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 leiolepidids (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 Bufo bufo 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.


CONTENTS

Introduction 389
The ethmoidal endocrania in temnospondyls and anthracosaurs: a review 392
Temnospondyls 392
Anthracosaurs 398
Comparison of anuran, temnospondyl and anthracosaur ethmoidal endocrania 399
Discussion and conclusions 402
Summary 405
Acknowledgements 405
References 406

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
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
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
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

![Diagram of ethmoidal endocranial structures](image)

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 ophthalmic 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 ophthalmic nerve; in anurans, this nerve only exceptionally enters the braincase cavity (e.g. temporarily during the development of *Piipa*). 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 palatoquadrates. 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 Branchiosaauridae which are supposed to be paedomorphic Dissorophoidae, the only information available concerns the relation between the most lateral part of the postnasal wall and the palatoquadrates (Boy, 1978: fig. 8a–c, personal communication). In the late larval stages the palatoquadrates 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 Dinosaurus
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 Doleropetontidae 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
endoarina 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 endocranialis. The dorsal part is a fragment of the natural
cast that represents the ethmoidal endocranium including the posterior parts of
both fenestrae endocraninae and reaching up to the anterior part of the right
fenestra endocranialis.

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 endocraninae 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
Figure 5. *Benthosuchus suskini* (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 suskini*, 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.en.—fenestra endochoanalis; f.en.—fenestra endonarina; f.pm.—fenestra praemaxillaris; L.nch.—lamina nariochoanalis; max.—maxilla; pspm.—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 parachoanalisis sensu Bystrow & Efremov, 1940, fig. 17). The anterior extent of the fenestra endochoanalis almost reaches the level of the posterior limit of the fenestrae endorinariae. 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 endorinariae, 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 endorinariae 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 endorarina 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 endorarina 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 brachypodoids 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 endorarina 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 postchoanalisis (at least in Dvinosaurus) is composed of both roof and floor, the lateral diverticulum of the nasal sac being housed between them; the pars postchoanalisis is parallel to the anterior section of the medial ethmoidal commissure (i.e. the commisura quadrate-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
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 Deinosaurus, 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, 55, 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 nariochoanalisis 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. vomerocanales, 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 these 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 Pita (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 Pita, 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 Palaeotherpeton, 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 Palaeotherpeton.

Dinosaursaurus, although providing much information in other respects, cannot provide any concerning the sphenethmoid. The complete absence of this ossification in Dinosaursaurus 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 Dinosaursaurus 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 nariochoanalisis 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 Dinosaursaurus 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 nariochoanalisis 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 nariochoanalisis 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 endochoanalisis 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 carololoi 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 nariochoanalisi. 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 Deinosaurus 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 endochoanalisi 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 endochoanalisi is free. A nerve originally interpreted by Shishkin as the postchoanal anastomosis between V and VII nerves, and later interpreted by him as part of the maxillary nerve, passes through the aforementioned deep slot. In Deinosaurus egregius, the pars postchoanal is no longer free, but is connected with the palatoquadrate, thus forming an additional commissure, the commissura 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 palatoquadri 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 Deinosaurus.

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 Leiopteridae. 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 Ascepha and Leioptera 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 leiopterid 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 nariochoanalisis 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 parapteroid, 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 ristreeps, Cordicephalus graecilis, C. longicostatus, Xenopus sp., Saltenia ibanezi; all of Cretaceous age, see Báez, 1981: table 1).

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 proprium (to mention at least one of them) arises in the same manner in both anuran 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, temnospondylys correspond with all anuran lineages. It may be argued that certain viscerocranial elements, inherited by ancestral temnospondylys from osteolepiforms, could persist in all anurans too (with all structural consequences in their adults), regardless of the group or groups of temnospondylys 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 *Acephalus* 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 *Lepidopelma*, a close relative of *Acephalus*, 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 temnospondylys 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 temnospondylys yielding a more detailed knowledge of their ethmoidal endocranial structures will determine whether the similarities of temnospondylys 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 temnospondylys 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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