

Origin and evolution of the frontoparietal complex in anurans

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Abstract. The frontoparietal is a unique feature of anurans, not only if this group is compared with other amphibians, but also with other vertebrates as well. It is often used as an important character in anuran systematics. However, little is still known about its evolutionary origin and significance. This is the reason why its state in *Triadobatrachus* and fossil anurans was examined, and compared with the condition in osteolepiforms and labyrinthodonts. Besides that also an information from the larval development was taken into consideration. It follows from all these data that the frontoparietal in adult anurans is a compound bone; the originally independent elements forming it (frontals, parietals, and some other ones) either coalesced with each other, or have disappeared during the course of evolution, often in convergent fashion. As the original state is better reflected in early developmental stages, one may suppose that larval condition also better reflects phylogenetic relations than the definitive bone complex of adults.

Introduction

The frontoparietal complex belongs among the most specialized features of the anuran skeleton. Although the general structure of the skull in the Anura is rather uniform, this complex varies considerably (Trueb, 1973). It can be paired or unpaired, of various extent (so that a fontanelle following the median suture could arise between left and right frontoparietal), with dorsal surface sculptured or smooth, with the *incrassatio frontoparietalis* on its ventral surface (Jarošová and Roček, 1982) of various shape and configuration, and in various contact with neighbouring elements. To understand properly this variation (which is necessary if the frontoparietal should be used as a character useful in anuran systematics) we need to know (a) evolutionary origins of the state found in anurans, (b) embryological development of the complex in representatives of the most important groups, and (c) possible functional reasons of its diversity.

The problem has been studied already by Griffiths (1954) who also used both paleontological and embryological approaches. However, new fossils were recently discovered that either are claimed to belong among anuran ancestors or represent the

earliest known fossil record of the Anura. Besides this, *Triadobatrachus* was recently re-examined (Rage and Roček, 1986; in press). Also, further embryological data are now available as well. This all, together with continuing discussion dealing with criteria of homology of dermal cranial bones, provides a basis for further consideration that is more complete than was available three decades ago.

1. Origin and evolution of the frontoparietal as evidenced by fossils

If the frontoparietal of anurans should be traced back to their ancestors (supposed back-sequence is *Triadobatrachus* - Palaeozoic labyrinthodonts - osteolepiform crossopterygians), the most important is whether homologous elements are compared. There has been some dispute concerning the homology of frontal and parietal bones in fishes and tetrapods since Westoll's ideas were published (1943). Several criteria have been suggested for this purpose, some of them being later refuted as inappropriate. Reliable in establishing homologies of dermal roofing bones seemed to be their relation to brain (Schowing, 1961; 1968a, b, c; but cf. Moy-Thomas, 1941: 681-682), neuromasts (Allis, 1898: 428-429; 1899; Pehrson, 1922; Schmalhausen, 1950: 179, and many others; however, certain limitations of this character were stated by Devillers and Corsin, 1968: 414, and criticism was expressed e.g. by Moy-Thomas, 1941: 681 and Parrington, 1949; 1950: 544; 1956; 1967), and also to the nerves supplying neuromasts of the sensory lines and possibly to some others nerves and vessels (Jarvik, 1967: 188). However, for comparison among living animals and fossils (in which soft organs in most cases can be only deduced from the surrounding osteological structures), as well as for that between fishes and tetrapods (in which, with exception of some amphibians, lateral line system disappeared), the topographic relation between exocranial and endocranial structures seems to be most profitable (but cf. Borgen, 1983: 739-743). This is confirmed by studies of the normal dermal ossification (e.g. Frommer and Margolies, 1971: 1266 "maintain that the close spatial relationship between initial chondrogenesis of Meckel's cartilage and initial intramembraneous ossification in the mandible indicates induction of membrane bone by Meckel's cartilage" - citation from Hall, 1975: 338; but see already Allis, 1898: 431), as well as by studies using methods of experimental embryology. The latter revealed that if endocranial cartilage is extirpated, the corresponding exocranial bone arises only in its initial formation but not in its normal morphological adjustment (Leibel, 1976). The vacant space is only in limited extent captured by neighbouring dermal bones¹. One can thus say that for exocranial bones certain endocranial structures are used as a substrate or surface for con-

¹ This cannot be confused with excision of dermal bones which in some cases does result in partial invasion of neighbouring dermal bones into vacant space. Experience based on fishes, amphibians and reptiles (Tatarko, 1934; Leibel, 1976; Lebedkina, in verb.) seems to suggest that on lower evolutionary levels this feature is more strikingly developed. In mammals, on the other hand, a new bone arises of almost the same shape and extent as original one, without a sign of invasion by neighbouring bones (Troitzky, 1932: 508, figs 1a-c). This confirms potential capacity of certain space to produce dermal bone *de novo*.

densation of osteogenic mesenchyme (Leibel, op. cit.: 95). Thus the criterion of exocranial-endocranial relation seems to be most reliable, at least for cranial roofing bones, though it is necessary to suppose that besides the main factor some additional ones are also active in dermal osteogeny, and all function together.

Using this method, it may be assumed that what is designated as the frontal in labyrinthodonts with supposed affinities to anurans (Bolt, 1969, fig. 2; 1977, text-fig. 1) corresponds to the equally termed element (*sensu* Jarvik, 1980, fig. 120) in osteolepiform crossopterygians, and has the same spatial relations to the neural endocranium as the anterior part of the frontoparietal in anurans. Comparing evolutionary stages represented by some crossopterygian fishes, Palaeozoic amphibians, and anurans (it should be emphasized that all below-mentioned forms serve only as representatives of pertinent evolutionary levels; in other words, e.g. *Doleserpeton* should be understood as a representative of the evolutionary level preceding that represented by *Triadobatrachus*, but not necessarily should be taken as an ancestor of the latter) it can be stated that both in late Devonian crossopterygian fish *Eusthenopteron* and early Permian rhachitomous dissorophoid *Doleserpeton* the frontals adjoin the orbitotemporal region of the neural endocranium dorsally, extending approximately from the level of the foramen pro r. medialis n. ophthalmici to the level slightly anterior to the foramen n. trigemini. In *Eusthenopteron* the parietals occupy the space posterior to this level up to that of n. vagus, while reaching only the tectum synoticum in *Doleserpeton*. Thus (as can be seen also from fig. 1) the only noticeable difference between these two forms are the lateral extent of the frontals (they cover also the space between the braincase wall and the palatoquadrate in *Eusthenopteron*; in *Doleserpeton* they reach only slightly beyond the braincase walls) and the posterior extent of the parietals. These differences seem to be related to the changes in the neural endocranium proportions (see below).

In the early Triassic *Triadobatrachus*, which is considered as intermediate between Palaeozoic amphibians and anurans, the frontals and parietals fused with each other, giving rise to the frontoparietal complex (Eaton's, 1942 and Sedra's, 1949 view that parietals disappeared in the course of evolution from Palaeozoic amphibians to *Triadobatrachus* and that what is called the frontoparietal is actually the frontal seems to be highly improbable, as shown by Griffiths, 1954: 788). Although within the parietal portion of the complex a slight median suture can be still traced, in its anterior part both halves fused completely. Remarkable is the postero-lateral extent of the bone; it reaches the crista parotica. This is a unique character of *Triadobatrachus*, because the parietal in crossopterygians and labyrinthodonts, and the parietal portion of the complex in anurans do not reach laterally to that level.

In those Jurassic anurans in which the frontoparietal is satisfactorily preserved, i.e. in *Vieraella* (Estes and Reig, 1973: 14, fig. 1-1), *Notobatrachus* (fig. 1), *Eodiscoglossus* (Hecht, 1970: 3; information is, however, rather vague) and "Las Hoyas" frog² (fig.

² "Las Hoyas" and "Green River" frogs are fossils to be described by R. Estes (the former) and by R. Estes and L. Grande (the latter).

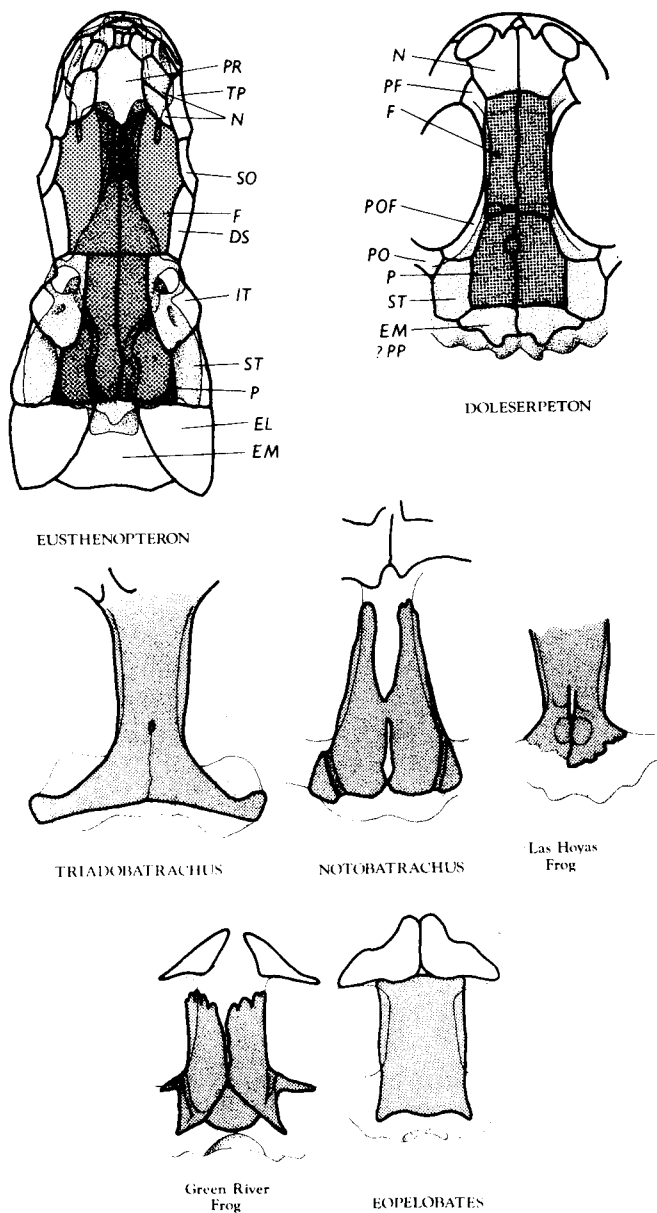


Figure 1. Frontoparietal of *Triadobatrachus* and some fossil anurans, compared with skull roof of *Eusthenopteron* and *Doleserpeton*. Frontals, parietals and frontoparietals are stippled. Not to scale. Abbreviations: DS - dermosphenoticum; EL - extrascapulare laterale; EM - extrascapulare mediale; F - frontale; IT - intertemporale; N - nasale or nasal; P - parietale; PP - postparietale; PR - postrostrale; SO - supraorbitale; ST - supratemporale; TP - tectale posterior. *Eusthenopteron* after Jarvik (1980), *Doleserpeton* after Bolt (1969, 1977).

1), the variation in the shape and extent of this element does not differ from that in Recent anurans. In *Vieraella*, the oldest known anuran (Liassic), the frontoparietal is badly crushed; despite this Estes and Reig (1973: 14) considered it paired, with an anterior fontanelle, and with a postero-lateral extension on the otic capsule.

Also in *Notobatrachus* (Tithonian) the frontoparietal is paired. In fig. 1 a juvenile specimen (length of the humerus without epiphyses 15.5 mm, neural vertebral arches not yet fused, epiphyses not yet ossified, unclosed suture between parietal parts of the frontoparietal) is given, in which frontoparietal ossification is not yet completed. However, Estes and Reig (1973: 20) stated that a fontanelle separating both frontal parts persists still in adults. The same holds for the groove for the arteria occipitalis (as evidenced by Museum La Plata specimen 55-VI-1-1 with length of the humerus with epiphyses 28 mm; see also Estes and Reig, op. cit.: 20, fig. 1-4).

In "Las Hoyas" frog (Kimmeridgian; Estes, in verb.) the frontoparietal is preserved in ventral aspect, displaying its frontoparietal incassation. Median suture is well preserved, and in mid-section it is unclosed. Remarkable is the very limited extent of the posterior part of the complex, leaving greater part of the otic capsule and the tectum synoticum uncovered.

Quite unusual is the frontoparietal in "Green River" frog (Eocene). Besides two frontoparietals that extend out postero-laterally into distinct outgrowths adjoining the dorsal surface of the prominentiae can. semicirculares posteriores (which recalls the condition in pelobatids) and display a groove for occipital artery, there is also an unpaired median element adjoining the tectum synoticum. Although undoubtedly this is an adult specimen (as evidenced by ossified epiphyses), the whole complex strongly resembles the praemetamorphic state in *Pelobates* and *Eopelobates* (see figs 2 and 3), including limited extent of the complex anteriorly (so that there is no contact with nasals) and not yet closed suture between the frontal parts. The only difference is an outgrowth adjoining the antero-dorsal surface of the prootic, which seems to be separated from the frontoparietal by a suture.

The adult frontoparietal condition in *Eopelobates* (Oligo-Miocene) is well known from many specimens (fig. 1). It is unpaired complex with postero-lateral outgrowths directed onto the dorsal surface of the prominentiae can. semicirculares posteriores. Also in palaeobatrachids (see Špinar, 1972, pls 10, 11, 22, 23, 24a) the complex is unpaired; even in young metamorphosed specimens there is no trace of the median suture. Its posterior margin bears a prominent median convexity above the tectum synoticum, and two pointed but very distinct postero-lateral horns (that never extend posteriorly over the level of the median convexity).

In adult fossil pipids (see Bacz, 1981, tab. I for review) the frontoparietal, if preserved, always lacks a median suture. This holds true also for *Eoxenopoides* (Estes, 1977: 55, figs 2A, 3; but cf. Haughton, 1931: 235). In *Shelania* (syn. of *Xenopus*, according to Estes, 1975a: 270-271) some specimens were reported to have an obliterated median suture (Casamiquela, 1961: 85) as evidenced by a longitudinal depression, others (e.g. Museum La Plata specimen 62-XII-22-1) have the frontoparietal unpaired, with flat

convexity along its median axis, closely resembling the condition in *Xenopus romeri* (Estes, 1975b, fig. 1) and Recent representatives of this genus (Reumer, 1985, fig. 2).

From this comparison of the frontal and parietal condition in pre-anuran level with oldest known anurans or those fossils in which this composite bone deviates from the common scheme of two frontoparietals separated by median suture, the following facts may be deduced: (a) The fusion of originally independent frontals and parietals is the most striking feature and it is hard to guess which (if any) functional reasons caused this fusion. The frontoparietal complex belongs among the first typical anuran characters (see postcranial skeleton in *Triadobatrachus*), and already in very early evolutionary stages of anurans the fusion of the frontal and parietal could have been accompanied with fusion of both frontals medially. Fusion or retained separation of both frontoparietals seem to occur quite irregularly in anuran phylogeny; while entirely or partially fused frontoparietals (more specialized condition) occurred in some early forms (*Triadobatrachus*, Cretaceous pipids), separated bones (unspecialized condition) persist in many modern Recent anurans. (b) Owing to changes in both endocranial and orbital proportions, the frontals became elements participating in bordering orbits, and only slightly extending over the braincase walls laterally. Once this condition is attained, it persists throughout anuran phylogeny regardless of other frontoparietal characters. The shape of the frontal part of the complex (viewed dorsally) always corresponds to that of the orbitotemporal section of the braincase; its extent both in anterior and medial directions varies according to degree of ossification so that frontoparietals do not contact nasals and/or anterior median fontanelle could arise. (c) The parietal portion of the complex in anurans adjoins approximately the same extent of the neural endocranium as in crossopterygians and labyrinthodonts. Differences in its shape are the result of antero-posterior shortening of the otic capsules and their lateral expansions, which is evidenced by experiments by Leibel (1976: 88-89). However, in *Triadobatrachus* the postero-lateral wings of the frontoparietal reach the level of the crista parotica, the condition which is found neither in crossopterygians and labyrinthodonts, nor in anurans. The extent of the posterior part of the frontoparietal considerably varies already in Jurassic forms (cf. *Notobatrachus* with "Las Hoyas" frog). (d) Although most fossil and extant adult anurans have the frontoparietal paired or of paired origin from parietals and frontals only (see below), there may be some forms that display additional elements within the complex. It concerns either an unpaired median element which can be well distinguished in adults ("Green River" frog) and tadpoles (figs 2 and 3), or paired elements adjoining the prootics antero-dorsally.

Summarizing the contribution of adult fossils to the problem of the frontoparietal in anurans one can conclude that except for variation in its extent and proportions that may be in some cases interpreted as possible presence of other elements than frontals and parietals within the complex, only very rarely more precise indications of the origin of this composite bone can be found. This conclusion, however, does not refer to fossil tadpoles that will be dealt with below, together with Recent anuran larvae.

2. Origin and evolution of the frontoparietal as evidenced by its development in larvae

It is generally agreed that larvae, although they acquired some adaptive characters during the course of evolution, may indicate by their non-adaptive characters a state that occurred on lower evolutionary levels. Adults, on the other hand, are more specialized and thus deviated from the original condition. Hence, one may suppose that early stages of the frontoparietal development in anurans could indicate ancestral state of this compound bone.

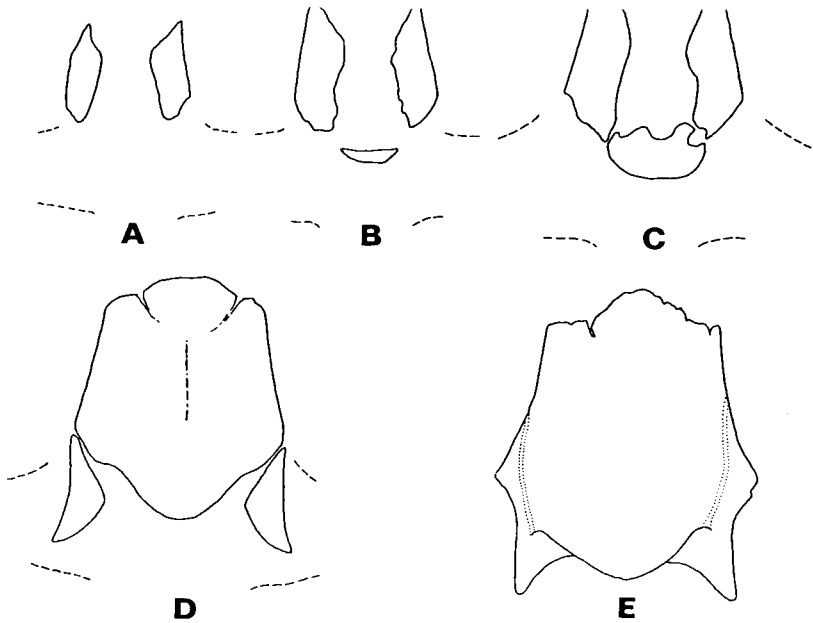


Figure 2. Development of the frontoparietal complex in *Pelobates fuscus*. Outlines of the otic capsules are indicated by a broken line, arteria occipitalis and a. orbitonasalis canals are dotted. After Roček (1981).

According to present knowledge of the development of the frontoparietal in anurans this complex arises basically from left and right ossification centers. However, while in urodelans the parietals and frontals arise always separately (and in primitive representatives, e.g. *Ranodon*, there are even three ossifications within the area of future frontal, similar to actinopterygians; see Lebedkina, 1979: 163, figs 82, 83), this is not regular in anurans. Also in this group frequently two ossifications arise that are supposed to represent frontal and parietal (e.g. Parker, 1871: 162, pl. VII, fig. 3; Gaupp, 1896: 50; Erdmann, 1933: 567-568; Griffiths, 1954: 782, pl. I, fig. 1; Lebedkina, 1979, figs 84, 85). However, in some groups it is not possible to trace the separate origin of frontals and parietals, and some authors even deny such a possibility (Eaton, 1939: 95; 1942:

151; Sedra, 1949: 638-639; Trueb, 1970: 588; 1966: 569; Gaudin, 1973: 207). One can agree with Lebedkina (1979: 165) that the rate of dermal bone development in Amphibia is so high that using limited number of stages for examination does not allow to find separate frontal and parietal ossifications. She did find them also in bufonids, hylids and discoglossids. Also Griffiths (1954: 782) found discrete frontal and parietal centers in some species previously claimed as having but a single center, and in some cases (e.g. *Bufo marinus*) he found at least one center clearly divided into anterior and posterior parts. Lebedkina's explanation has the only alternative given by Griffiths (op. cit.: 788): within Salientia there exists a trend towards the gradual approximation of the frontal and parietal ossification centers, which in some groups or even species could already reach its conclusion. From this point of view the fused frontoparietal would be regarded as more advanced while frontal and parietal discrete centers as primitive condition.

Comparing the condition in Urodela and Anura, and using spatial relation of the ossification centers to the underlying endocranium as a criterion of homology, Lebedkina (op. cit.: 165) also concluded that while in the former group the frontal in adults is a composite bone resulted by fusion of originally three frontals, in anurans the adult frontal corresponds only to frontal 3. On the background of this knowledge the conclusion by Sedra (1949: 640), Eaton (1942: 153) and Ramaswami (1956) that the frontoparietal of anurans is represented only by the frontal appears to be incorrect.

In any case, paired frontals and parietals arise in anurans always as first components of the future complex, and soon fuse into a thin, elongated plate rimming dorsally the braincase walls within the orbitotemporal region of the skull. This holds true not only for groups having paired frontoparietal in adults, but also for those whose definitive frontoparietal is completely fused (*Xenopus* - Brown and Estes, in prep.; Sedra and Michael, 1957: 11; pers. observ.; *Pipa* - fig. 4; *Pelobates* - fig. 2; *Eopelobates* -fig. 3; *Shomronella* - Estes et al., 1978: 378, figs 11B, 12A, 13A; despite the fact that the fully metamorphosed stage is not known in this latter form the frontoparietal was undoubtedly fused in adults, as indicated by later developmental stages). Both in *Xenopus* and *Pipa* the ossification starts within the orbitotemporal region, anterior to the otic capsules. This indicates that the ossa frontalia are concerned. Then, the ossification proceeds posteriorwards, so the strip of ossified tissue soon reaches the contact with the antero-medial surface of the otic capsule. Later stages rather differ in both genera. While in *Xenopus* the ossification is directed towards the midline along its whole length (Sedra and Michael, 1957: 20), in *Pipa* it follows anteriorly and posteriorly along the margins of the frontoparietal primordium, which is well delimited (fig. 4C). Then, the ossification proceeds quite rapidly from the margins toward the center of the primordium, so that no median suture can be observed (see also Ramaswami, 1956; Parker's statement, 1876: 658, pl. 61, fig. 2, that the frontoparietal in *Pipa* is formed from four centers is no doubt based on the structures seen through still transparent bone). This stage corresponds to the final stage in *Xenopus* (fig. 4D), and is in further development completed with antero-lateral horns whose earliest developmental stages are

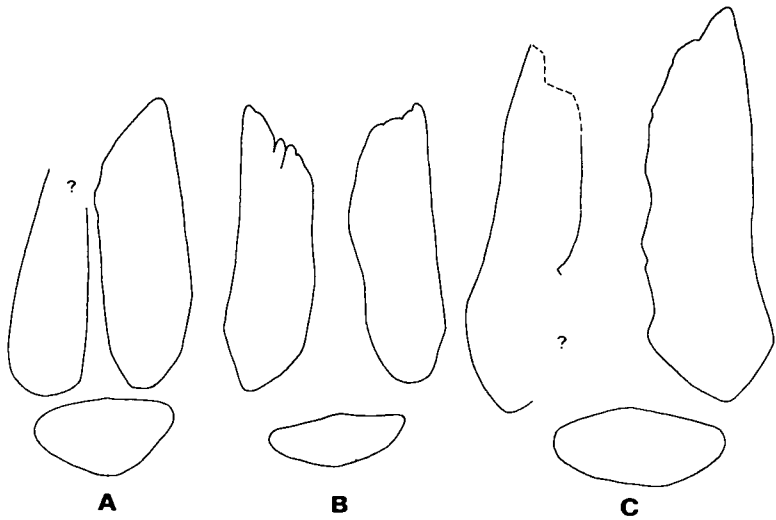


Figure 3. Embryonic stage of tripartite frontoparietal complex (corresponding to the stage in fig. 2C) in three tadpoles of *Eopelobates bayeri*. After Roček (1981).

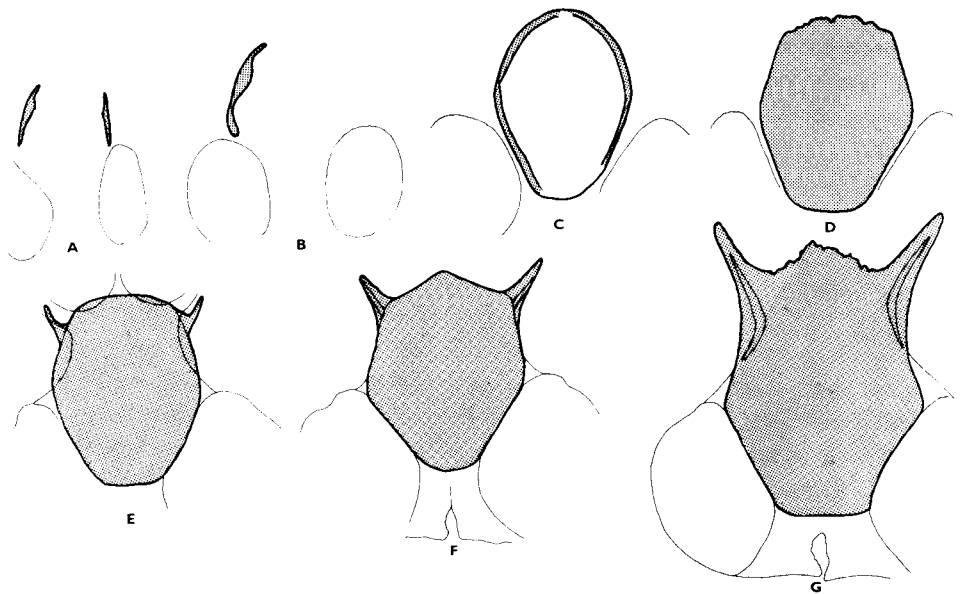


Figure 4. Development of the frontoparietal complex, in relation to otic capsules and some other endocranial structures, in *Pipa pipa*.

represented by vertical ridges adjoining the orbitonasal walls posteriorly (fig. 4E), and only later they spread also onto their dorsal surface (fig. 4F). Vertical ridges adjoining both orbitonasal and lateral braincase walls are well seen on the stained specimens; thus it can be deduced that that part of the frontoparietal between mentioned vertical ridges and the lateral margin of the bone represents the lateral increase of the complex in the latest stages of its development.

Although there is no direct evidence, it may be supposed that the development of the frontoparietal in *Saltenia* proceeded in a very similar way, though it is already fused in tadpoles and young metamorphosed specimens (Baez, 1981: 134). The same holds for palaeobatrachids (pers. observ.). *Shomronella* (Estes et al., 1978, and pers. observ.) is probably close to developmental scheme of *Xenopus*. Despite of the statement of Haughton (1931: 235) it seems more probable that *Eoxenopoides* is not an exception from other pipids (Estes, 1977: 55, figs 2a, 3). However, even if it would be the only pipid in which a paired frontoparietal persisted until the adult stage, this could be explained by the observations by Brown and Estes (in prep., fig. 2). According to them the stage in which both frontoparietals fuse with each other differs considerably in some *Xenopus* species, and the fusion can be retarded even within single species (e.g. in laboratory *X. laevis* the fusion is in later stages than in wild specimens). Thus the fusion can be considered as a rather variable character both intra- and interspecifically.

In *Pelobates* and *Eopelobates* the development of the frontoparietal is well documented. As in all other anurans the ossification starts as two strips adjoining lateral braincase walls within the orbitotemporal region (fig. 2A). Soon afterwards these two ossification centers are completed by an unpaired element adjoining the tectum synoticum. The former two centers grow medially and slightly posteriorly, while the latter grows anteriorwards. This results in the fusion of all three elements. In *Pelobates*, two other ossifications seem to arise independently lateral to the course of the arteria occipitalis (fig. 2D), which later fuse with the former complex. The condition found in larval *Pelobates* and *Eopelobates* is, so far as it is known, unique among anurans, except for the "Green River" frog (which is, remarkably, an adult specimen).

Discussion

In evaluating the larval condition it is necessary to start with a decision as to whether arising ossifications really represent ossification centers or only islets of ossifying tissue. As criteria for this purpose topographical stability of these ossifications can be cited, as well as their regular occurrence in all specimens.

According to the above criteria those ossifications can be regarded as true ossification centers that arise above the upper margins of the braincase walls within the orbitotemporal region. Except for pathological cases (see fig. 4B) they are always present. They can be homologized with frontals and, when they reach the otic capsule, with frontoparietals. Similar constant ossification is the unpaired median element adjoining the tectum synoticum in *Pelobates* and *Eopelobates*. It can be homologized with

corresponding element in the "Green River" frog. Also that part of the frontoparietal in *Pelobates* that arises laterally from the a. occipitalis is in agreement with the above criteria.

Besides just mentioned, there are some other ossifications within the area of adult frontoparietal which, however, do not maintain such positional and occurrence stability. Tschugunova (1981: 120, figs 1, 2, 3) found dermal ossifications (called interfrontals) in *Bombina orientalis* and *B. bombina*. They vary considerably in number, shape and location. Another type of ossification is called "co-ossified ethmoid" (Trueb, 1966: 572) or "dermal sphenethmoid" (Trueb, 1970; 1973: 75-76; Duellman and Trueb, 1985: 317). It is said that it arises from a separate, dermal layer above the sphenethmoid, which later fuses indistinguishably with the latter, resulting thus in a bone of compound origin. It is confined to some casque-headed hylids. Tschugunova (op. cit.: 120), however, found a similar element between the nasals and the anterior portion of the frontals in the two species of *Bombina* noted above. She also mentions that in adults it is impossible to discern any border between endesmal and enchondral portions of the bone. Therefore it is quite possible that this bone might be similar to that found in *Pelobates* (Roček, 1980: 16, 18, figs 9, 12). Bolkay (1919: 283, fig. 6) called it "glabella". In fact, it is an uncovered dorsal surface of the sphenethmoid. According to Basoğlu and Zaloğlu (1964: 236, figs 13-16) this triangular field of exposed sphenethmoid can be observed only in young individuals, later this field is invaded and thus covered by nasals and frontoparietal. Its surface is sculptured similarly to neighbouring dermal bones, so it might be sometimes confused with dermal bone (Jarvik, 1968: 508). It should be also noted that "interfrontal", "internasofrontal" or "nasofrontal" was described also in *Osteophorus romeri* v. Mayer and *Eryops megacephalus* Cope (Temnospondyli, Eryopidae), *Trematosaurus sobeyi* Houghton (Temnospondyli, Trematosauridae), *Batrachosaurus browni* (Temnospondyli, Brachyopidae) (Broili, 1917: 372, figs 15, 16; Säve-Söderbergh, 1935: 42, text-figs 18, 19, 21), and *Ricinodon* (Microsauria, Hapsidopareiontidae). Besides these fossils, similar condition can also be found in caecilians. However, H. v. Mayer (1859: 101; *ex* Broili, 1917) was the first who pointed out that in the latter group this is in fact an exposed sphenethmoid. The above fossils should be checked from this point of view (see also Broili, 1917: 573-574; however, Säve-Söderbergh, 1935: 42-43, considered this element to be homologous with the median postrostral of osteolepiforms).

Concerning the unpaired median element of pelobatids, two explanations are possible: first, this might represent an evolutionary neo-morph that had arisen within the posterior section of the interparietal suture during the period of evolution from the level of *Triadobatrachus* to pelobatids. Second, this ossification center represents an inheritance from ancestors.

Although earlier authors did not use other criteria of homology than topographic relations to neighbouring exocranial elements, and despite the fact that in some cases knowledge of underlying endocranial structures is insufficient, some unpaired elements similar in position to that in pelobatids may be found in labyrinthodonts,

namely the “centroparietale” in one specimen of *Aphaneramma* Woodward (Temnospondyli, Trematosauridae) (Wiman, 1915: 18; Broili, 1917: 566, fig. 6; Säve-Söderbergh, 1935, text-fig. 56; 1936: 65, text-fig. 24; 1937, fig. 8A), the “parieto-extrascapular” in *Ichthyostega* (Jarvik, 1980: 241, fig. 171), and the “median extrascapular” in osteolepiforms, many porolepiforms, and primitive actinopterygians. However, in most labyrinthodonts the pertinent space is occupied by a pair of variously termed bones (see below).

In evolutionarily more advanced vertebrates a similar unpaired element was found in most reptiles where it is called “postparietal”, “interparietal”, or “dermal supra-occipital” (Romer, 1956: 62). Although the skull in some reptiles is considerably modified in its parietal region, this bone maintains remarkable constancy (e.g. Brink, 1982). In those mammals in which this element occurs (called mainly “interparietal”), it is always of paired origin, and only later in ontogeny it fuses together, and in some cases (Rodentia, Ruminantia) it even fuses with the parietals (Maggi, 1898: 215; Huene, 1912: 522; Watson, 1913: 70; Säve-Söderbergh, 1935: 109; Stadtmüller, 1936: 923).

Ossification arising incidentally within sutures between developing parietals and occipital in some mammal embryos (in human skull it is called “os incae” and may be single or multiplied) varies in its occurrence, size and shape, and should not be homologized with the interparietal of reptiles.

As is quite clear from the above account, an unpaired element adjoining the tectum synoticum is very rare in labyrinthodonts. Disregarding *Ichthyostega* and one specimen of *Aphaneramma*, in all other members of this group, incl. the earliest ones (e.g. *Acanthostega*, see Jarvik, 1980, fig. 175A) the posterior section of the skull roof is occupied by a pair of bones (termed “retroparietals” *sensu* Maggi, “dermo-supra-occipitals” *sensu* Miall, “dermooccipitals” *sensu* Williston, “parieto-extrascapulars” *sensu* Säve-Söderbergh³, and “postparietals” *sensu* Broom), and no odd element occurs⁴.

If the first explanation of its occurrence in cases above the evolutionary level of rhipidistians would be correct (i.e. that a neo-morph is concerned), then the question arises what would be the reason for re-development of the element once lost in phylogeny. As this appears highly improbable, another alternative explanation should be taken into account, namely that the mentioned odd element is an inheritance from ancestors. Supposing this, the question arises what is the evolutionary origin of the paired bones in the middle of the posterior part of the dermal skull roof in labyrinthodonts. Two possible explanations may be given, both of them resting on different interpretations of the dermal roofing bones, mentioned above in connection with various criteria of homology.

³ Säve-Söderbergh (1935: 97-99) did not consider the two most posterior bones in the middle of the dermal cranial roof of anthracosaurs homologous with similarly located bones in other labyrinthodonts.

⁴ In *Acanthostega*, Jarvik (1980: 244) regards pair of most posterior bones of the skull roof to be parietals.

Romer (1941: 158-159, fig. 4) maintained that a pair of bones anterior to the extrascapular series in osteolepiforms are postparietals, while parietals are those elements that enclose the pineal foramen. The extrascapular series is supposed to be lost during the transition from fish to tetrapods (cf., however, criticism of e.g. Schmalhausen, 1950: 180, and Jarvik, 1967), and both postparietals either fused with one another (in *Ichthyostega*), or retained their paired nature (in *Acanthostega* and post-Devonian labyrinthodonts). If this hypothesis is further developed, then one can suppose that in anurans (with few exceptions, see below) both postparietals disappeared, while in most reptiles they fused together, giving rise to a single element. The same situation is in mammals; indications of the paired nature of the bone are still observable in their ontogeny. This all sounds quite reasonable up to the point when one starts to consider role of sensory lines in the origin of dermal bones and their course in crossopterygians and early tetrapods. Then the presence or absence of these lines within certain bones causes problems in acceptance of this hypothesis.

An alternative explanation has been proposed by Säve-Söderbergh (1932, 1935, 1936). According to him the pair of bones in question in most labyrinthodonts is in fact represented by compound ossifications called parieto-extrascapulars (comprising posterior pair of parietals, the median extrascapular, and the medial pair of lateral extrascapulars), but only by median extrascapular subdivided into two parts in antracosaurs. If this hypothesis is followed, then it has to be supposed that in *Ichthyostega* both parietals and median extrascapular fused together, while in post-Devonian temnospondyls parietal parts retained their paired nature and the median extrascapular was subdivided into two parts, both of them fusing with each parietal. However, it should be noted that although some variation of the extrascapulars was observed in osteolepiforms, it never concerned a division of the median extrascapular (Jarvik, 1948: 66, fig. 17). Following further the hypothesis, parietals had to gain their independence again, fusing later in ontogeny with frontals. According to Säve-Söderbergh in reptiles (descendants of Anthracosauria), and consequently also in mammals, the bones in question have to be homologized with the median extrascapular only. It is supposed that in the Anthracosauria this was subdivided into two parts, and in most reptiles it fused again forming this single element (in adults).

It is beyond the scope of this paper to decide which of these two hypotheses is correct. Disregarding thus the problem of the homology of the bones during fish-tetrapod transition (and consequently the problem whether these bones should be termed postparietals, parieto-extrascapulars, or median extrascapular) we can accept the conclusion that the bones which are designated with these terms may be homologous with single element called generally interparietal of most reptiles and mammals. This was already suggested by Huene (1912: 524).

Returning to anurans one may suppose that these medial elements could disappear in the course of evolution from anuran ancestors to *Triadobatrachus*, contrary to the opinion of Hecht (1962: 42) who maintains that the frontoparietal in *Triadobatrachus* does include postparietals and even tabulars, and of Säve-Söderbergh (1936: 156, text-fig.

67) who believed that the frontoparietal in *Rana* includes the equivalents of his frontal, frontoparietal, but also his parieto-extrascapular. The only group so far known among anurans, in which these bones seem to persist, though fused into a single bone as in reptiles, are pelobatids (the systematic status of the “Green River” frog is still in the process of examination; see footnote p. 387).

Contrary to the odd element just discussed, the ossifications arising lateral to arteria occipitalis are not restricted to pelobatids only. In *Triadobatrachus* there is no trace of the a. occipitalis and it probably extended between the endocranium and the exocranial layer, as in crossopterygians and very probably also in labyrinthodonts (Säve-Söderbergh, 1936: 158, supposed the presence of this artery without any detailed knowledge of its course). In adult pelobatids and many other fossil and Recent anurans this artery extends through the canal within the posterior section of the frontoparietal. The canal is a remnant of the embryological condition where a space is present between the main body of the frontoparietal and its postero-lateral portion (fig. 2D; Reinbach, 1939, figs 2a, b, 3, 4). The connection between the two arises first beneath the artery and later above it. This condition seems to be preserved in *Notobatrachus*, “Green River” frog (fig. 1) and some Recent anurans. The artery may also extend entirely above the frontoparietal, leaving no trace of its course on the bone surface, or lateral to the bone if this is represented only as a narrow strip along the median suture. The latter is the case with ranids.

Looking back at labyrinthodonts and crossopterygians one can find at the corresponding area of the endocranium the lateral extrascapular (called by some early English writers “the supratemporal” – see Allis, 1899: 62) or the tabular (in other terminology). We are here concerned again with different interpretations of the dermal roofing bones, however, for our purpose one may admit that the elements adjoining the postero-lateral section of the otic capsules in labyrinthodonts are lateral extrascapulars (or tabulars; see also Borgen, 1983: 745-746). If these elements are homologous with the lateral extrascapulars in osteolepiform fishes, then we could trace a particular evolutionary trend (fig. 5). While in the osteolepiforms the bones in question are almost without any contact with the neural endocranium, and arise most probably depending on the supratemporal commissural canal and postotic canal, in labyrinthodonts they already adjoin, at least partly, the postero-lateral section of the otic capsule. If this trend is supposed to continue also in anurans, then it would result in that part of the frontoparietal which is lateral to the groove in *Notobatrachus* and the “Green River” frog, or to the course of the a. occipitalis in some other anurans (Reinbach, 1939, called this element os supratemporale).

It follows from the comparison of both larval and adult condition known that the elements in question are not included in the frontoparietal of all anurans. Early anurans are expected to have them (see *Notobatrachus*), but some of them (e.g. “Las Hoyas” frog) already have the frontoparietal reduced to such extent that it covers only very limited area of the otic capsule. On the other hand, modern anurans (e.g. ranids) are supposed to have them lost, but there are some living groups in which they still persist (e.g. pelobatids).

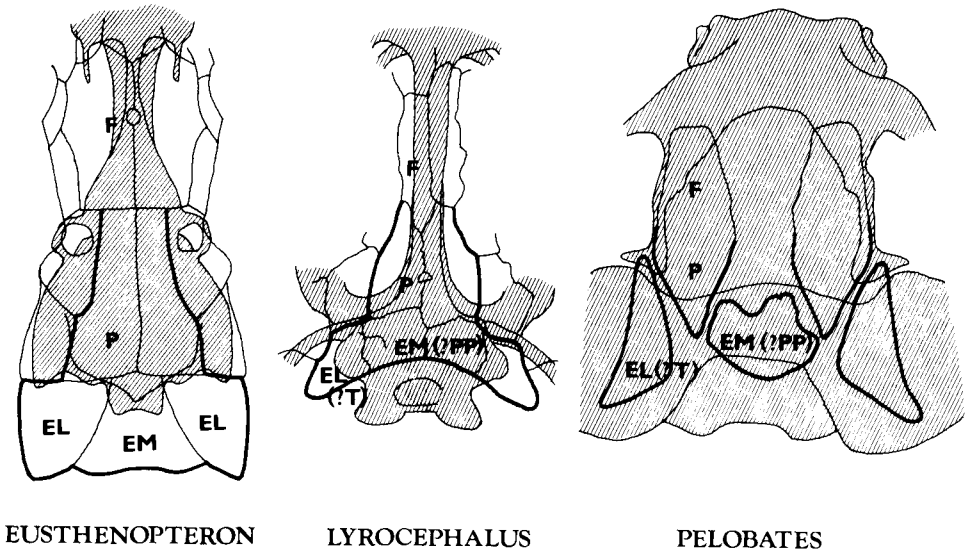


Figure 5. Possible evolution of the posterior part of the frontoparietal complex from the state in crossopterygians, via some labyrinthodont stage, to pelobatid-like anurans (larva at the last stages of metamorphosis). Endocranium hatched. Abbreviations: EL - extrascapulare laterale; EM - extrascapulare mediale; F - frontale; P - parietale; PP - postparietale; T - tabulare. *Eusthenopteron* after Jarvik (1980), *Lyrocephalus* after Säve-Söderbergh (1936), *Pelobates* after Roček (1981).

Conclusions

If it is accepted that the separate ossification centers observed during the development of larval frontoparietal represent dermal bones occurring in labyrinthodont and osteolepiform anuran ancestors, and if it is accepted that there is certain functional relation between location, shape and extent of dermal roofing bones on one hand, and corresponding parts of underlying endocranium on the other hand, then some conclusions can be made. (1) The fusion of the originally independent elements resulted during the transition from labyrinthodonts to immediate anuran ancestors (represented by *Triadobatrachus*) in the formation of the frontoparietal complex. In *Triadobatrachus* this complex, although formed already in accordance with the shape of the otic capsule, is unique in that it extends laterally up to the crista parotica; this suggests that it probably includes also those elements that occur in labyrinthodonts at the same area. (2) The extent of the fusion of the elements constituting the frontoparietal is different in various lineages. While already in *Triadobatrachus* left and right frontoparietals partially fused together, and in early (Cretaceous) pipids they already fused completely, in other early anurans (but even in modern groups like e.g. in hylids, ranids and bufonids) they retained their separate nature. (3) The number of elements contributing to the frontoparietals seems to be different in various anurans too. As the element which in crossopterygians and labyrinthodonts is called the median extra-

scapular, parieto-extrascapular, or postparietal, and in reptiles and mammals the interparietal, was never recorded in anurans except for pelobatids and the “Green River” frog, one may suppose that it survived in very few anuran lineages. Contrary to this, the element which is located lateral to the a. occipitalis is preserved in various groups of anurans. However, similarly to the case of fusion, in some early forms this element could be reduced or vanished entirely (e.g. “Las Hoyas” frog) while it is still present in some Recent groups.

It is obvious from these conclusions that frontoparietal characters (such as fusion of left and right frontoparietal, number of elements within the complex, etc.) should be used very carefully in taxonomical studies and in evaluating attained evolutionary level of various anuran lineages. Complete knowledge of the developmental changes of the characters, not only of their larval or adult state, and proper understanding of their evolutionary significance is necessary. This would prevent those results of taxonomical studies on frogs where systematics is based on superficial evaluating of characters, such as “the frontoparietal is paired or unpaired”.

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