The Incrassatio Frontoparietalis in Frogs, its Origin and Phylogenetic Significance

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Abstract. The incrassatio frontoparietalis is a clearly delimited part of the frontoparietal, covering the gap or gaps in the dorsal wall of the endocranium. In frogs, this structure originates in very early ontogenetic stages, and keeps its shape without considerable changes till maturity. Therefore, it is probably a good diagnostic character. Moreover, it is presumed that this structure also is a good phylogenetic character, and its study based on an extensive recent and fossil material might contribute to our present knowledge of the frog phylogeny.

Introduction

Ventrally, a characterictic surface structure occurs on the frontoparietals in both fossil and resent frogs (ŠPINAR 1975, 1976; TRUEB 1966, 1970) which originally was considered to represent an imprint of dorsal parts of the brain (ŠPINAR 1975). The similarity of shape between this configuration and the subjacent brain parts is almost outstanding in the family Ranidae. ŠPINAR (1975) first described the structure as "brain figure", but later (1976) referred to it as "endocranial pattern". The latter term, however, is somewhat misleading: it suggests the total makeup of an endocranium rather than a character of the frontoparietal. In the sequel, therefore, the term "incrassatio frontoparietalis" will be used.

An interpretation based on a supposedly direct contact between the brain and the frontoparietals seemed very attractive. For, if correct, the incrassatio frontoparietalis, although an osteological feature, would offer information about the morphology of the central nervous system, one of the morphologically most conservative organ structures of the vertebrate body. In giving information on the shape of the brain and the proportions of brain parts in fossil frogs, an incrassatio frontoparietalis would make it possible to judge the degree of phylogenetic development of the central nervous system, and provide reliable conclusions as to the phylogeny and systematics of various frog groups.

Further study revealed, however, that the incrassatio frontoparietalis, which is very characteristic of individual frog families, genera and even species (ŠPINAR 1976) and hence a valuable diagnostic feature, does not always match the shape of the brain. A revision of the original interpretation is therefore necessary.

Material and Methods

Three specimens of *Rana esculenta* L., 1758 and three specimens of *Pelobates fuscus* (LAURENTI, 1768), representing two genera possessing entirely different frontoparietal incrassations were chosen for the study of the origin and development of the frontoparietal incrassation. Three stages have been employed to reveal the ontogenetic changes: tadpoles of stages 55—57*, specimens during the last stage of metamorphosis (stage 64), and adult frogs collected during a breeding season. Their heads, fixed in 10% formalin, were decalcified and embedded in celloidin. This medium guaranteed that the natural position of the organs located within the braincase was retained (embedding in paraffin proved to be unsuitable). Transverse sections of 30 microns were made, and then stained with Weigert's hematoxylin and mucicarmin. Altogether 803 sections have been prepared, 423 of them passing through the frontoparietals.

As for the skull terminology, see ROČEK (1981); concerning the braincase and adjacent structures, the terminology of STADTMÜLLER (1936), unless otherwise stated, has been used.

Results

Figures 1—6 schematically represent transverse sections through the braincase, and illustrate the proportional relations of the brain, the endocranium, and the dermal bones
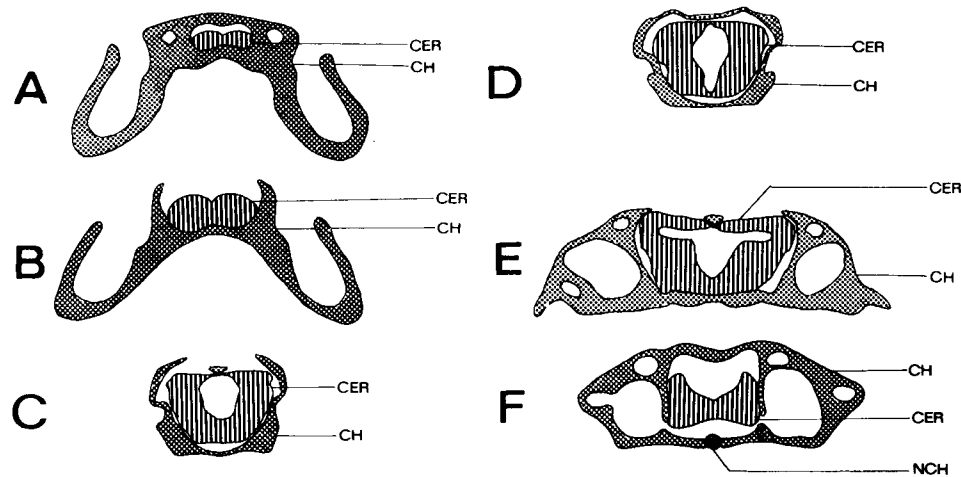

Fig. 1. Cross sections through the braincase of a tadpole of *Rana esculenta* (stage 55—57). A — through the anterior end of the braincase; B — through the fenestra frontalis; C — through the posterior margin of the fenestra frontalis, with a pointed projection of the taenia tecti transversalis in the midline; D — through the taenia tecti transversalis; E — through the fenestrae parietales, separated by the taenia tecti medialis; F — through an area close to the posterior margin of the fenestrae parietales. CER: brain; CH: endocranium; NCH: notochord.

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* For designation of ontogenetic stages we have used the criteria of NIEUWKOOP and FABER (1967).

(the frontoparietal, the parasphenoid and the nasals). Sections at the following levels are given: through the anterior end of the braincase, through fenestra frontalis (if present), through taenia tecti transversalis, through fenestrae parietales, and through a level just posterior to these fenestrae. In *Pelobates*, where the morphology of the endocranial roof is different from that of *Rana*, sections at corresponding levels are given. Further sections have been used where the margins of the fenestrae were irregular (for example, the posterior margin in *Pelobates*). For a detailed description see the explanation of figures.
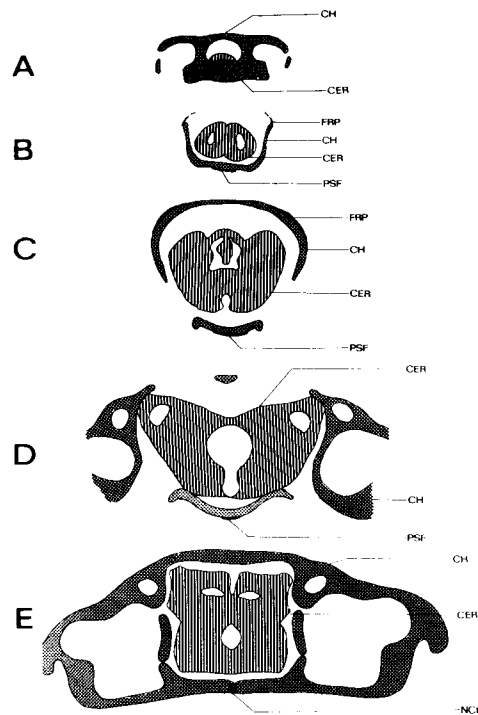

Fig. 2. Cross sections through the braincase of a tadpole of *Rana esculenta*, at the end of metamorphosis (stage 64). A — through the anterior end of the braincase; B — through the fenestra frontalis; C — through the taenia tecti transversalis; D — through the fenestrae parietales with the taenia tecti medialis; E — through an area close to the posterior margin of both fenestrae parietales. FRP: frontoparietal; PSF: parasphenoid. For other abbreviations see fig. 1.

In *Rana esculenta* apparently the ossification of the exocranium has not yet started in stage 55—57. The fenestra frontalis is very wide, and the side walls of the braincase are conspicuously thin. All fenestrae are covered by a connective tissue membrane, which also covers the cartilaginous bars between the fenestrae (= teniae tecti), from the dorsal side. During metamorphosis, the endocranium in its dorsal part does not differ much from that of an adult frog. However, the fenestra frontalis is wider, and the side walls of the endocranium extend dorsally to end without slanting medially as in an adult frog. In the area of the fenestra frontalis the braincase is closed only by a connective tissue

membrane, which partly extends over the outer surface of the endocranium. In the tissue small islands of bone formation may be observed — the beginning of the frontoparietal. The ossification is most intensive in the lateral areas of the fenestrae, and in the connective tissue extending over the endocranial walls. Only isolated islands of ossification occur medially. These primordia of the frontoparietal extend anteriorly as far as two thirds of the fenestra length (not so far as the sphenethmoid, as is the case in adult frogs), and posteriorly only close to and behind the taenia tecti transversalis. The major part of the parietal fenestrae is closed only by a connective tissue membrane.

In an adult *Rana esculenta* the anterior ends of the frontoparietal are two thin osseous laminae lying on a dorsal surface of the cartilagionous sphenethmoid. They are surrounded by subcutaneous connective tissue, a thin layer of which separates them from
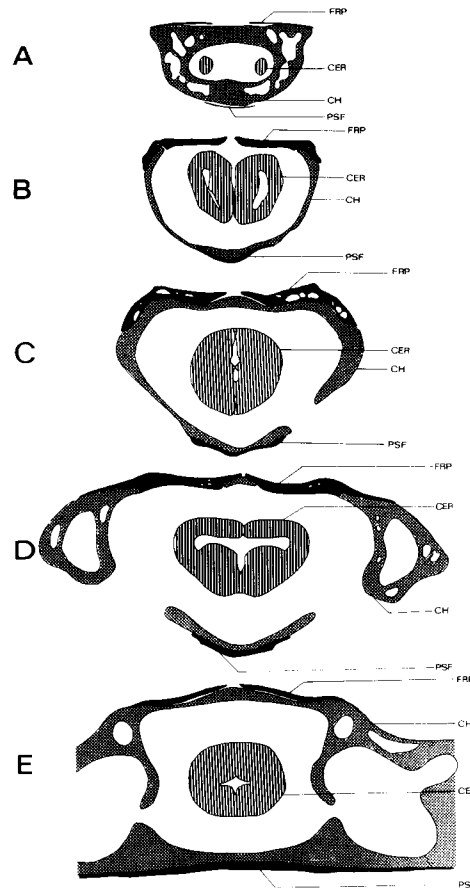

Fig. 3. Cross sections through the braincase of an adult *Rana esculenta*. A — through the anterior end of the braincase; B — through the fenestra frontalis; C — through the taenia tecti transversalis; D — through the fenestrae parietales with the taenia tecti medialis; E — through an area close to the posterior margin of the fenestrae parietales. For abbreviations see figs. 1 and 2.
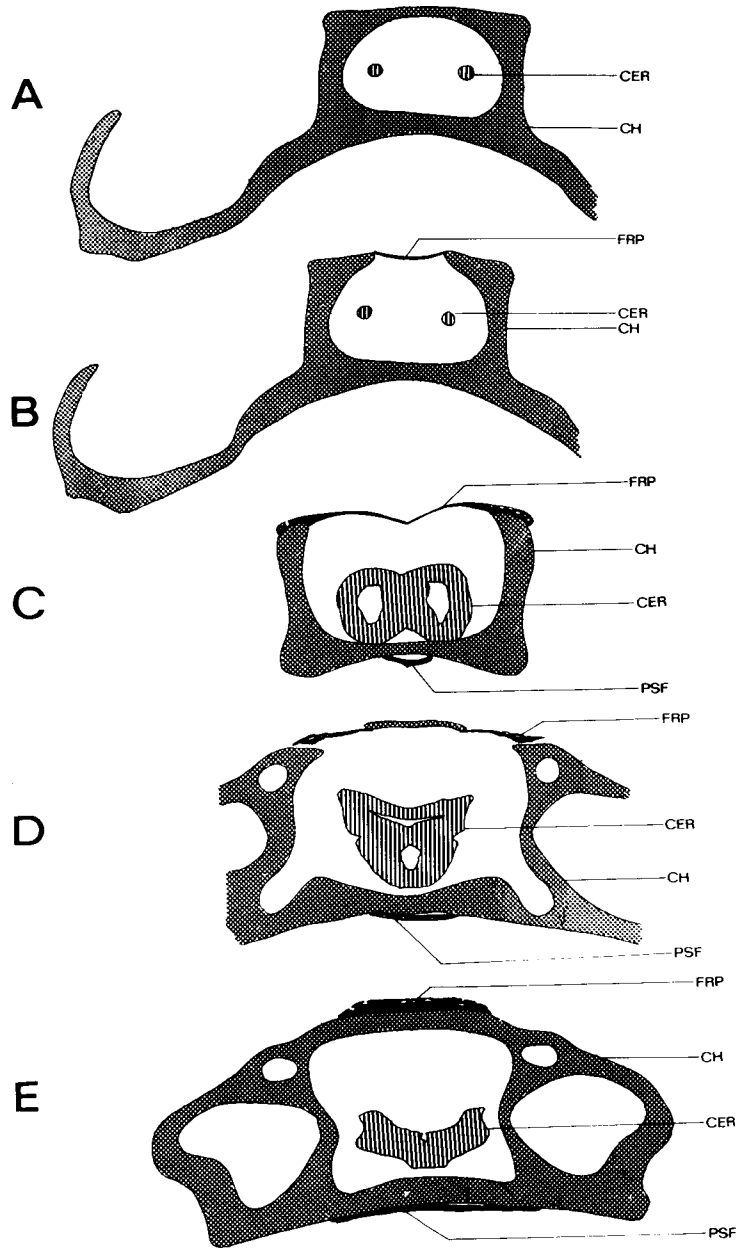
Fig. 4. Cross sections through the braincase of a tadpole of *Pelobates fuscus* (stage 55—57). A — through the anterior end of the braincase; B — through the anterior area of the fenestra; C — through the widest part of the fenestra; D — through the posterior end of the fenestra, with a pointed projection of the posterior margin; E — through an area close to the posterior margin of the fenestra. For abbreviations see figs. 1 and 2.

the sphenethmoid (fig. 3 A). Farther posteriorly the walls of the endocranium become thinner and the dorsal wall disappears altogether, except for narrow taeniae between the fenestrae. In the area of the fenestrae, the roof of the braincase consists of the fronto-parietal only, which, however, extends laterally and partly covers the outer surface of the endocranium. On sections through the widest part of the fenestra frontalis, the two halves of the frontoparietal almost touch each other in the midline (fig. 3 B). Their dorsal surfaces are smooth and almost horizontal, except laterally where they slant ventrally at an obtuse angle. The inner surfaces of these lateral laminae are attached to the outer surface of the endocranium. At the edge of the endocranium (the lateral margin of the fenestra), a thickened part of the ventral surface of the frontoparietal appears. The inner surface of this thickening forms a smooth transition with the inner surface of the endocranium. A lateral margin of the thickening ends in a sharp edge. In the area of the taenia tecti transversalis, the ventral surface of the frontoparietal is smooth, without a thickening, and slightly undulated in accordance with the cartilaginous bar to which it is attached (fig. 3 C). In the area of the fenestrae parietales the ventral surface of the frontoparietal is thickened again, even more so than in the area of the fenestra frontalis. Both thickenings are limited by a sharp edge at the lateral margin as well as at the medial margin which touches the taenia tecti medialis (fig. 3 D). At the posterior end of the fenestrae parietales the taenia tecti medialis gradually widens, and the lateral walls of the endocranium reach farther medially. The endocranial part of the braincase closes again (tectum synoticum). The ventral surface of the frontoparietal, smooth and without a thickening, rests on the endocranium.

In a tadpole of *Pelobates fuscus* (stage 55—57), a connective tissue membrane is formed in the anterior part of the fenestra only between the inner margins of the side walls of the endocranium (fig. 4 B). However, isolated islands of forming bone can be observed even here. In the posterior part of the fenestra a thick layer of connective tissue reaches over to the outer surface of the endocranium. The ossification is most intensive here. The bone already contains small cavities and, on the outer surface, a sculpture begins to appear. The anterior end of the frontoparietal does not reach so far forwards at the time of metamorphosis as in an adult frog. The fenestra is widely open on sections through the anterior end and the olfactory bulbs fuse. An osseous tissue is formed above all in the lateral parts, attached to the margins of the cartilaginous sphenethmoid. Farther backward, islands of bone tissue are formed throughout the frontoparietal. However, the frontoparietal is not yet thickened on its ventral side. Only a slight edge suggests the border of the future thickening of the bone.

In an adult *Pelobates fuscus* the anterior end of the frontoparietal is a thin, unpaired, osseous lamella, dorsally concave. It lies on the dorsal wall of the sphenethmoid and is attached to the latter by a relatively thick layer of connective tissue (fig. 6 A). The frontoparietal widens behind, while the nasals become narrower. The frontoparietal already covers the whole inner third of the dorsal sphenethmoid wall above the anterior end of the braincase. Both outer and inner surfaces of the frontoparietal are smooth (fig. 6 B). The dorsal wall of the endocranium disappears farther backward and the brain is dorsally sheltered by the frontoparietal only. The endocranium exhibits a single large fenestra, undivided by taeniae. The ventral surface of the frontoparietal is smooth at the anterior end of the fenestra but the frontoparietal already is thickened a little. The border of the thickening becomes sharper farther backward. The thickening is at first separated from
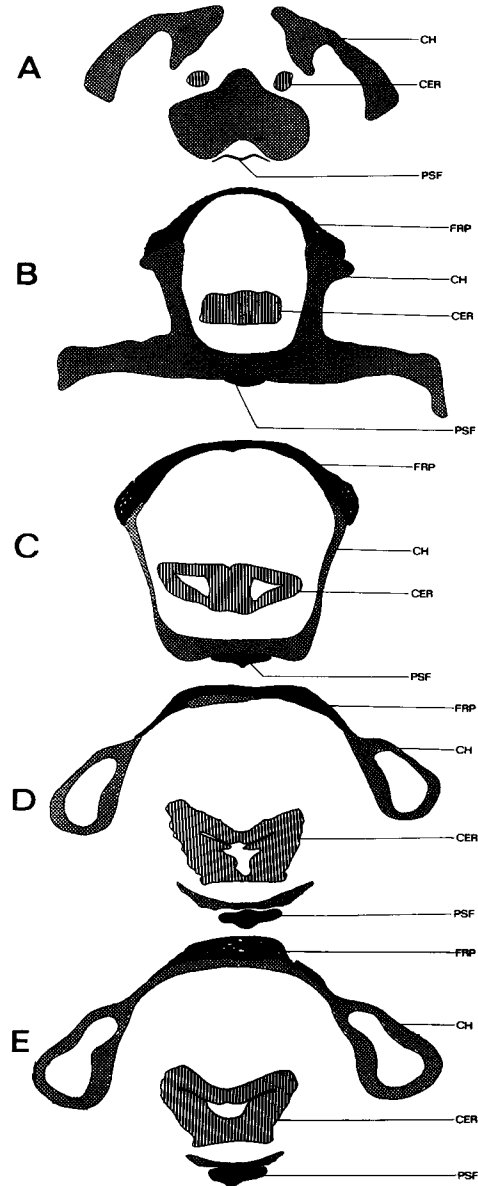
Fig. 5. Cross sections through the braincase of a tadpole of *Pelobates fuscus*, at the end of metamorphosis (stage 64). A — through the anterior end of the braincase; B, C — through characteristic parts of the fenestra; D — through the posterior margin of the fenestra with a pointed projection; E — through an area close to the posterior margin of the fenestra. For abbreviations see figs. 1 and 2.
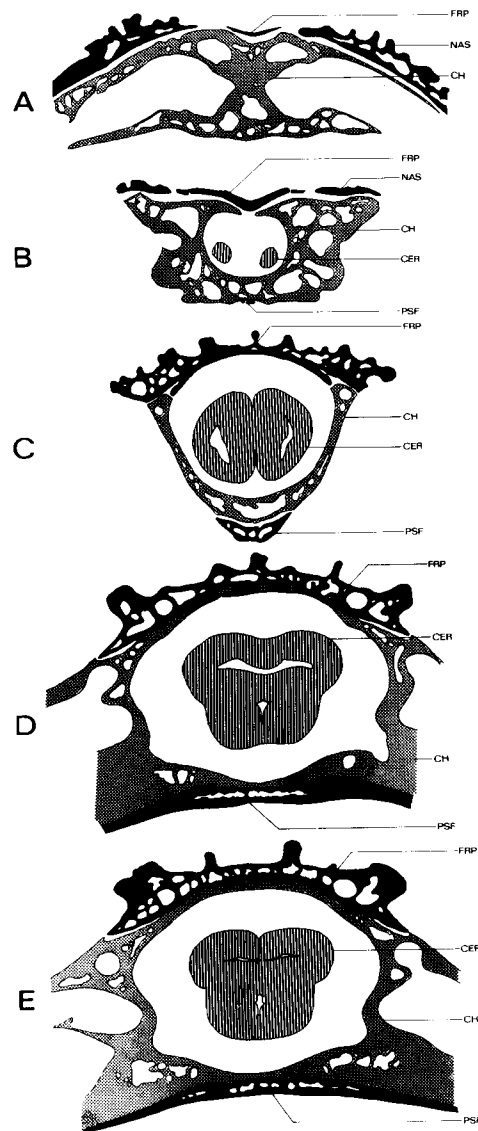
Fig. 6. Cross sections through the braincase of an adult *Pelobates fuscus.* A — through the anterior projection of the frontoparietal; B — through the anterior end of the braincase; C — through the widest part of the fenestra; D — through the posterior margin of the fenestra with a pointed projection in the midline; E — through an area close to the posterior margin of the fenestra. NAS: nasal. For other abbreviations see figs. 1 and 2.

lateral parts of the bone by a sharp edge, later by a conspicuous lamina directed ventro-laterally, and separated by a deep groove from the rest of the bone (fig. 6 C). The ventral surface of the thickening is smooth, while the lateral parts are irregular, with shallow depressions and rounded projections. These lateral parts are attached to the thickened margins of the fenestra by a thick layer of connective tissue. All parts of the ventral surface of the frontoparietal are smooth again in the posterior part of the fenestra where the endocranial wall is cartilaginous and very thin. The thickening is limited by a sharp edge only, the lamina has disappeared. Also the thick layer of connective tissue between the frontoparietal and the endocranium has disappeared and the bone is closely attached to the cartilage. Only in the area of the tectum synoticum where the endocranial wall is osseous, a wide gap filled with connective tissue separates the frontoparietal from the endocranium. The posterior end of the fenestra is cartilaginous and forms a pointed projection in the midline, directed forwards (fig. 6 D).

A study of the serial sections at hand reveals explicitly that the incrassatio frontoparietalis develops in the fenestra or fenestrae in the dorsal wall of the endocranium (cf. ROMER and EDINGER 1942, TRUEB 1966). This thickening makes up for an absent part of the endocranium. From an ontogenetic viewpoint it can be stated that the characteristic shape of the gaps in the dorsal wall of the endocranium, and consequently the shape of the frontoparietal incrassation is being formed already in early ontogenetic stages. Only small modifications occur during subsequent development. For example, the anterior margin of the fenestra frontalis is slightly curved or straight in *Rana* tadpoles, while it forms a pointed projection in adults. The area of the future frontoparietal is composed by mesenchyme which, during development, condenses into a shape of the future bone (clearly discernible in the sections). In this area of mesenchyme a slight thickening can be discerned. Its shape and size correspond to the future frontoparietal incrassation.

The ossification of dermal bones does not proceed at the same rate; there are marked differences between the two species studied as well as between individual dermal bones. In *Rana*, the gaps are covered at stages 55–57 merely by a layer of a condensed mesenchyme, while in *Pelobates* it is already possible to observe a young bone. *Rana* reaches this stage as late as at the time of metamorphosis: it is possible to find differentiated osteoblasts in our specimen of *Rana*, stage 64. The osteoblasts lie in a mesenchyme close to the lateral margins of the fenestrae. In this species, osteogenesis proceeds insularly from the lateral margin of the frontoparietal toward the sutura mediana (figs. 2 B, 4 C).

The uneven ossification of individual dermal bones in *Rana* is demonstrated by the fact that while the frontoparietal is still represented only by narrow bands of young bone attached to the lateral margins of the fenestra, the parasphenoid is already formed in its entirety (fig. 2 B).

The process of frontoparietal ossification in *Pelobates* is probably similar to that of *Rana*, but takes place at earlier ontogenetic stages. As previously stated, the fenestra is already covered by bone in the tadpole (stage 55–57). Even the cavities identical to those occurring in adult specimens are formed (fig. 4). The frontoparietal becomes thinner toward the midline. This may be interpreted as an immature and still developing part of the bone. Thus it can be stated that even here the osteogenesis proceeds in a medial direction. However, the only evidence is the shape of the bone. We have no histological evidence because of the lack of earlier ontogenetic stages of *Pelobates*.

The frontoparietal incrassation presents no subdivision in *Pelobates*. It corresponds to a single large gap in the dorsal wall of the endocranium. Three gaps occur in *Rana:* a fenestra frontalis and a right and left fenestra parietalis. They are separated by narrow bars: taenia tecti medialis and taenia tecti transversalis. This partition is cruciform, as taenia tecti transversalis forms an anteriorly directed projection from the posterior margin of the fenestra frontalis. This projection looks like a prolongation of taenia tecti medialis but it occurs also in forms in which the taenia tecti medialis is completely absent (e. g. *Discoglossus*). On the ventral surface of the frontoparietal an imprint made by the subjacent endocranial bars separates individual parts of the incrassation from each other.

There exists a series of transitions between these two extreme types of frontoparietal incrassations represented by *Rana* and *Pelobates*, which can be interpreted phylogenetically. Some of these morphological types were published by Špinar (1976).

In *Pelobates fuscus* (a representative of the frogs whose frontoparietal incrassation corresponds to a single large gap) the frontoparietal incrassation invariably presents a distinct notch in the middle of the posterior margin, while the lateral margins usually are unincised. However, a variant often exists in which the lateral margins are interrupted in their posterior third by a similar notch.
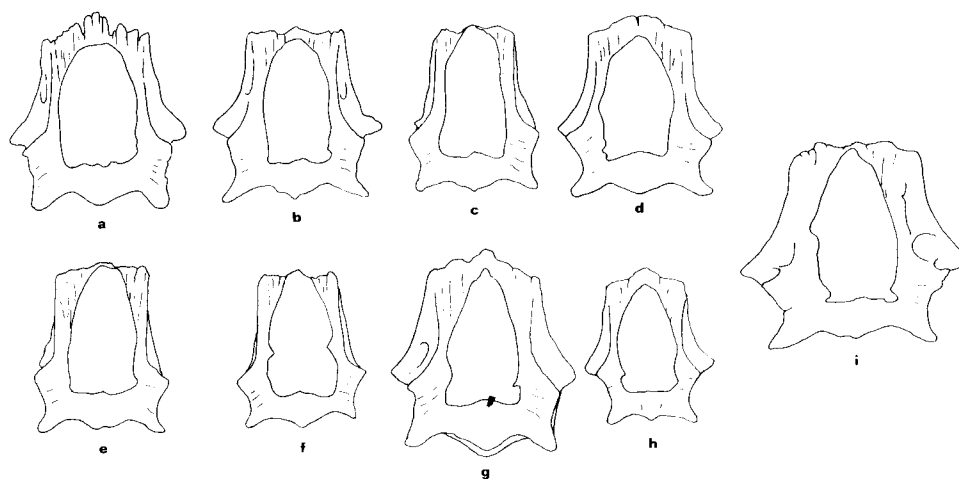

Fig. 7. Morphological variation in the frontoparietal incrassation of *Pelobates fuscus* (a–c, e–i Recent, Czechoslovakia, d Miocene, loc. Valeč, Czechoslovakia).

Stadmüller (1936) explains this fact by partial or complete absence of the taenia tecti transversalis. A similar type of the incrassatio frontoparietalis is found in *Scaphiopus, Xenopus* etc.

The notches in the lateral margin of the frontoparietal incrassation may reach so far toward the midline that they completely separate the anterior part of the incrassation from the posterior one (the gap is divided by the taenia tecti transversalis into unpaired frontal and parietal fenestrae). This type of incrassatio frontoparietalis occurs, for example, in *Discoglossus, Alytes,* and fossil *Latonia*.

The posterior part of the frontoparietal incrassation may be further subdivided by the taenia tecti medialis into bilateral parts. The incrassatio frontoparietalis derived in this way corresponds to three gaps in the roof of the endocranium: an unpaired fenestra frontalis and paired fenestrae parietales. This is a second extreme type of incrassatio frontoparietalis, occurring, for example, in *Hyla, Bufo* and *Rana*.

Owing to the fact that a frontoparietal incrassation is caused by the shape and size of endocranial gaps, it is not important whether the frontoparietal is paired or unpaired. The frontoparietal incrassation must be considered as a whole even in such cases in which it is formed by parts of both a right and a left frontoparietal.

As to the relationship of the frontoparietal incrassation to the brain, no correlation between the shape of the brain and that of the inner surface of the braincase has been observed. The growth of the brain and the braincase is disproportionate: the brain is delayed in its growth, compared with that of the braincase; while in a tadpole the brain fills out the braincase almost completely, in an adult frog it is surrounded by a vast meningeal space containing the liquor cerebrospinalis.

Neither did we recognize any relationship between the frontoparietal incrassation and the shape of the endolyphatic sacs. According to DEMPSTER (1930) the pelobatids and the bufonids display the same type of endolymphatic sac, although their frontoparietal incrassations are quite different. On the other hand, the ranids exhibit a completely different type of endolyphatic sac, but their frontoparietal incrassation is almost identical with that of the bufonids. These facts demonstrate clearly that the endolymphatic sac need not be taken into account when considering the origin and configuration of the frontoparietal incrassation.

Discussion and Conclusions

According to the above results the shape of the frontoparietal incrassation is determined by the shape of subjacent parts of the endocranium.

ROMER and EDINGER (1942) studied endocranial casts in recent amphibians and their relation to the shape of the brain, in order to establish to what extent the shape of the brain is reflected on the inner surface of the braincase. In their paper they figured the frontoparietal incrassation of *Rana catesbeiana* SHAW, 1802, and concluded that the anterior part of the incrassation reflects the shape of the brain, while the posterior part corresponds to "the fenestrae parietales of the chondrocranium".

TRUEB, who had observed this structure in several representatives of the family Hylidae, interpreted it as "those parts of the frontoparietals that overlie the fontanelle" (TRUEB 1966: 566).

ŠPINAR (1976) emphasized the diagnostic significance of the character, and carried out an extensive comparative study on representatives of several families, drawing attention to the possibility of phylogenetic conclusions. Nevertheless, his original presumption as to the origin of the frontoparietal incrassation, namely, that the shape of it "is modelled by the parts of the brain and the size of the endolymphatic sacs" (ŠPINAR 1976: 286) has proved to be incorrect. According to the results of the present writers, the frontoparietal incrassation is a structure arisen without direct relationship to the morphology of the brain, conforming rather to the morphology of the dorsal wall of the en-

docranium in both recent and fossil frogs. It can be suggested, therefore, that diffe-
rences in this feature, evolved during frog phylogeny, are not of an adaptive nature, and
that they may be used to interprete phylogenetic lineages.

It is presumed that the endocranium of frogs in the course of its evolution followed a
trend common for the evolution of all vertebrates: a regressive skeletal development of
the endocranium beginning in its dorsal wall and progressing laterally and ventrally.
While, for example, the dorsal wall of the endocranium is complete in selachians, one
or more gaps occur in other groups which have reached a higher evolutionary level. This
trend culminates in advanced mammals whose endocrania are reduced and limited to
the base of the skull.

This assumption is supported by the examination of very early ontogenetic stages.
The early ontogenetic development of the endocranium is characterized by the diffe-
rentiation and growth of its lateral walls in the dorsal direction. Later, however, the abil-
ity to proliferate cartilage stops. As a result, the endocranium does not close on the dor-
sal side, leaving one or more gaps.* In the course of vertebrate evolution this decrease of
proliferation apparently continued to shift toward earlier ontogenetic stages: the cartil-
age proliferation stopped sooner, and the size of the gaps became larger. From this point
of view, the common phylogenetic trend in forming the dorsal wall of the vertebrate en-
docranium can be understood as a progressive loss of the ability of the cells on the mar-
gin of growing walls to produce cartilage.

The study of the individual variation of the frontoparietal incrassation in pelobatids,
together with the examination of this character in ranids (Roček 1980), makes it pos-
sible to reconstruct the development of the incrassatio frontoparietalis in these two
main lineages of the suborder Ranoidei (Sokol 1977). The mechanism of forming the
dorsal wall of the endocranium is probably the same also in other lineages of frogs.

The variation of the frontoparietal incrassation reflects the stage of endocranial roof;
in *Pelobates* the state variability of endocranial roof ranges from forms with quite
smooth margins of a single gap, to forms with a slight subdivision of the gap by means of
three projections of the wall margin: one of these projections juts out from the middle
of the posterior margin, the two others from the posterior thirds of the lateral margins.
These three projections can be explained as remnants of formerly well-developed tae-
niae. The incrassation with smooth margins would then be the more progressive varia-
tion.

Accordingly, in Ranidae the development of the incrassatio frontoparietalis has not
yet reached the stage where a single large fenestra exists in the dorsal wall of the endo-
cranium. An examination of the European material (Roček 1980) revealed that an ab-
solute majority of forms have a characteristic incrassatio frontoparietalis (i. e. consist-
ing of three parts). Several specimens, however, have been found whose anterior and
posterior parts of the incrassation are fused to various extent, in other words, the taenia
tecti transversalis is already partly missing. In one case the taenia tecti transversalis was
found to be completely absent and only the posterior part of the taenia tecti medialis

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* Our results agree with the conclusions of other authors. According to Weisz (1945) and Kotthaus
(1933) the gap in the roof of the chondrocranium in *Xenopus laevis* originates in the following way: lat-
eral walls of the chondrocranium, growing upwards from the basal plate, do not fuse in the area of the
gap.

was preserved. The reduction of the taenia tecti transversalis was found in different ranid species. Therefore, it cannot be considered a specific feature. It seems that the endocranium is only slightly reduced in Ranidae, but the above mentioned variations suggest the direction of the future development. (Morphological transitions are schematically drawn in fig. 8).
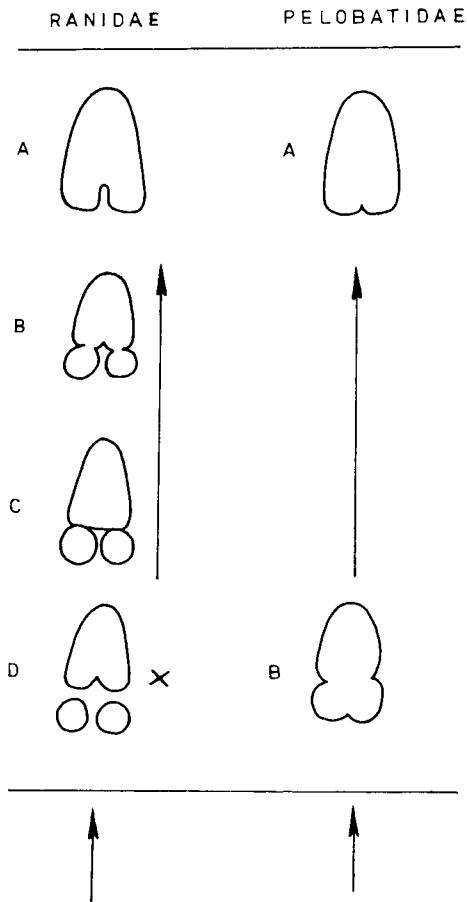

Fig. 8. Diagram illustrating the morphological variation of the frontoparietal incrassation in Ranidae and Pelobatidae. The arrows indicate a possible phylogenetic trend, the cross marks the most common variation. Compare stages A—A, B—B in both families.

On the basis of the above facts it can be suggested that the regressive skeletal development of the endocranium started independently in more than one developmental lineages of frogs: either two (Discoglossidae, see Spinar 1976) or three (e. g. Ranidae, Bufonidae) gaps originated in the dorsal wall of the endocranium, and the reduction could reach a higher degree in some lineages than in other ones. Therefore, the endocranium

of recent representatives of some lineages displays a single large fenestra, without any trace of connection between its lateral walls, and in other lineages remnants of taenia tecti medialis and taenia tecti transversalis still exist. Further studies on the frontoparietal incrassation based on a large number of both fossil and recent representatives might reveal the possible phylogenetic significance of the character.

Unfortunately, the frontoparietal incrassation cannot be studied in fossil frogs with complete and intact skulls. In fossil genera that occupy a key position (e. g. *Vieraella*), the number of specimens is too limited to allow a study of internal skull structures by methods resulting in a conversion of the original state of preservation (by using, for instance, serial grinding). If in the future a large number of specimens becomes available, these methods might be useful in trying to give an answer to the question of the phylogenetic significance of the incrassatio frontoparietalis.

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