First, in the course of phylogeny the fenestra endonarina is shifted anteriorly and rather medially, thus the distance between the naris externa and the choana increases (Shishkin, 1973: 162). Second, as observed in *Dvinosaurus*, the pars postchoanalis joins the anterior portion of the palatoquadrate (called by Shishkin the medial quadrato-ethmoidal commissure) laterally, fusing with it later. As a result of this latter process, the above discussed nerve, which originally passed through a slot between the two structures, ultimately runs through a canal (Shishkin, 1973: 177–178, fig. 73).

Some data on the sphenethmoid and the ethmoidal region, though incomplete, are available for the trematosaurids *Lyrocephaliscus* (Fig. 7B),

Aphaneramma, and to a certain extent also for *Platystega* (Säve-Söderbergh, 1936: 23, 25–30, 53, 92, 115, fig. 8). The ventral surface of the ethmoidal endocranium was reconstructed from imprints of the dorsal surface of the palatines and vomers. According to his interpretation, the lamina nariochoanalis was lacking and two connections were developed between the postnasal wall and the palatoquadrate. However, according to Shishkin (1973: 58) the groove interpreted by Säve-Söderbergh (1936: fig. 4B) as housing the processus maxillaris posterior was better interpreted as the sulcus nasolacrimalis. Whether prenasal cartilages were present, as Säve-Söderbergh believed, is questionable. Nothing is known about details of the dorsal arrangement of that region. The sphenethmoid in *Lyrocephaliscus* is satisfactorily known, but as it represented only the posterior part of the orbitotemporal region it contributes little to our knowledge of the ethmoidal region, except for the position of the olfactory canals which is not relevant to this discussion.

The ethmoid region of *Buettneria* was tentatively reconstructed (Wilson, 1941: fig. 10). Again, the most conspicuous feature in this fossil is a broad, flat region between the nasal capsules. The orbitonasal wall (designated by Wilson as the commissura quadrato-cranialis anterior) continues laterally as two bridges supporting the postero-lateral margin of the choana and forming a foramen between them as in some brachyopoids (Shishkin, 1973: fig. 73b) and trematosaurids (Säve-Söderbergh, 1936: figs 8, 14). The foramen is indicated in the above forms by a processus dorsalis on the dorsal surface of the palatinum. The lateral bridge is termed the processus maxillaris posterior (as in Säve-Söderbergh's identification of the homologous structures in *Lyrocephaliscus*). The choana is supported laterally by a process (also as in *Lyrocephaliscus*; see Säve-Söderbergh, 1936) termed the processus maxillaris anterior. The antero-lateral margin of the nasal capsules was missing. The anterior part of this region was dubiously reconstructed particularly the structures identified as the cart. alaris and obliqua, respectively (Wilson, 1941: 95).

Anthracosaurs

No attempt has been made to restore the ethmoidal endocranium in anthracosaurs; however, the sphenethmoid is sufficiently known in *Palaeoherpeton* (Fig. 4C; Panchen, 1964: 615–616, figs 6–8, 9a, b; 1970: 17, fig. 2). Its lateral wings attain their maximum width at the level of the front of the orbits. If figs 3, 11 and 13 of Panchen's (1964) paper are set together then, contrary to *Edops* and *Eryops* discussed above, the postnasal wall *might* form a continuation of the antero-lateral extensions of the sphenethmoid, situated in front of the orbits and at the same time closely approaching the palatine/vomer suture. There was a pair of canals presumed to transmit the nn. vomeronasales, as in *Eryops*.

The sphenethmoid is known not only in the above-described forms, but also in many other temnospondyls and anthracosaurs. However, as this part mostly represents an ossification extending over the posterior moiety of the orbitotemporal region only, having presumably no direct relation to the ethmoidal region, the information which they can provide does not contribute much to reconstruction of this part of the endocranium.

COMPARISON OF ANURAN, TEMNOSPONDYL AND ANTHRACOSAUR ETHMOIDAL ENDOCRANIA

If the three structural types of the ethmoidal endocrania in anurans (one adult and two larval) mentioned in the introductory part are compared with the data on corresponding structures in temnospondyls and anthracosaurs, the following results may be obtained.

The nasal region of the skull in *Benthosuchus*, *Dvinosaurus* and *Lyrocephaliscus* is notably depressed. In *Dvinosaurus*, ventral and dorsal imprints of the ethmoidal endocranium on the inner surface of the dermal bones correspond approximately to one another (disregarding the lamina supraorbitalis which belongs to the orbitotemporal region). *Benthosuchus*, to judge by its endocranial cast, had the same morphology. Hence, it can be supposed that the ethmoidal endocranium in these temnospondyls was plate-like. Nothing that is known about temnospondyl endocrania would suggest that they possessed a structure homologous with the cornua trabecularum. Similar general morphology of the nasal endocranium is observed in larval pipids in which the basic structure is called the ethmoid plate.

The sphenethmoid of those labyrinthodonts in which it represents part of the postnasal wall might provide a useful basis for comparison. However, as was shown in the previous section, whereas the isolated sphenethmoid in primitive temnospondyls can be interpreted in terms of anuran morphology, its topographic relations to exocranial elements cause some doubts about such an interpretation. Nevertheless, if the former view, originally expressed by Romer & Witter (1942: 941) is taken into account, then the comparison between *Edops* and both larval and adult anurans does not raise significant problems. The same holds for *Palaeoherpeton*. In all forms, as well as the medial pair of olfactory canals there is also a lateral pair for the r. medialis n. ophthalmici. In the older larvae of *Pipa* (in early larvae there is only a single nerve: see Fig. 2) this branch of the n. ophthalmicus arises by bifurcation of the n. ophthalmicus into the ramus medialis and the ramus lateralis narium proprius. The point of splitting is always within the anterolateral wall of the braincase, and the r. medialis either (in subadult individuals) enters the braincase activity, later piercing the postnasal wall laterally to the n. olfactorius, or proceeds anteromedially. In both cases it enters the nasal capsule in the vicinity of the anterior orifice of the canalis olfactorius, and sometimes even joins the anterior section of this canal, as in *Edops*.

Contrary to the condition in *Pipa*, in adult ranids, pelobatids and other anurans the n. ophthalmicus does not pierce the braincase wall, and both branches enter the postnasal wall separately from the orbit. Thus, the condition in *Edops* recalls the subadult stages in pipids, but differs in this respect from that in both larvae and adults of anurans with the trabecular horns (cf. Roček, 1981, fig. 18; 1982, fig. 3).

In *Eryops*, a similar interpretation is precluded by the possible (see previous section) presence of the third, most lateral canal connecting the braincase with the nasal cavity, and by the presence of an additional medial pair of canals believed to transmit the vomeronasal nerves.

It is worthy of note that in the specimen of *Palaeoherpeton* described by Panchen (1964: 615, fig. 9a, b) the walls of canals do not yet seem to be entirely fused with the ventral part of the sphenethmoid. A similar feature may be found in pipids

(Kotthaus, 1933: 544, 564). In early stages of their development the olfactory nerves extend uncovered on the dorsal surface of the larval postnasal wall (Fig. 2A). Only later do they become covered by the horizontal cartilaginous plate from which the partitions between the two nerves, as well as lateral wall of the canals, are formed. These partitions continue to grow down to meet the braincase floor at its lateral limit. Of course, this process can be observed in early developmental stages when all structures are still cartilaginous; in *Palaeoherpeton*, on the other hand, the corresponding structures are ossified, but the similarity between the two processes is noteworthy. In most other anurans similar processes were not followed. Only early stages of *Pelobates* Plasota, 1974: 113, figs 17, 18, 19) and possibly *Rana* (Gaupp, 1893), in which separate cartilaginous elements cover the olfactory nerves from above, could be compared with the condition in *Palaeoherpeton*.

Dvinosaurus, although providing much information in other respects, cannot provide any concerning the sphenethmoid. The complete absence of this ossification in *Dvinosaurus* is considered one of the neotenic features of this genus (Bystrow, 1938: 228).

The remarkable shift of the naris externa from the original position approximately coplanar with the choana towards the tip of the snout found in brachyopoids (inferred from the developmental series of *Dvinosaurus* described by Shishkin, 1973: 162) is one of the few developmental processes documented in fossils. If the development of the pipid head is followed it can be found that in early larvae (for instance in *Pipa pipa* at the stages 40–45-staging after Nieuwkoop & Faber, 1967) the external naris is just above the choana and the nasal sac is formed by a simple broadened vertical canal connecting them. Only later does the sac become more complex in structure, and the naris externa move anteriorly ultimately reaching the level of the anterior end of the cart. alaris which arises comparatively late in development. This displacement is reminiscent of the process described by Shishkin (1973: 162) in brachyopoids. Similar positional shift may be observed in anurans with trabecular horns as well, however, their larval ethmoidal skeleton is different.

The size of the lamina nariochoanalis is probably related to the developmental process discussed above. As the distance between the lateral margins of the naris externa and choana is very short in larvae and young individuals (also in adults of brachyopoids such as *Dvinosaurus* which is no doubt paedomorphic with respect to other labyrinthodonts; see Shishkin, 1973: 146), the wall separating both apertures is very narrow or even lacking, and broadens during the subsequent development of the individual. The question now arises, what is the nature of the lamina nariochoanalis in anurans? Jarvik (1942: 312), who introduced this term, designated by it that part of the lateral wall of the nasal capsule in adult *Rana* which is represented by a narrow bridge between the planum terminale and the paries nasi. However, it is not always easy to distinguish it from the lamina inferior cristae intermediae. Consequently the use of the term lamina nariochoanalis in adult anurans seems to be rather artificial.

In tadpoles with trabecular horns there is no lateral wall of the nasal capsule. In pipids, however, there is an endocranial partition between the fenestra endochoanalis and the fen. endonarina, called the ligamentum cornu quadratum mediale *sensu* Sedra & Michael (1957: 14, fig. 5) or the quadrato-ethmoidal process *sensu* De Beer (1937: pl. 74, fig. 5). Its homology with the proc. quadrato-

ethmoidalis and lig. quadrato-ethmoidale in *Rana* (see Jarvik, 1942: 319) is, however, doubtful. In *Pipa carvolhoi* the lateral partition between both fenestrae is still present in comparatively late stages and consists of cartilage, while in *P. pipa* it is formed by a ligament which disappears in early stages of development. In *Xenopus* it persists until metamorphosis, when the entire ethmoid plate disintegrates completely. Thus it seems that neither adult anurans nor tadpoles characterized by the cornua trabecularum possess a homologue of the lamina nariochoanalis. Such a homologue is, however, present temporarily in pipid larvae.

Finally, the comparison of the development of structures laterally adjoining the postnasal wall in temnospondyls and anurans deserves some attention. Data on the former group may be taken from Shishkin (1973: 177–178, fig. 73). The palatoquadrate in *Dvinosaurus primus*, considered as representing the earliest developmental stage available, is connected with the postnasal wall by the single commissura called by Shishkin the commissura quadrato-ethmoidalis medialis. That part of the nasal capsule which contains the fenestra endochoanalis is separated from the commissura quadrato-ethmoidalis medialis by a slot which is represented on the inner surface of the dermal bones by a ridge called the crista ethmoidalis. Hence, that part of the nasal capsule which is posterior to the fenestra endochoanalis is free. A nerve originally interpreted by Shishkin as the postchoanal anastomosis between V and VII nerves, and later reinterpreted by him as part of the maxillary nerve, passes through the aforementioned deep slot. In *Dvinosaurus egregius*, the pars postchoanalis is no longer free, but is connected with the palatoquadrate, thus forming an additional commissure, the commisura quadrato-ethmoidalis lateralis (neither of which should be confused with the proc. quadrato-ethmoidalis *sensu* De Beer). The free margin of the notch between these structures closes, but a dorso-ventral opening remains, forming a slot-like canal. In old individuals of *D. egregius* both commissures fuse with one another, leaving only a narrow canal for transmitting the above mentioned nerve.

In anuran tadpoles with trabecular horns there is, in early stages, only one connection between the postnasal wall and the palatoquadrate. This connection is called the commissura quadrato-cranialis anterior (Fig. 2B). In the course of metamorphosis the palatoquadrate moves backwards to a position underneath the otic capsule (Roček, 1981: fig. 22). Consequently, the commissura quadrato-cranialis anterior gradually increases in length. At the same time a small element (the proc. maxillaris posterior) arises lateral to the proximal-most section of this commissure. Finally it fuses with both the commissura and the postnasal wall. After the subsequent destruction of the proximal section of the commissura, the resulting subocular bar connecting the pars quadrata palatoquadrati with the postnasal wall consists of the residual commissura (posteriorly) and the proc. maxillaris posterior (anteriorly). The nerve enclosed between the proc. maxillaris posterior and the commissura quadrato-cranialis anterior is in anurans usually called the r. communicans and lies between the r. maxillaris V and the r. palatinus VII. Judging by its topographic relations it is no doubt homologous with the abovementioned nerve in *Dvinosaurus*.

Säve-Söderbergh (1936: 42–43, text-figs 8, 14) considered the medial connection in *Lyrocephaliscus* homologous with the commissura quadrato-cranialis anterior, and the lateral connection with the proc. maxillaris posterior. Watson (1940: 226, fig. 23) in his interpretation of similar structures in *Branchiosaurus*

followed Säve-Söderbergh. Considering the facts presented above it seems that there is nothing contradicting this interpretation. It follows from this comparison that the condition in adult temnospondyls is clearly preserved in larval anurans.

There remains one anural group that should be compared with temnospondyls, namely the Leiopelmatidae. It is conventionally regarded as one of the most primitive Recent anuran families, and hence its component taxa should supposedly display some characters shared with temnospondyls or at least derivable from them. Both *Ascaphus* and *Leiopelma* undoubtedly belong to a single lineage. This is evidenced, among other features, by striking similarities in their larval endocranial development (Pusey, 1943; van Eeden, 1951; N. G. Stephenson, 1951; E. M. Stephenson, 1951). Their trabecular horns are directed ventrally, and the nasal capsules arise ventrolaterally to the anterior portion of the braincase. The braincase cavity has no front wall and only in the course of subsequent development is it closed by septum nasi. As far as is known, the medial walls of the nasal capsules in the adult are the same structures that were already present in the early embryo. Thus, in contrast to pipids, their larval structures do persist in adults.

It is beyond the scope of this paper to analyse morphological affinities of leiopelmatid ethmoidal structures and to decide whether they can be derived from the pipid condition or from the trabecular horns, or if it represents yet another condition. For the present it is possible to state that it is not comparable with any known condition found in temnospondyls.

DISCUSSION AND CONCLUSIONS

On the basis of data currently available, the structure of the ethmoidal endocranium of labyrinthodont-grade tetrapods is essentially uniform, even in distantly related groups. It is compressed dorsoventrally and plate-like. No free elements of premandibular branchial arches are present. Although traces of comparatively subtle connections of the palatoquadrate with the ethmoidal endocranium are preserved in some cases, none were found that could be identified as the cart. alaris and obliqua (except for ambiguous findings in *Buettneria* that might equally be identified as muscle impressions). Likewise, no structures comparable with the cornua trabecularum were identified. The lamina nariochoanalis may be either present or absent.

This is all reminiscent of the condition in larval pipids, but not of that in larvae with trabecular horns, nor of that in adult anurans. This implies that the pipid larval type may be primitive, retaining the morphology characterizing the labyrinthodont grade of organization (Fig. 8). The structure in adult pipids seems to be derived from the temnospondyl/larval pipid structural scheme by the addition of structures typical for adults (the septum nasi, cart. obliqua, etc.). In other words, a stage was attained in adult pipids that was not yet present in temnospondyls. This would argue against a direct comparison between adult temnospondyls and adult anurans (cf. Säve-Söderbergh, 1936: 148–149).

However, there are other features in which some temnospondyls do correspond to adult frogs. For instance the number and position of nerve-transmitting canals within the postnasal wall of the sphenethmoid are similar in *Edops* and adult anurans (Figs 1, 4B). In all anuran larvae the n. ophthalmicus
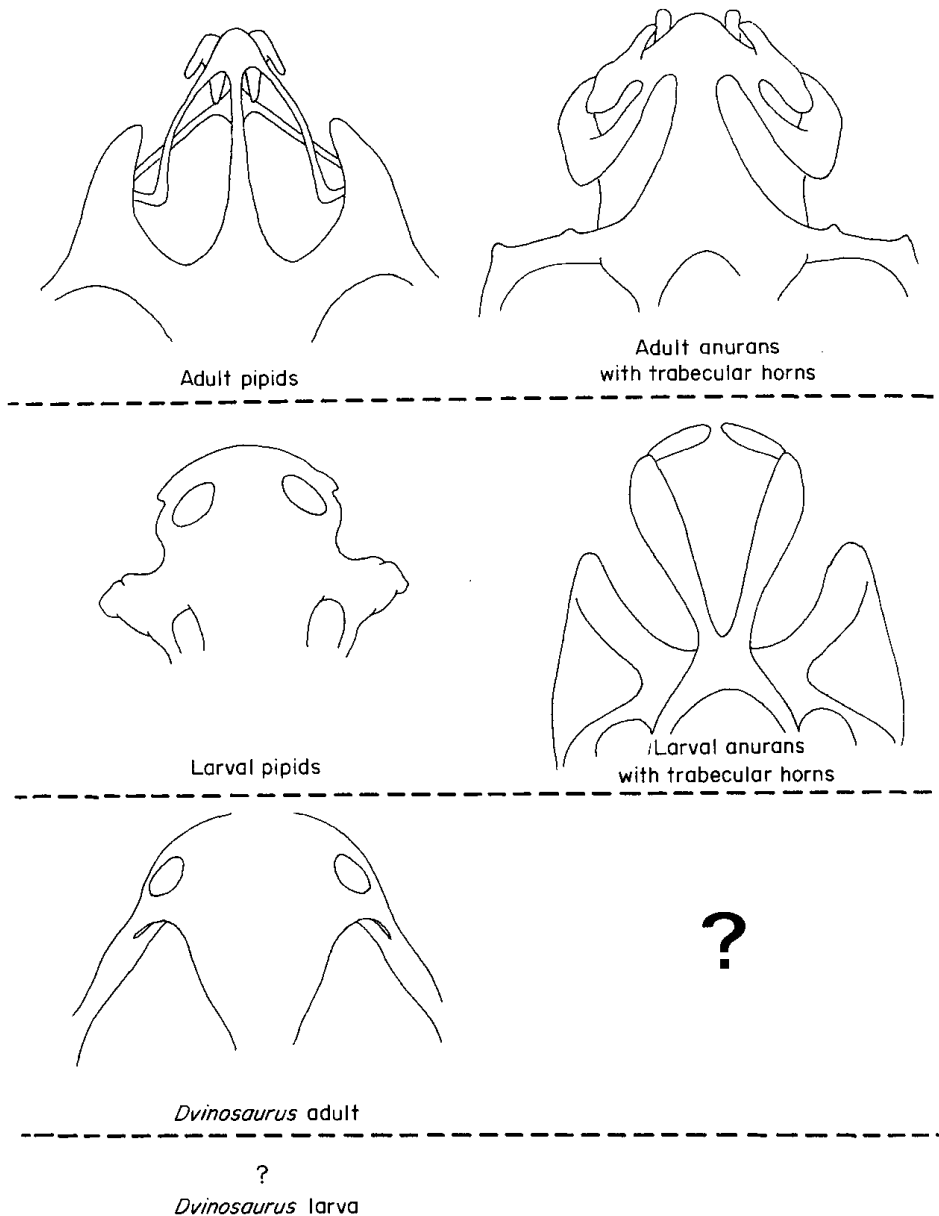
Figure 8. Morphological types of ethmoidal endocrania representing possible evolutionary grades between temnospondyls and anurans.

runs exposed on the dorsal surface of the commissura quadrato-cranialis anterior. In this case the condition in tadpoles no doubt corresponds to that in temnospondyl larvae, and consequently adults of both groups may be compared.

The similarity of pipids and temnospondyls in their ethmoidal endocrania is neither astonishing nor in disagreement with most taxonomic views (see Duellman, 1975—but note Cannatella & Trueb, 1988). Pipids, besides some derived characters, retained primitive characters inherited from ancestors (e.g. free ribs, shape of the parasphenoid, high degree of the endocranial ossification, dermal ossification on the hyoid, well developed columella, etc.). It is very difficult to suppose that the set of these characters evolved in pipids quite independently from other archaic groups of anurans, and therefore that these characters are not homologous. Likewise, the fossil record seems to suggest the

archaic nature of pipids, though this evidence must be used very carefully due to its incompleteness. However, it might be of some importance that with the exception of *Triadobatrachus* a considerable number of early anurans belong to this group (*Shomronella jordanica*, *Thoraciliacus rostriceps*, *Cordicephalus gracilis*, *C. longicostatus*, *Xenopus* sp., *Saltenia ibanezi*; all of Cretaceous age, see Báez, 1981: table I).

What then is the evolutionary origin of the cornua trabecularum? It should be emphasized that the cornua and the ethmoid plate do not appear to be entirely homologous structures (Roček, 1989), despite their similar early embryonic origin. This is shown by the persistence of the cornua as a part of the ethmoidal endocranium in the adult, whereas the planum internasale—or the ethmoid plate in broad sense—disappears completely in the course of larval development and all adult ethmoidal structures arise above this former plate. The ethmoid plate cannot be explained by fusion of the cornua (because of positional differences mentioned). Such fusion has been frequently (and incorrectly) invoked by earlier workers (Parker, De Beer, Sokol). If similarities between temnospondyls and pipids (as revealed by the above comparison) are taken into account, the trabecular horns could, hypothetically, be a result of evolution from some other temnospondyl group to discoglossids and other anuran groups that possess these structures. However, whereas the origin of the septum nasi from the ethmoid plate in adult pipids is explicable by the ontogenetic development of Recent representatives of this group (Fig. 3), it is hard to understand which structures in labyrinthodonts could have given rise to the cornua trabecularum.

Jarvik (1942) pointed out similarities that are shared by osteolepiforms and adult anurans represented by *Rana*. However, it is also not difficult to find features shared by adult osteolepiforms and adult temnospondyls, provided that the dorsal and ventral parts of the ethmoidal region in the former group were adpressed and slightly remodelled, as a consequence of the flattening of the snout. Bearing this in mind, it might even be possible, judging by the ethmoidal endocranial structure, to identify morphological relations within the sequence osteolepiforms—temnospondyls—larval pipids. Provided that similarities in this sequence reflect real affinities of its members, and that differences in anuran larval structural schemes preclude their direct relationships, the only explanation would be that splitting of both anuran lineages took place as early as at the level of temnospondyls. This view is also supported by a list of Weisz's (1945: 189–191) differences between the Pipidae and other anurans, other than those in the structure of the endocranial ethmoidal region, and also possibly by other workers (Nishikawa & Wassersug, 1988).

On the other hand, there are other characters that unify both groups of anurans, and that are also present in temnospondyls. For instance the canalis pro ramo lateralis narium proprio (to mention at least one of them) arises in the same manner in both anural groups, as well as in labyrinthodonts. Its lateral part is formed by an element which is either originally free cartilaginous rod (e.g. in ranids, pelobatids; Fig. 2, epm.) or arising rather late in ontogeny from condensing mesenchymous primordium (in pipids), independently from the lamina orbitonasalis and commissura quadrato-cranialis anterior (Roček & Veselý, 1989: 303, fig. 2B, incorrectly termed the proc. maxillaris anterior). In both cases the elements in question have the same purpose—to form the antero-dorsal part of the canal, and are most probably homologous. Thus, even with

respect to characters that are obscured in adult frogs, temnospondyls correspond with all anuran lineages. It may be argued that certain viscerocranial elements, inherited by ancestral temnospondyls from osteolepiforms, could persist in all anurans too (with all structural consequences in their adults), regardless of the group or groups of temnospondyls from which they arose. Differences in the timing of the appearance of these structures in ontogeny (retardation or even disappearance) can also occur in closely related lineages, and cannot be considered as evidence against such relationships. For example, in *Ascaphus* free viscerocranial elements are evolutionarily preserved to such a degree that they are well defined from the very early stages of chondrogenesis. Later they coalesce with the neural endocranium or disappear completely. In *Leiopelma*, a close relative of *Ascaphus*, the same viscerocranial elements appear much later in advanced developmental stages (i.e. they do not arise simultaneously with the main components of the ethmoidal region, and their early development is in the procartilaginous stage). Nonetheless, their ultimate destiny is the same (e.g. the origin of the crista subnasalis in both genera). The presence of widely distributed characters, like these mentioned above, in an ancestral group (or at an ancestral grade) should not be taken as evidence of common origin.

Although differences in endocranial ethmoidal structure in larval anurans suggest that a transition between temnospondyls and anurans could occur independently in several lineages, no systematic ramifications are suggested here. Such interpretation would require a more detailed study of the development of the larval cranial structures of anurans. Further investigations on temnospondyls yielding a more detailed knowledge of their ethmoidal endocranial structures will determine whether the similarities of temnospondyls to larval pipids on one hand, and their distinctness from those anuran larvae with trabecular horns on the other, suggests some events of phylogenetic importance in their evolutionary history.

SUMMARY

(1) According to data available at the present time, the ethmoidal region of the endocranium in labyrinthodont-grade tetrapods, disregarding its proportions and degree of ossification, is basically uniform even in rather distantly related groups.

(2) Comparison of the entire ethmoidal endocranium in temnospondyls with that in anurans reveals that whereas similarities may be found between the former group and larval pipids, comparison with other anurans (both larval and adult) meets with problems.

(3) Comparisons based on isolated sphenethmoids reveal close morphological and developmental similarities only between anurans as a whole and *Palaeoherpeton*.

(4) On the basis of present knowledge it is difficult to explain the evolutionary origin of the cornua trabecularum.

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REFERENCES

BÁEZ, A. M., 1981. Redescription and relationships of *Saltenia ibanezi*, a late Cretaceous pipid frog from northwestern Argentina. *Ameghiniana, 18(3/4):* 127–154.

BOLT, J. R., 1974a. Evolution and functional interpretation of some suture patterns in Paleozoic labyrinthodont amphibians and other lower tetrapods. *Journal of Paleontology, 48:* 434–458.

BOLT, J. R., 1974b. Osteology, function, and evolution of the trematopsid (Amphibia: Labyrinthodontia) nasal region. *Fieldiana, Geology, 33:* 11–30.

BOY, J. A., 1978. Die Tetrapodenfauna (Amphibia, Reptilia) des saarpfalzischen Rotliegenden (Unter-Perm; SW-Deutschland). 1. *Branchiosaurus. Mainzer geowissenschaftliche Mitteilungen, 7:* 27–76.

BROOM, R., 1913. Studies on the Permian temnospondylous stegocephalians of North America. *Bulletin of the American Museum of Natural History, 32:* 563–595.

BYSTROW, A. P., 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. *Acta Zoologica, 19:* 209–295.

BYSTROW, A. P. & EFREMOV, J. A., 1940. *Benthosuchus sushkini* Efr. a labyrinthodont from the Eotriassic of Sharzhenga river. *Trudy Paleontologicheskogo Instituta, 10(1):* 1–152. [In Russian.]

CANNATELLA, D. C. & TRUEB, L., 1988. Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zoological Journal of the Linnean Society, 94:* 1–38.

DE BEER, G. R., 1937. *The Development of the Vertebrate Skull.* Oxford: Clarendon Press.

DE JONGH, H. J., 1968. Functional morphology of the jaw apparatus of larval and metamorphosing *Rana temporaria* L. *Netherlands Journal of Zoology, 18:* 1–103.

DEMPSTER, W. T., 1935. The braincase and endocranial cast of *Eryops megacephalus* (Cope). *Journal of Comparative Neurology, 62:* 171–196.

DUELLMAN, W. E., 1975. On the classification of frogs. *Occasional Papers of the Museum of Natural History, The University of Kansas, 42:* 1–14.

GAUPP, E., 1893. Beiträge zur Morphologie des Schädels. I. Primordial-cranium und Kieferbogen von *Rana fusca. Morphologische Arbeiten, 2.*

JARVIK, E., 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zoologiska Bidrag från Uppsala, 21:* 235–675.

JURGENS, J. D., 1971. The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. *Annale Universiteit van Stellenbosch, 46, Ser. A, 2:* 1–146.

KOTTHAUS, A., 1933. Die Entwicklung des Primordial-Craniums in *Xenopus laevis* bis zur Metamorphose. *Zeitschrift für Wissenschaftliche Zoologie, 144:* 511–572.

NIEUWKOOP, P. D. & FABER, J., 1967. *Normal Table of* Xenopus laevis *(Daudin).* Amsterdam: North-Holland Publishing Company.

NISHIKAWA, K. & WASSERSUG, R., 1988. Morphology of the caudal spinal cord in *Rana* (Ranidae) and *Xenopus* (Pipidae) tadpoles. *Journal of Comparative Neurology, 269:* 193–202.

PANCHEN, A. L., 1964. The cranial anatomy of two coal measure anthracosaurs. *Philosophical Transactions of the Royal Society of London, Ser. B, 247:* 593–637.

PANCHEN, A. L., 1970. *Batrachosauria (Anthracosauria). Handbuch der Palaeoherpetologie, Part 5A.* Stuttgart: Fischer Verlag.

PLASOTA, K., 1974. The development of the chondrocranium (neurocranium, and the mandibular and hyoid arches) in *Rana temporaria* L. and *Pelobates fuscus* (Laur.). *Zoologia Poloniae, 24:* 99–168.

PUSEY, H. K., 1943. On the head of the liopelmid frog, *Ascaphus truei.* I. The chondrocranium, jaws, arches, and muscles of a partly grown larva. *Quarterly Journal of Microscopical Science (N.S.), 84:* 105–185.

ROČEK, Z., 1981. Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Universitatis Carolinae, Biologica (1980):* 1–164.

ROČEK, Z., 1982. *Macropelobates osborni* Noble, 1924 – redescription and reassignment. *Acta Universitatis Carolinae, Geologica (1982):* 421–438.

ROČEK, Z., 1989. Developmental patterns in the ethmoidal region of the anuran skull. In H. Splechtna & H. Hilgers (Eds), *Trends in Vertebrate Morphology. Progress in Zoology, 35:* 412–415. Stuttgart: Fischer Verlag.

ROČEK, Z. & VESELÝ, M., 1989. Development of the ethmoidal structures of the endocranium in the anuran *Pipa pipa. Journal of Morphology, 200:* 301–319.

ROMER, A. S. & WITTER, R. V., 1942. *Edops*, a primitive rhachitomous amphibian from the Texas Red beds. *Journal of Geology, 50:* 925–959.

SAWIN, H. J., 1941. The cranial anatomy of *Eryops megacephalus*. *Bulletin of the Museum of Comparative Zoology, Harvard, 88:* 407–463.

SÄVE-SÖDERBERGH, G., 1936. On the morphology of Triassic stegocephalians from Spitsbergen, and the interpretation of the endocranium in the Labyrinthodontia. *Kungl. Svenska Vetenskapsakademien Handlingar, 16(1):* 1–180.

SEDRA, S. N. & MICHAEL, M. I., 1957. The development of the skull, visceral arches, larynx and visceral muscles of the South African clawed toad, *Xenopus laevis* (Daudin) during the process of metamorphosis (from stage 55 to stage 66). *Verhandelingen der Koninklijke Akademie van Wetenschappen, afd. Natuurkunde, ser. 2, 51:* 1–80.

SHISHKIN, M. A., 1973. *The Morphology of the Early Amphibia and some Problems of the Lower Tetrapod Evolution.* Moscow: Nauka [In Russian.]

STEPHENSON, E. M., 1951. The anatomy of the head of the New Zealand frog, *Leiopelma*. *Transactions of the Zoological Society of London, 27(2):* 255–305.

STEPHENSON, N. G., 1951. On the development of the chondrocranium and visceral arches of *Leiopelma archeyi*. *Transactions of the Zoological Society of London, 27(2):* 203–252.

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 Zoologica, 32:* 41–136.

WATSON, D. M. S., 1940. The origin of frogs. *Transactions of the Royal Society of Edinburgh, 60(1):* 195–231.

WILSON, J. A., 1941. An interpretation of the skull of *Buettneria*, with special reference to the cartilages and soft parts. *Contributions from the Museum of Paleontology, University of Michigan, 6:* 71–111.

WEISZ, P. B., 1945. The development and morphology of the larva of the South African clawed toad, *Xenopus laevis*. *Journal of Morphology, 77:* 163–191.