# DEVELOPMENTAL STORY OF THE ANURAN SKULL: DOES IT PROVIDE ANY PHYLOGENETIC INFORMATION ?

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## INTRODUCTION

Reconstructions of anuran phylogeny only scarcely involve larval characters and even less attention is paid to developmental processes, that is to sequence of changes leading from early, procartilaginous primordia to terminal morphogenetic stages of adults. However, development as a whole is an effective tool for filling gaps in our knowledge of evolutionary processes in the past, which are not documented by fossils. Moreover, it provides a possibility for understanding diversity of adults. Overlooking developmental processes means that we voluntarily give up a valuable source of phylogenetic information. Early larval stages appear to be very conservative and uniform (see, e.g., branchial slits in embryos of terrestrial tetrapods, such as reptiles, birds and mammals). Therefore, any difference in the early developmental stages deserve taxonomist's attention because it may be important for reconstructing phylogeny. In the Anura, significance of developmental data may be demonstrated on several structures characteristic for these vertebrates, such as the nasal region of the enchondral part of the skull, jaw apparatus in tadpoles and adult frogs, palatoquadrate and associated structures, postnasal wall, ear ossicle and other components of the sound-conducting apparatus, fissura prootica, and fronto-parietal and "squamosal" complexes.

## NASAL ENDOCRANIUM

The nasal (= ethmoidal) endocranium is that part of the skull which contains the nasal organs. In contrast to the nasal exocranium (consisting of superficial dermal bones), it ossifies from cartilage. In *Rana*, which can exemplify majority of anuran taxa (fig. 1), the earliest structures of the nasal endocranium are the upper labial cartilages
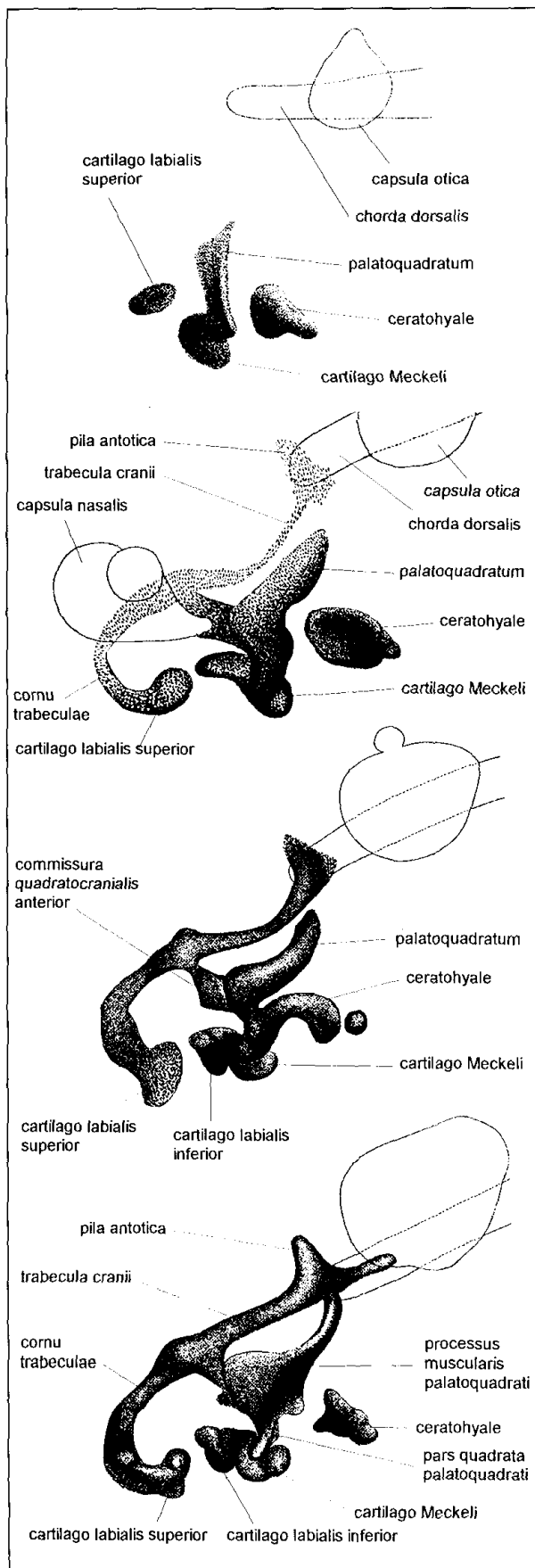
cartilago labialis
superior

capsula otica

chorda dorsalis

palatoquadratum

ceratohyale

cartilago Meckeli

pila antotica

trabecula cranii

capsula nasalis

capsula otica

chorda dorsalis

palatoquadratum

ceratohyale

cornu
trabeculae

cartilago Meckeli

cartilago labialis superior

commissura
quadratocranialis
anterior

palatoquadratum

ceratohyale

cartilago Meckeli

cartilago labialis
superior

cartilago labialis
inferior

pila antotica

trabecula cranii

cornu
trabeculae

processus
muscularis
palatoquadrati

ceratohyale

pars quadrata
palatoquadrati

cartilago Meckeli

cartilago labialis superior    cartilago labialis inferior

Fig 1: Early development of the skull in *Rana*. Sinistral view. From Spemann ( 1898).

which take their origin on each side anterior to the mandibular arch and primordium of the hyoid arch. All these three viscerocranial elements are well separated from the otic capsule which is the only neurocranial element developed at that time. Only later (when the nasal organ appears) both cranial trabecles arise, and their anterior ends become fused with the upper labial cartilages. It is of great importance that whereas the posterior part of the trabeculae (giving origin to the floor of the braincase) arises from sclerotomic mesoderm, their anterior part (i.e., cornua trabecularum) arises from the neural crest, as it is the case with other viscerocranial structures (Stone 1926). This means that the cornua trabecularum may be considered parts of the viscerocranium, i.e. of that part of the skull which evolved from the branchial arches (fig. 15).

The trabecular horns are connected with each other proximally, near their connection with the anterior ends of the trabecles. Distally, they acquire a movable articulation with the upper labial cartilages which, during the larval period, serve as part of the jaw apparatus (see below). Later, during metamorphosis, a new cartilaginous material arises between them. This, as a whole, gives rise to the septum nasi. Although the septum in adults is only a thin partition between both nasal capsules, vestiges of both trabecles are preserved at the transition between the septum and the floor of the capsules (solum nasi). The question remains whether or not the upper labial cartilages disappear entirely or if their vestiges are incorporated in the floor of the nasal endocranium.

In the Pipidae, development of the nasal endocranium is different. Instead of both trabecular horns, there is a single horizontal internasal plate (planum internasale) (fig. 2). It is not clear whether it arises from the neural crest cells or from the sclerotomic mesoderm, which is essential for decision if it is homogous with the trabecular horns. Besides, there are no upper labial carti-
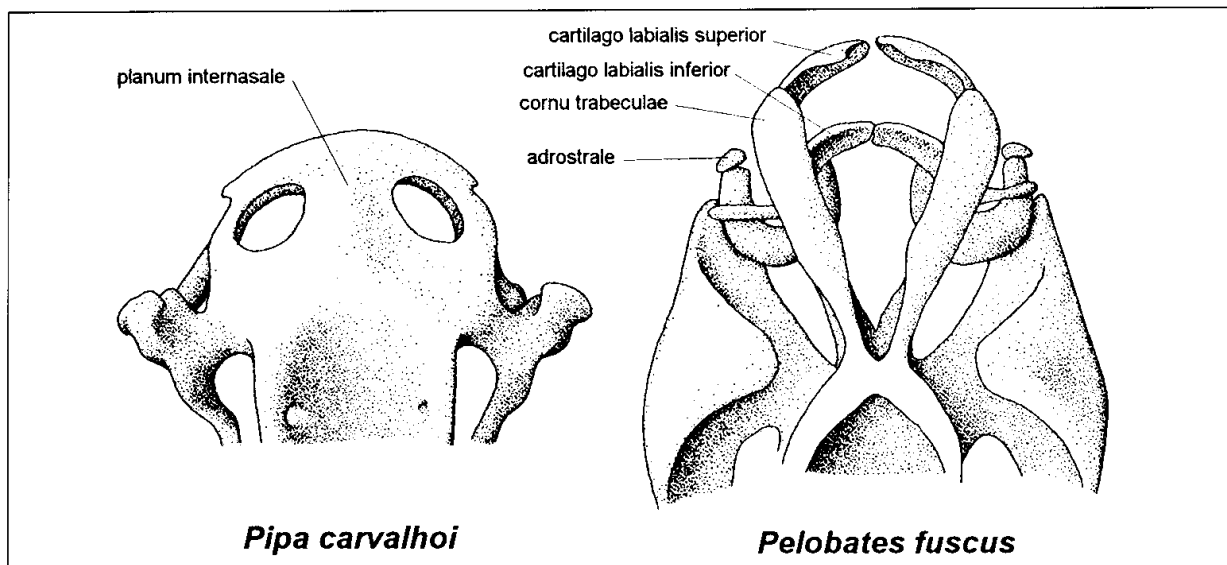
Fig 2: Dorsal view of ethmoidal endocrania of two different anuran groups, to show structural differences in their structure. From Rocek (1990, 1993).

lages. It was claimed (Sokol 1977) that they become incorporated into an arch-like structure stretched between the anterior margin of the internasal plate and anterior portion of the palatoquadrate (i.e. antero-lateral to the nasal capsule). However, the upper labial cartilages are well developed also in some anurans with the internasal plate (e.g., *Heleophryne*; Westhuizen 1961) where they should be absent as independent structures because they are supposedly involved in the antero-lateral parts of the nasal capsule. Moreover, the septum nasi in the pipids develops as a condensation of new cartilage above the internasal plate, and the plate itself completely disappears. This means that the adult nasal endocranium of pipids does not involve vestigial larval structures.

If, in order to learn what was the situation in earlier stages of amphibian evolution, we turn our attention to the endocranial nasal structures in primitive amphibians, we find this part of the skull dorso-ventrally compressed, so the external naris is connected with the fenestra endochoanalis only by a short canal (fig. 3). Nothing what would recall

the trabecular horns may be found in them but, in contrast, morphology of the nasal endocranium of those few taxa in which the information is available* closely recalls that of the Pipidae. This may suggest that pipids still maintain ancestral structural scheme which was already modified in other anurans.
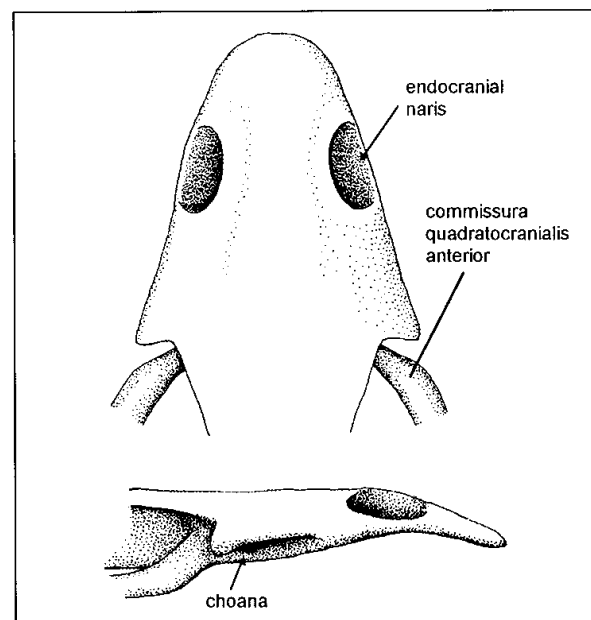


Fig 3: Reconstruction of the ethmoidal endocranium of the Triassic amphibian *Benthosuchus* in dorsal and dextral views. After Rocek (1991).

* Only scarce data are available because considerable part of the endocranium (including nasal structures) does not reach ossification in tetrapods, and remains cartilaginous. Nevertheless, these originally cartilaginous structures may be studied on the basis of natural or latex casts, provided that the skull is three-dimensionally preserved.

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The upper labial cartilages (there may be a pair of them or they may fuse with one another in an unpaired structure) serve as a support of horny larval upper jaw. It was already said that they arise anterior to the mandibular arch, underneath the nasal capsule. In contrast, the lower labial cartilages (also covered by horny sheath) take their origin later, from the lower part of the mandibular arch, at the tip of Meckel's cartilage (fig. 1). Since in more developed tadpoles the palatoquadrate attains secondarily the horizontal position (or, better said, a position parallel to the trabecles), the structures (i.e., Meckel's cartilage and lower labial cartilage) which were in the earliest recognizable stages located ventral to the palatoquadrate move - in accordance with anterior
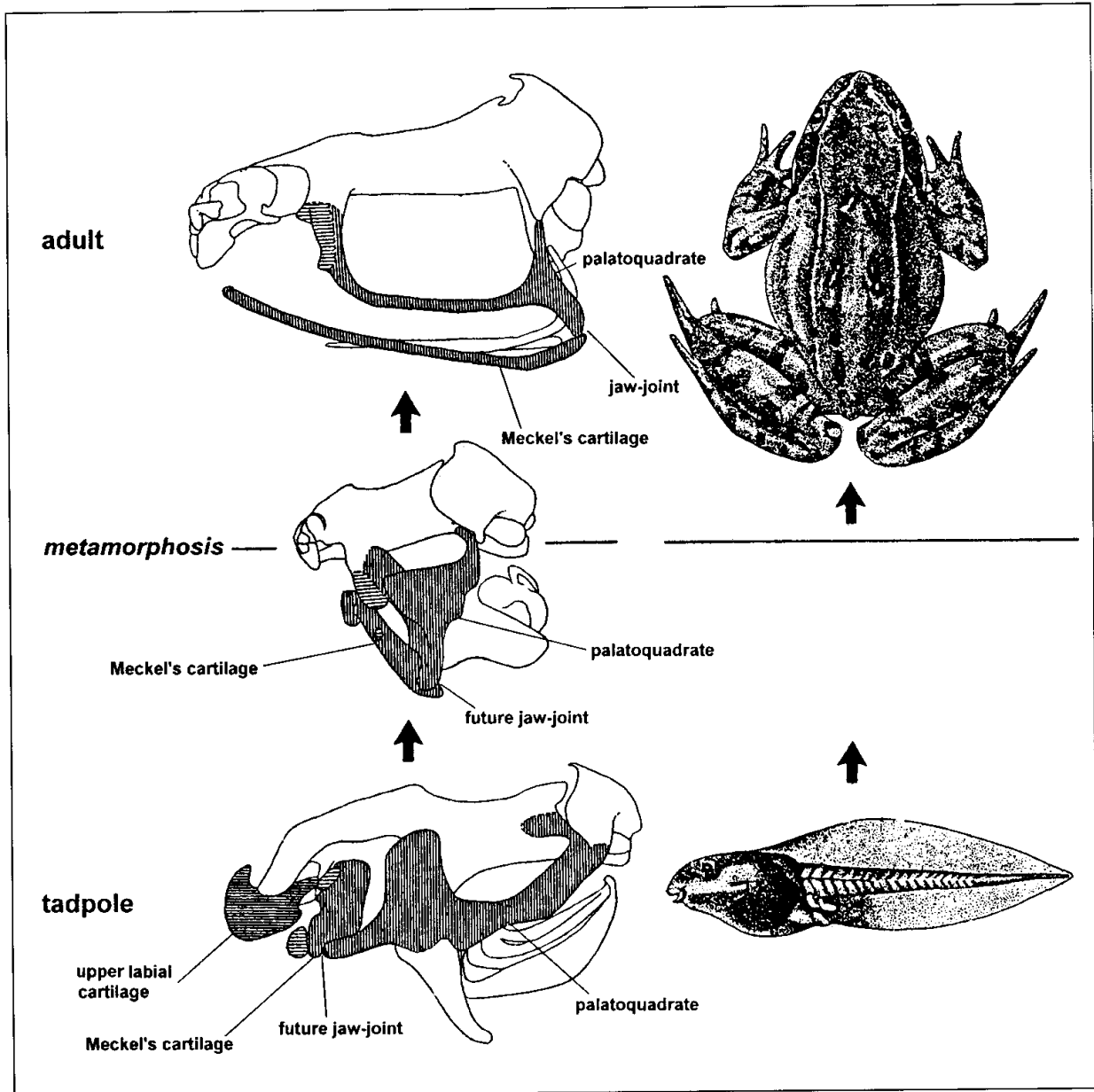


Fig 4: Transformation of some viscerocranial elements in course of metamorphosis demonstrated in sinistral view of three developmental stages. Larval jaws are represented by the upper and lower labial cartilages (supporting horny beaks), adult jaws by the commissura quadratocranialis anterior (i.e. that part of the palatoquadrate which is sometimes called the processus pterygoideus palatoquadrati or the subocular bar) and Meckel's cartilage (supporting the maxilla, and dentary and praearticular, respectively). Note changes in position of the palatoquadrate during its rotation, and corresponding changes in position of the adult jaw joint. Partly from Rocek (1981).

rotation of the palatoquadrate - below the nasal capsule. Only after this anterior rotation of the primitive palatoquadrate the lower labial cartilage begin to serve as the lower part of the mouth apparatus. Meckel's cartilage is in this stage of development a stout, transversely located element supporting the lower labial cartilage anteriorly, and articulating with the most anterior part of the palatoquadrate (pars quadrata palatoquadrati) posteriorly.

In course of metamorphosis, the palatoquadrate rotates in an opposite sense, that means posteriorly (fig. 4). After this rotation it attains the vertical position again, as in the earliest developmental stages. During this second rotation, a new jaw apparatus is established. The upper jaw consists exclusively of dermal bones (praemaxilla and maxilla) supported by the knob-like cartilago (pro-

cessus) praenasalis inferior and superior, and by the vestigial commissura quadratocranialis anterior (= processus pterygoideus palatoquadrati, also simply called the subocular bar). It was already mentioned that it is not yet clear whether the upper labial cartilages disappear completely or if they are incorporated in the floor of the nasal capsule (close to the bases of the lower praenasal cartilages). The lower jaw is supported by Meckel's cartilage which in the meantime becomes elongated as in other vertebrates. The lower labial cartilage, after loosing its original function of the lower larval jaw, becomes a vestige maintaining, however, its original position at the anterior end of Meckel's cartilage. Usually it is called the mentomandibulare or mentomeckelian, and in adults it may coalesce with the dentary.

## PALATOQUADRATE

The palatoquadrate arises among structures of the mandibular arch (fig. 1). Ventrally, it is confluent with Meckel's cartilage, whereas it is free dorsally. Later, when the cranial trabecles appear and the palatoquadrate reaches the position parallel to them, it becomes attached to that part of the trabecles which takes its origin from the neural crest cells. The transverse connection between originally lower part of the palatoquadrate and cornu trabeculae is called the commissura quadratocranialis anterior. Postero-dorsally, the palatoquadrate is still free and becomes attached to the trabecles only much later, by means of the processus ascendens palatoduadrati (at the level of the pila antotica, just in front of the prootic fissure; see below). Another posterior connection, the processus oticus palatoquadrati, is established with the otic capsule. Hence, in larvae there are three palatoquadrate connections, one anterior and two posterior.

During metamorphosis, the anterior qua-

dratocranial commissure becomes detached from the braincase wall (arisen, in the meantime, from the proximal section of the trabecular horn) and becomes attached to the posterior surface of the lamina orbitonasalis which originally is an independent cartilaginous structure separating the nasal capsule from the orbit, later becoming a substantial part of the postnasal wall (see below). Sometimes, this connection is called the commissura quadratoethmoidalis medialis but it is important to note that originally it was the anterior quadratocranial commissure shifted laterally onto the orbitonasal lamina so that it lost its former contact with the braincase (fig. 5, right).

Laterally, however, a totally new connection (represented as an independent cartilage called the processus maxillaris posterior) arises between the posterolateral part of the orbitonasal lamina and the anterior section of the commissura quadratocranialis anterior. This new connection is sometimes called the commissura
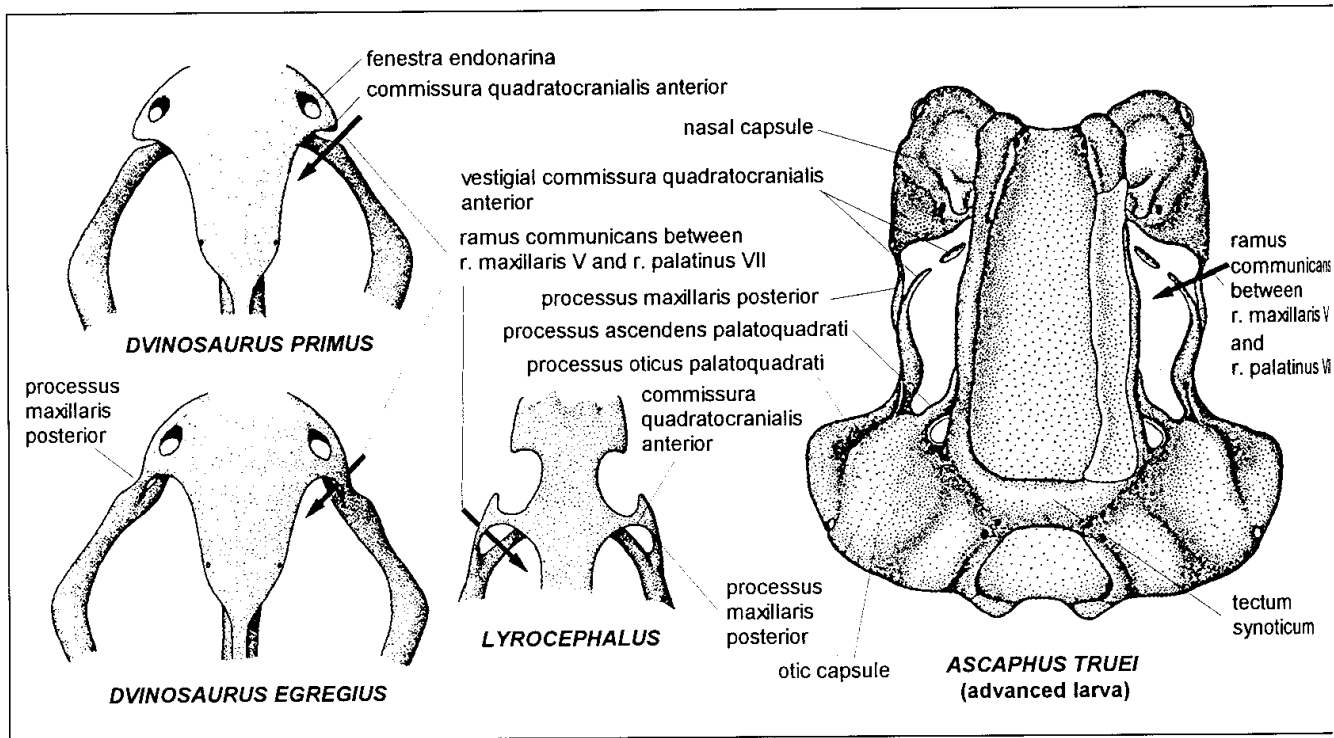
**Fig 5:** Dorsal view of the endocranium in primitive contemporary anuran (right), compared with reconstructions of those in the Triassic temnospondyl amphibians (otic region omitted), to show similarities in details of anterior palatoquadrate connections. From Shishkin (1973), Säve-Söderbergh (1936) and van Eeden (1951).

quadratoethmoidalis lateralis. Both these connections of the anterior quadratocranial commissure with the orbitonasal lamina rim a triangular fenestra through which a topographically important nerve (ramus communicans between r. maxillaris V and r. palatinus VII) passes.

Finally, when the palatoquadrate attains its vertical position below the otic capsule, the vestigial anterior quadratocranial commissure looses its contact also with the orbitonasal lamina and its connection to the postnasal wall is only via the processus maxillaris posterior. Therefore, the so-called subocular bar in adults is in fact consisting of the vestigial commissura quadratocranialis anterior (this part is often termed the processus pterygoideus palatoquadrati), and its most anterior part consists of the processus maxillaris posterior which, in the meantime, lost its identity so that both structures are preserved in adults as a continuous strip of cartilage supporting the maxilla.

The posterior palatoquadrate connections develop in a different way. Whereas

the processus ascendens (connecting the posterior end of the palatoquadrate with the braincase wall) remains preserved in adults (though incorporated in the braincase wall), the larval otic process disintegrates and becomes re-established again (from entirely different material) when the palatoquadrate reaches its vertical position below the otic capsule. Consequently, posterior surface of its upper part (lower lateral part in tadpole) comes into contact with the otic capsule, in the region closely adjacent to the anterior end of the crista parotica. Since it is obvious that the larval and adult otic processes are not homologous, they are termed the processus oticus larvalis and processus oticus adulti, respectively.

To sum up development of the anuran palatoquadrate one can say that in early development it arises as a vertical structure (which is in agreement with its position within the branchial arch), later (during larval perod) it rotates anteriorly to support the larval lower jaw (apparently because the larval mouth opening is located at the

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anterior end of the head), and only in course of metamorphosis it rotates posteriorly, ultimately reaching again its vertical position below the otic capsule, as in other vertebrates. Judging from situation found in the paedomorphic and adult Triassic temnos-

pondyl amphibians (fig. 5, left), the anterior palatoquadrate connections corresponding to those in advanced anuran larval stages were present, but not those which occur in adult anurans (fig. 16).

## POSTNASAL WALL

The postnasal wall is that part of the anuran skull which separates the nasal region (ethmoidal capsules, septum nasi, and associated structures) from the braincase and orbits (fig. 6). In early larvae, the nasal region is represented only by the trabecular horns, and the anterior part of the braincase by a flat horizontal plate (called the planum trabeculare anticum by Gaupp 1893, or the planum praecerebrale by Stadtmüller 1936, to give at least some of numerous termes introduced for this structure) interconnecting both trabecles at the level where the commissura quadratocranialis anterior on either side connects the palatoquadrate with the braincase. The nervus olfactorius runs free, uncovered dorsally, from the brain to the nasal organ. Similarly, the nervus ophthalmicus passes uncovered along the lateral margin of the trabecle from the orbit to the nasal region, crossing the dorsal surface of the commissura quadratocranialis anterior.

The earliest part of the postnasal wall arises from a distinct mesenchymous and later cartilaginous horizontal layer covering the olfactory nerves from above. It is paired in origin but these cartilaginous structures (laminae cerebronasales) soon fuse with one another. They produce, by downward growth, extensions called the columnae ethmoidales which form the lateral walls of the olfactory canals. Medially from both olfactory nerves, in a space between them, there is a large ethmoidal fenestra which, however, soon becomes filled so that a partition arises between the both olfactory canals. It is noteworthy that this process may

also be followed in various stages of some Palaeozoic anthracosaurian amphibians.
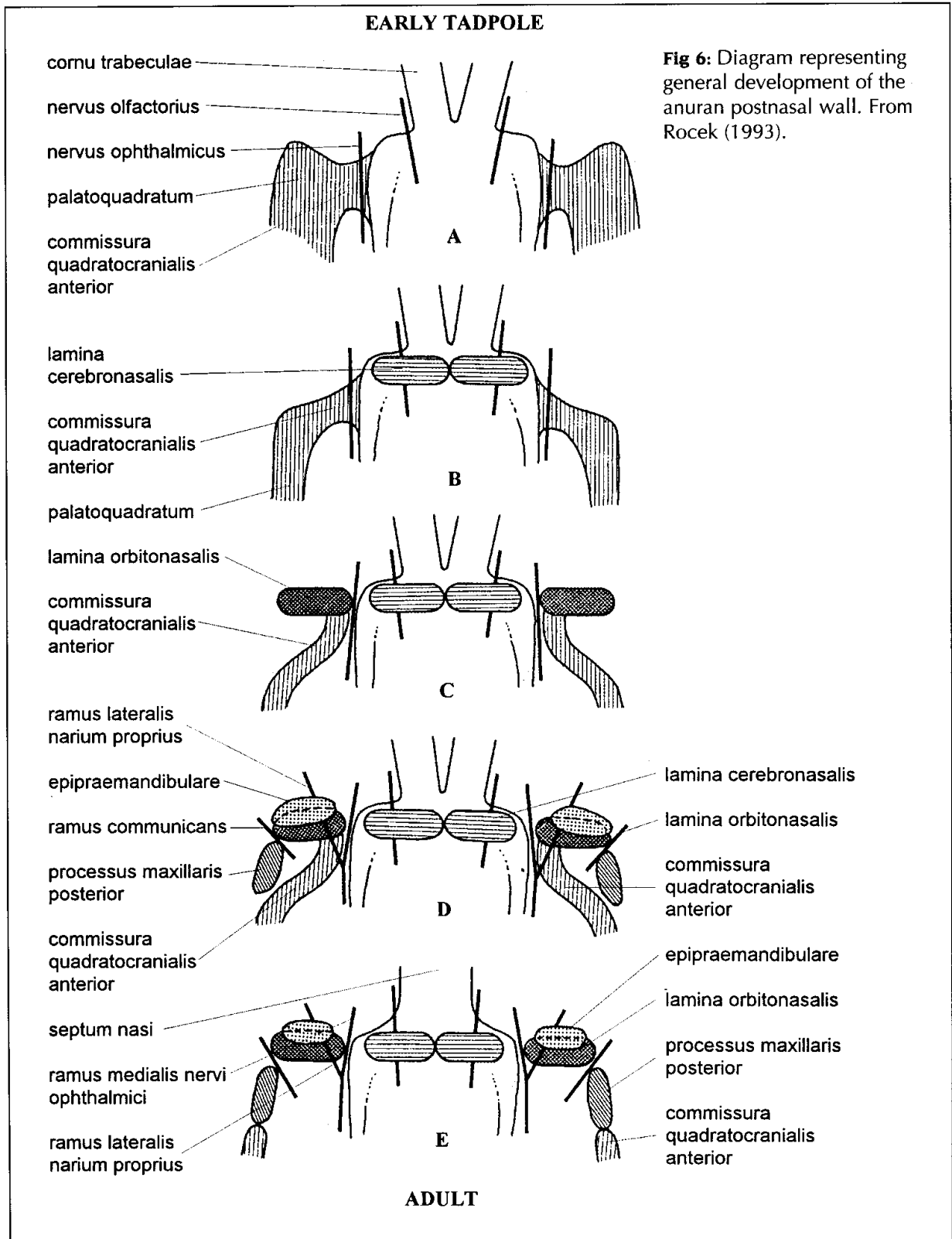
Development of the lateral part of the postnasal wall is more complicated. In early developmental stages, the only functional partition between the nasal organ and orbit is the commissura quadratocranialis anterior. Soon, however, a new material is added, chondrifying within a ligament located anterolaterally to the commissura, which results in enclosing the ophthalmicus nerve first in a slot and later in a canal between the braincase wall (produced in the meantime by dorsal growth of the trabeculae) and this new cartilage (called the lamina orbitonasalis). The commissura quadratocranialis anterior does not contribute to the postnasal wall because, as was already mentioned above, it becomes detached from the braincase wall and shifted to the posterior surface of the lamina orbitonasalis or terminates free (fig. 5-6). This stage may be documented in Triassic temnospondyls (fig. 3, 5).

Almost simultaneously with appearance of the processus maxillaris posterior (see above, Palatoquadrate), the anterodorsal surface of the lamina orbitonasalis is joined by another, ovoid or rod-like cartilage which encloses the lateral branch of the ophthalmicus nerve into a canal crossing anterolaterally the lamina orbitonasalis. This cartilage is usually called the adrostrale or epipraemandibulare; in some taxa it may be represented only by an indistinct condensation of mesenchyme. In adults, it is represented by an elevation on the anterodorsal surface of the postnasal wall (termed "bulge" or "anterior process on postnasal wall" by Jurgens 1971).

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Considerable part of the postnasal wall in adults ossifies as the sphenethmoid (involving also various parts of the septum nasi and anterior part of the braincase). The sphenethmoid may arise as a paired structure within the postnasal wall in some taxa, but in majority of them it is of unpaired origin.

Hence, it is obvious that the anuran postnasal wall arises from several independent elements which only in metamorphosis fuse together to give rise a compact partition between the nasal capsule and orbit.

## EARLY TADPOLE

cornu trabeculae

nervus olfactorius

nervus ophthalmicus

palatoquadratum

commissura
quadratocranialis
anterior

**A**

**Fig 6:** Diagram representing general development of the anuran postnasal wall. From Rocek (1993).

lamina
cerebronasalis

commissura
quadratocranialis
anterior

palatoquadratum

**B**

lamina orbitonasalis

commissura
quadratocranialis
anterior

**C**

ramus lateralis
narium proprius

epipraemandibulare

ramus communicans

processus maxillaris
posterior

commissura
quadratocranialis
anterior

**D**

lamina cerebronasalis

lamina orbitonasalis

commissura
quadratocranialis
anterior

epipraemandibulare

lamina orbitonasalis

septum nasi

ramus medialis nervi
ophthalmici

ramus lateralis
narium proprius

**E**

processus maxillaris
posterior

commissura
quadratocranialis
anterior

## ADULT

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The fenestra ovalis arises comparatively early in larval development, as a vestige of a large fenestra basicapsularis in the floor of the otic capsule. It is entirely covered by membrane (membrana opercularis). Dorsally, it is roofed by a horizontal ridge-like bulge termed the crista parotica. Two structures arise within the fenestra ovalis. In its posterior part, a plate of cartilage arises within the membrana opercularis independently of the wall of the capsule (Gaupp 1893). It is called the operculum fenestrae ovalis (in order to distinguish it from the dermal bone of the opercular series also termed the operculum). A small muscle originating on the suprascapular cartilage of the shoulder girdle is inserted onto the operculum; it is called the musculus opercularis.

Only later (in metamorphosing larvae of Rana with well developed hind legs), an independent horizontal bar of cartilage arises (also within the opercular membrane). This bar is usually called the pars interna plectri. The pars interna plectri turns sideways to that part of skin where the tympanum is formed and where it is fused synchondrotically with another cartilaginous

element, the pars externa plectri. The pars externa plectri develops from the posterior surface of the palatoquadrate after it attained vertical position underneath the otic capsule. It acquires a connection with the crista parotica by means of a thin vertical processus ascendens plectri (it may be cartilaginous, ligamentous or absent).

It is apparent that the columella auris (or plectrum) arises from two separate chondrifications which may later, in adults, ossify in the middle part (pars media plectri).

As regards the cartilaginous tympanic ring (annulus tympanicus) which is a characteristic feature of some Anura, it is no doubt a derivate of the palatoquadrate. It chondrifies only after metamorphosis and remains closely associated with the palatoquadrate, though separated from it. Ultimately, it dorsally fuses to the crista parotica. The tympanic membrane is stretched on its outer margin, whereas its inner surface is reached by the tuba Eustachii and pars externa plectri.

It is obvious that these parts develop from various sources: the operculum is a derivate of the otic capsule. The pars interna plectri, arising as an independent cartilage within the ligament stretched over the anterior part of the fenestra ovalis, seems to be a homologue of the hyomandibulare. On the other hand, the pars externa plectri and the annulus tympanicus develop from the pars quadrata of the palatoquadrate. In other words, the pars interna plectri is a derivate of the hyoid arch, whereas the pars externa plectri of the mandibular arch. If both together are considered the columella auris, then only part of it (pars interna) is homologous with stapes of other vertebrates.
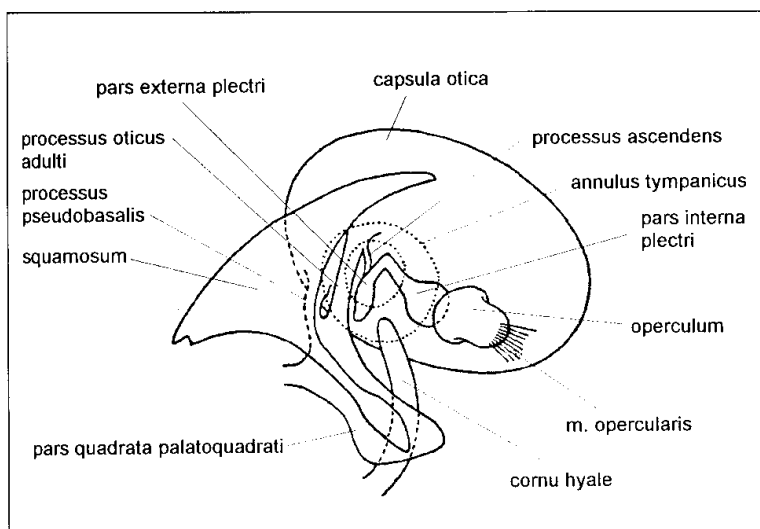


Fig. 7: Scheme of the left capsula otica with palatoquadrate (including its posterior connections) and squamosum, and with the sound-conducting apparatus (operculum, m. opercularis, pars interna and pars externa plectri, annulus tympanicus) in adult Rana. Sinistral view. From Stadtmüller (1936).

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In advanced anuran larvae, the otic capsule is separated from the lateral wall of the orbitotemporal part of the braincase, just behind the pila antotica and processus ascendens palatoquadrati, by a slot called the fissura prootica (fig. 8; see also fig. 10, below). Within this fissure is located the ganglion trigeminofaciale. The fissure reaches up to the membranous floor of the braincase. Since in metamorphosis the larval processus oticus disintegrates (see above, Palatoquadrate) it is apparent that the otic part of the skull is connected in this stage with the ethmoidal and orbitotemporal parts only by means of the hyoid arch and the membranous floor of the braincase. It may be supposed that these parts of the neurocranium would theoretically be movable, if these motions were not prevented by developing exocranial bones (especially by the parasphenoid and frontoparietal). Later, at the end of metamorphosis, a connection over the dorsal part of the prootic fissure is re-established (by

means of the taenia marginalis) so that a large fontanella prootica arises, and the palatoquadrate also becomes newly attached to the otic capsule, both by the processus oticus adulti and by the processus basalis on the lower surface of the otic capsule.

A similar division of the neural endocranium may be found in osteolepiform fishes, where it is represented by a complex articulation system separating the orbitotemporal and otic regions of the endocranium, called the intracranial juncture apparatus. It seems that osteolepiforms (and, presumably, the earliest tetrapods) are the only vertebrates that have the adult skull divided into the anterior and posterior moieties.

Homology between the prootic fissure and the intracranial juncture apparatus is evidenced by topographic relations. The apparatus lies at the level of the anterior tip of the notochord, between the posterior margin of the frontal and anterior margin of the parietal, as in advanced anuran larvae.



*Eusthenopteron* adult

intracranial juncture apparatus

*Xenopus* larva

fissura prootica

palatoquadrate
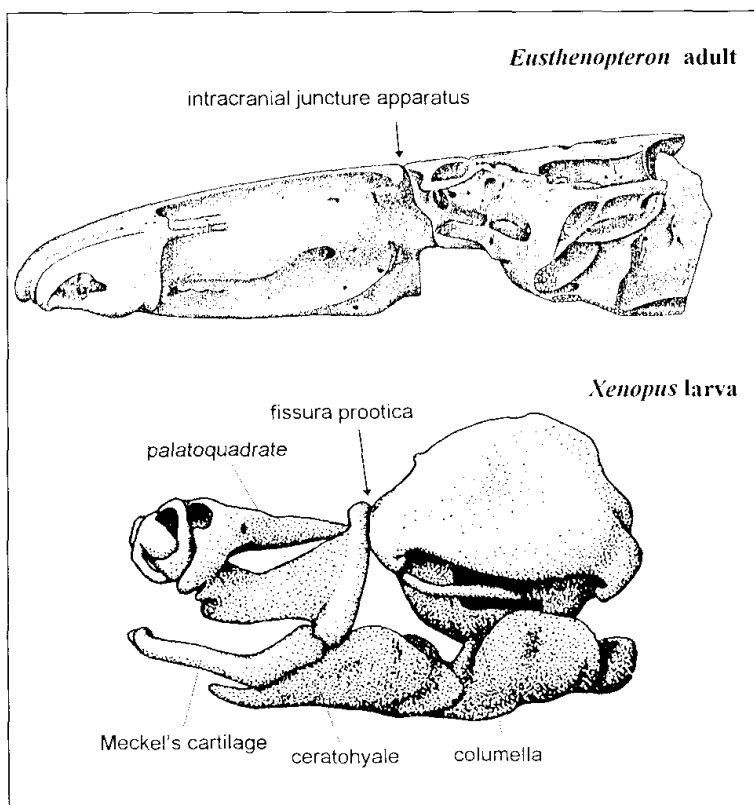
Meckel's cartilage
ceratohyale    columella

Fig. 8: Comparison of endocrania in adult Devonian osteolepiform fish *Eusthenopteron* and larval anuran *Xenopus*, demonstrating presumed homology of the intracranial juncture apparatus and fissura prootica. From Rocek (1986).

The frontoparietal complex (a dermal ossification) is a unique character of the Anura (if its occurrence in pachycephalosaur dinosaurs is not taken into account). In Rana (fig. 9-10), its frontal part arises from a tiny ossification centre on the dorsal margin of the braincase wall anterior to the prootic fissure (this part of the braincase wall arises from the early larval structure called the pila

antotica). Soon afterwards, it is joined by an ossification centre arising on the dorsal surface of the otic capsule (fig. 9B); the latter no doubt represents the parietal. They fuse with one another, giving rise to a composite bone termed the frontoparietal. Both expand also medially, to reach their counterparts from the opposite side in a median suture. At the same time, the frontals expand anteriorly to reach the level of the anterior margin of the orbit (fig. 9C).
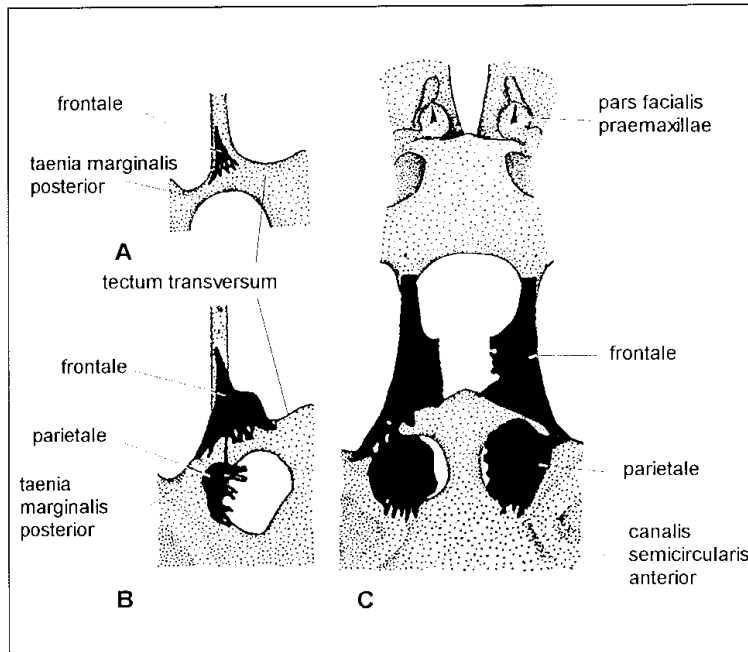
In Pelobates (fig. 10, 12), an additional, unpaired element arises on the dorsal roof of the braincase between both otic capsules (i.e., on the dorsal surface of the tectum synoticum), which fuses with the posteromedial margins of both parietal centres. Still later, paired elements, arising on the dorsal surface of the otic capsules and enclosing the arteria occipitalis into a canal, join the complex which is in its ultimate stage represented by a single, unpaired bone. It is obvious that the frontoparietal in Pelobates (but not in Scaphiopus) involves some additional elements, not present in Rana. Identity of these elements is matter of some discussion, nevertheless it seems that the unpaired element adjoining the tectum synoticum may represent the intertemporal of some primitive Palaeozoic amphibians.

In pipids (fig. 13), the frontoparietal arises from paired frontals too, however, these centres expand both anteriorly and posteriorly along the dorsal margins of the walls of the braincase (but not onto the



Fig 9: Development of the frontoparietal in Rana. From Lebedkina (1979).
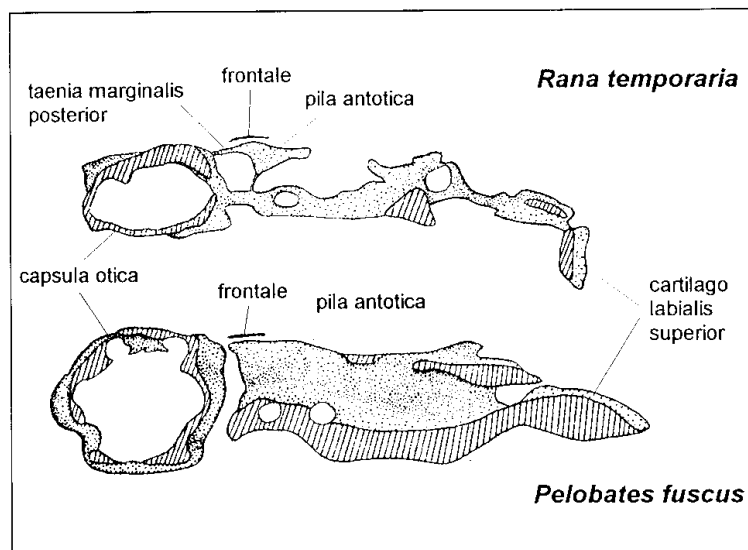


Fig 10: Position of the early frontal in relation to the endocranium (cutted in the mid-line). From Lebedkina (1979).

dorsal surface of the otic capsule). The space between them is later filled so that it forms a roof above the brain-case cavity. Ultimately, a paired ossification is added, extending on each side onto the dorsal surface of the postnasal wall. It is not clear whether the fronto-parietal in pipids involves also ossifications representing the parietals of other anurans.

It is obvious that there is some variation in structure of the anuran frontoparietal complex. In contrast to primitive water-dwelling vertebrates in which the principal criterion for assessing homologies of dermal bones is the lateral line system, in anurans (as in other terrestrial tetrapods) this criterion disappeared and only topographic relations of dermal bones to underlying endocranial structures (which have a capacity to induce dermal ossification) may be used. Hence, judged by their relations to endocranium, the frontoparietal components in pipids and pelobatids form a complex different from that in ranids. Another important fact may be that in all anurans the very first ossification entering the fronto-parietal complex is the frontal, located on the top of the pila antotica. However, if compared with fishes and primitive urodeles (fig. 11) in which the frontals arise from three pairs of ossifications centres, the earliest developmental stage of the anuran frontals correspond to the most posterior of them (termed "frontals 3" by Lebedkina 1973). Whether they include, later in development, also equivalents of



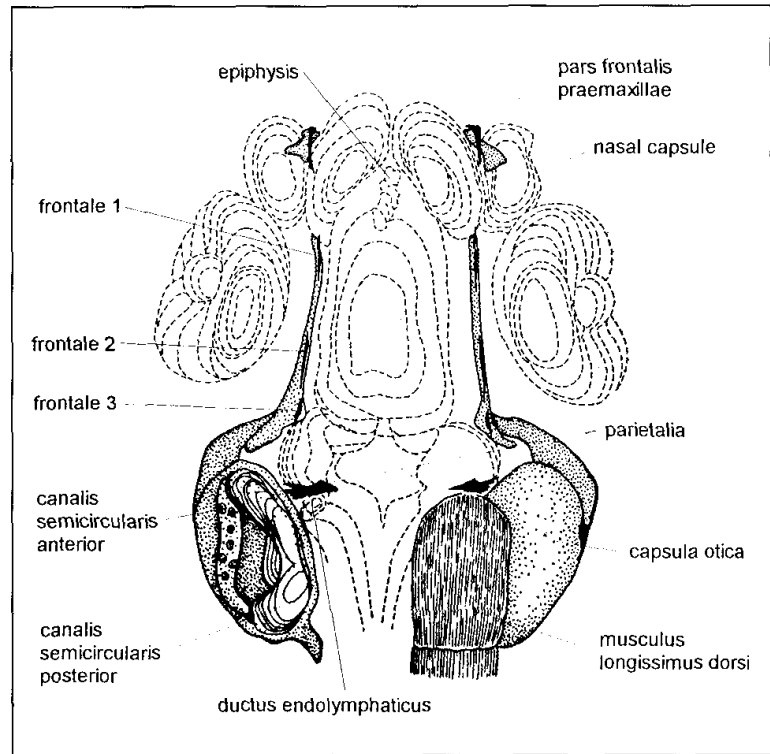**Fig. 11:** Position of three ossification centres of the frontal, and that of the parietal, in the larva of a primitive contemporary urodele *Ranodon sibiricus*. From Lebedkina (1979).
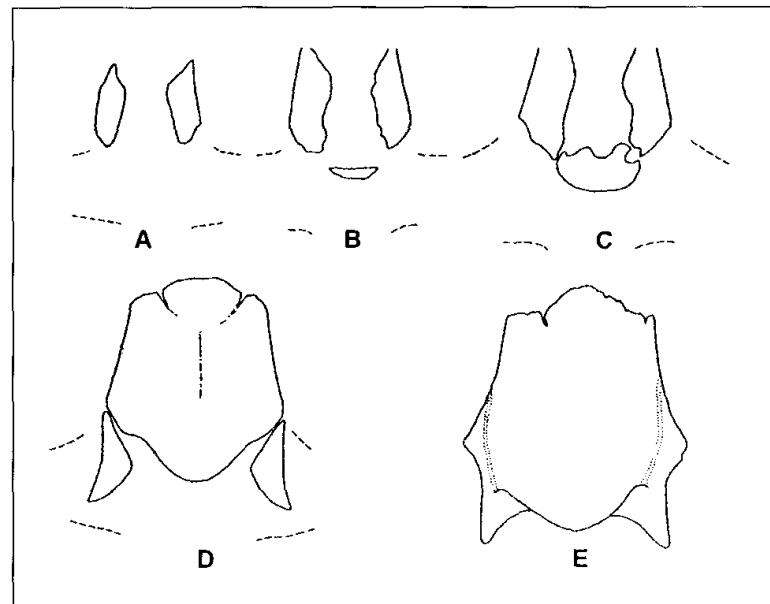


**Fig. 12:** Development of the frontoparietal complex in *Pelobates*. From Rocek (1981).

frontals 2 and frontals 1, or represent only frontals 3 expanded anteriorly, can be solved by further detailed developmental studies.
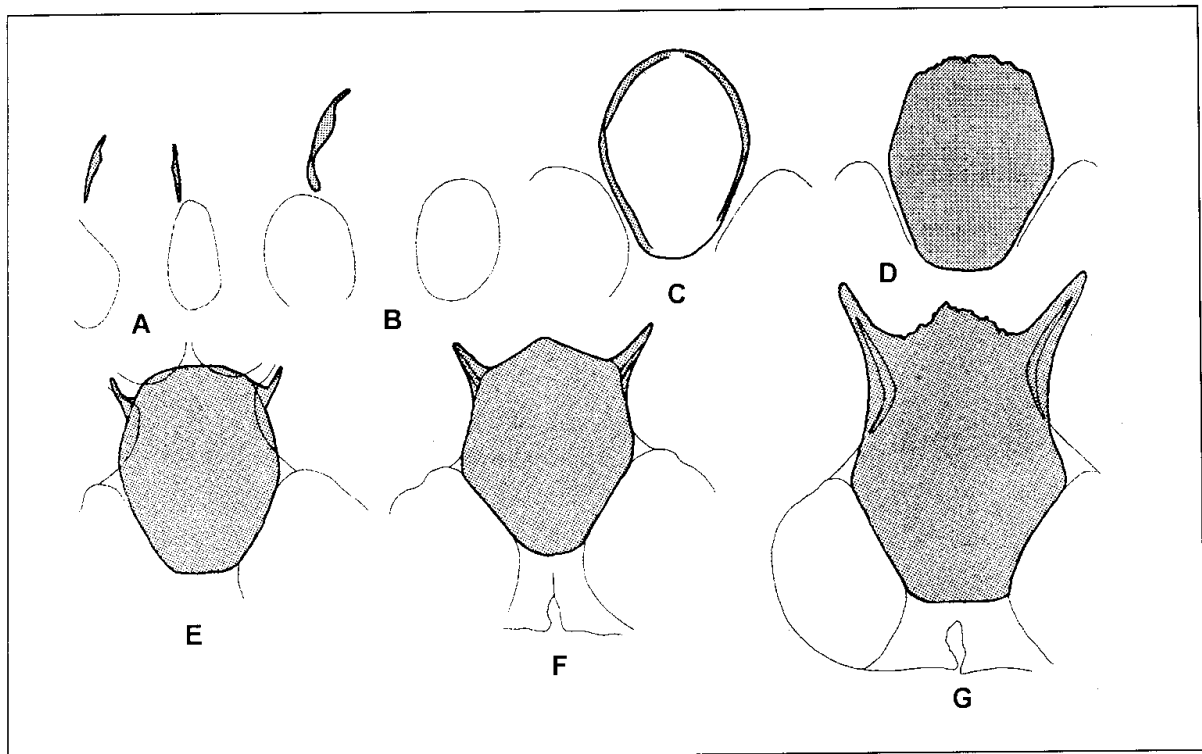
Fig. 13: Development of the frontoparietal complex in *Pipa*. From Rocek (1988).

## SQUAMOSAL

Similar to the frontoparietal, also squamosal arises from several ossification centres (fig. 14). Earlier of the two centres arises on the lateral surface of the palatoquadrate and later encloses it laterally. In adult, this part of the squamosal is represented by a slender and smooth posterolateral process.

However, its dorsal, often sculptured part termed the lamina alaris arises as a separate ossification centre on the lateral surface of the otic capsule, in the region of its crista parotica. If topographic relations to the underlying endocranial structures are applied as the criterion of homology, then only the dorsal ossification (and thus only the lamina alaris) can be called the squamosal, whereas the lower, adjoining the palatoquadrate should be called the praeopercular (because of its identical topographic relations to the palatoquadrate in osteolepiform fishes). Hence, the bone usually called the "squamosum" should rather be called the "praeoperculo-squamosum", in order to express properly its composition.



Fig. 14: Development of the squamosal complex in *Rana*. From Lebedkina (1979).

lamina orbitonasalis
part of postnasal wall
*suprapharyngopraemandibulare*

**commissura quadratocranialis anterior**
subocular bar
*epipraemandibulare*

**lamina cerebronasalis**

**cornu trabeculae**
*infrapharyngoterminale*

**processus ascendens palatoquadrati**
disappears or fuses to braincase wall
*suprapharyngomandibulare*

**adrostrale**
bulge on postnasal wall
?

**cartilago labialis superior**
*element of terminal arch*
*(epiterminale ?)*

**hyomandibulare**
pars interna plectri
*epihyale*

**cartilago labialis inferior**
mentomandibulare
*hypomandibulare*

**ceratopraemandibulare**
disappears in metamorphosis
*ceratopraemandibulare*

**cartilago Meckeli**
cartilago Meckeli
ceratomandibulare

**ceratohyale**
cornu anterior hyoidei
*ceratohyale*

**bulge on postnasal wall**
adrostrale
?

**part of postnasal wall**
lamina orbitonasalis
*suprapharyngopraemandibulare*

**palatoquadrate**
palatoquadrate
*epimandibulare*

**cartilago obliqua**

**processus praenasalis inferior**
cartilago labialis superior ?
*epiterminale ?*

**pars interna plectri**
hyomandibulare
*epihyale*

**pars externa plectri**
part of palatoquadrate
*part of epimandibulare*

**basal part of septum nasi**
cornu trabeculae
*infrapharyngoterminale*

**mentomandibulare**
cartilago labialis inferior
*hypomandibulare*

**cornu hyoidei**
*ceratohyale*

**anterior part of subocular bar**
processus maxillaris posterior
?

**hyoideum**
*basihyale + elements of 1$^{st}$ posthyoid arch*

**cartilago Meckeli** (= mandibulare)
*ceratomandibulare*

**posterior part of subocular bar**
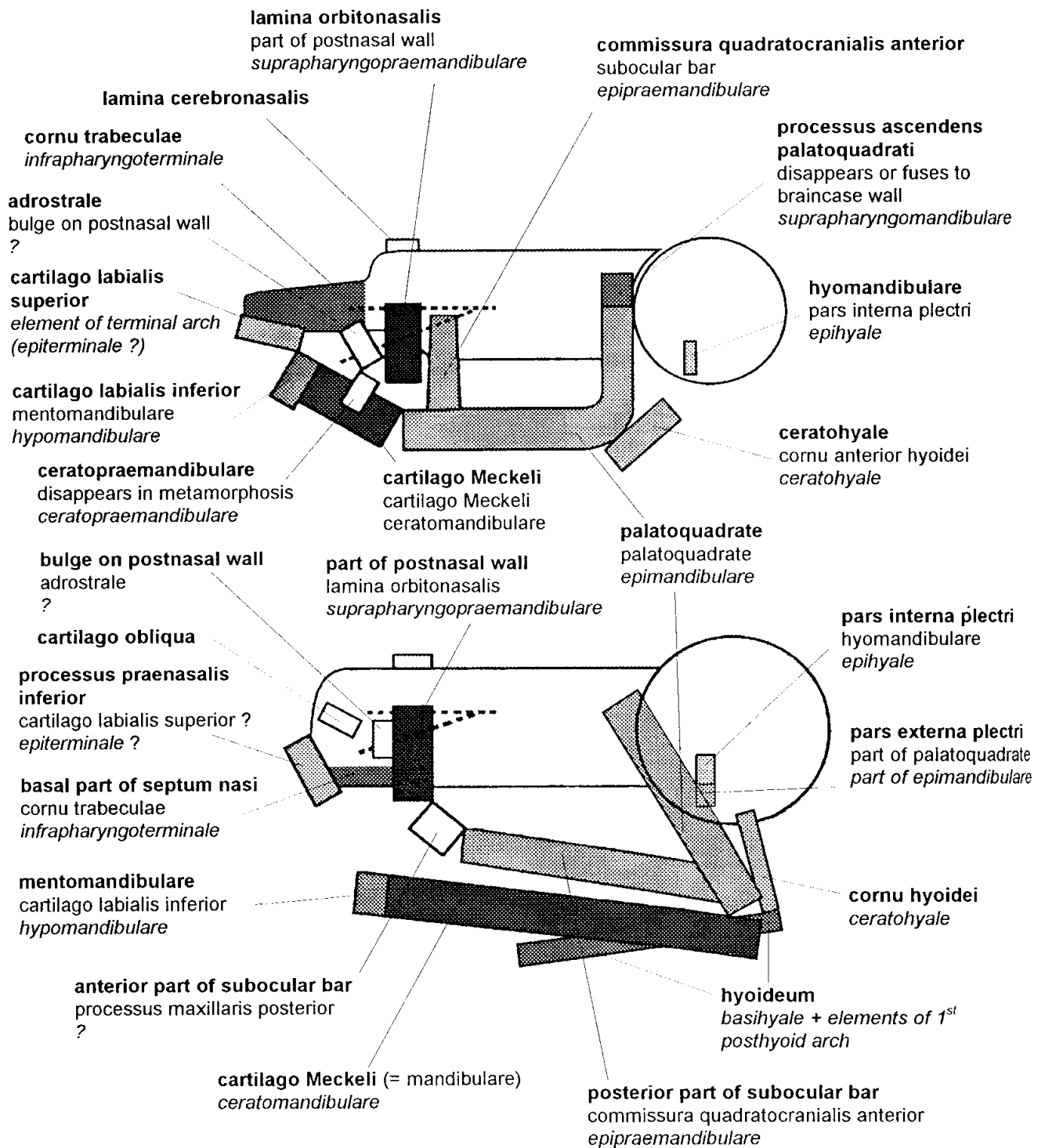commissura quadratocranialis anterior
*epipraemandibulare*

Fig. 15: An attempt to analyse endocranial viscerocranial elements of tadpole (above) and adult anuran (below) in terms of branchial arch elements of an ancestral fish. Given are the present anatomical structures (in bold), their earlier developmental precursors or ultimate developmental situation in adult, and proposed homology with elements of branchial arch (in italics). Presumed derivates of branchial arches (lamina cerebronasalis, cartilago obliqua, processus maxillaris posterior, etc.) are also included. Courses of topographically important nerves in broken lines.

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The question now arises what is the phylogenetic significance of these developmental features? First, it was already said that early developmental stages are more uniform than terminal stages of adults and, therefore, any structural deviation from the common developmental mode may be taxonomically important. Second, if cranial (and other) structures of larval stages are analyzed (fig. 15), they can be directly compared with adults of ancestral evolutionary stages. In case of the Anura, we can compare cranial structures of tadpoles directly with adult temnospondyl amphibians from the Carbo-niferous - Triassic period, and/or with Devonian osteolepiform fishes. Such comparison provides information not only about the ways and rate of morphological evolution, but may also exclude those forms from supposed ancestors which structurally differ from early developmental stages of supposed evolutionary descendents. It is obvious that search for evolutionary (and phylogenetic) continuity cannot be based only on comparison of adults because some are more derived than others (fig. 16), but should also assess complete set of developmental changes.
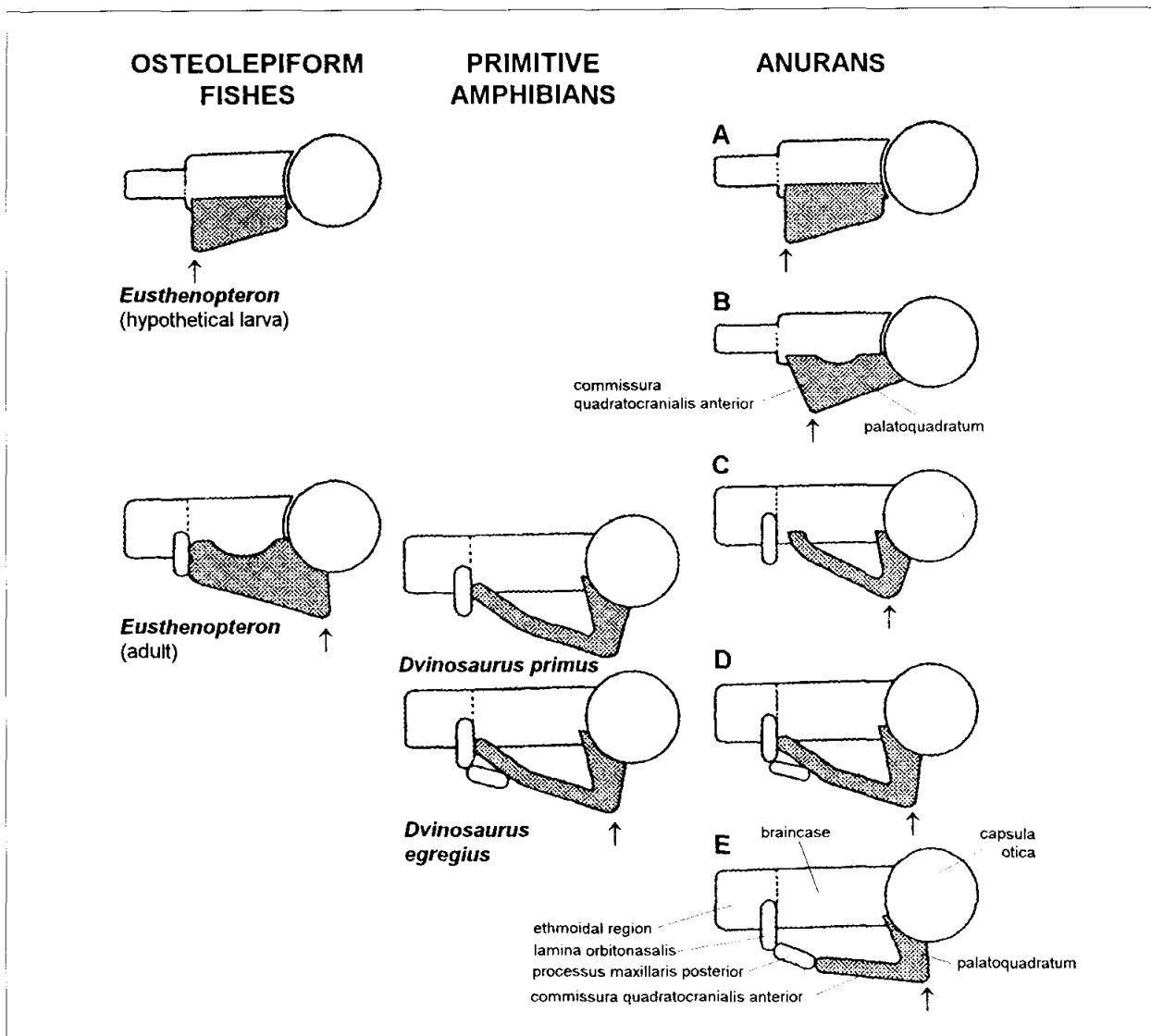


Fig. 16: Diagram representing development of the palatoquadrate and its anterior connections in anurans, from early larva (A) to adult (E), compared with labyrinthodonts (earlier developmental stage inferred from the condition in paedomorphic *Dvinosaurus primus*), and with hypothesized development in osteolepiform fishes exemplified by *Eusthenopteron*. Position of the jaw joint is marked by arrow. From Rocek (1993).

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