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CHAPTER 7

Larval Development and Evolutionary Origin of the Anuran Skull

Zbyněk Roček

I. INTRODUCTION

THE structure of the skull of adult anurans is a result of two processes. One is evolution, a long-term historical process in the course of which the skulls of ancestral crossopterygian fishes and certain late-Palaeozoic through early-Triassic temnospondyl labyrinthodonts evolved into the skull of an adult frog (Roček and Rage 2000a; Vorobyeva, this volume). The basic features of the anuran skull were attained in the early Triassic, as evidenced by *Triadobatrachus* (Rage and Roček 1989; Roček and Rage 2000b) and since the early Jurassic (some 200 million years ago) anuran skeletal anatomy has not changed substantially. The palaeontological record provides direct evidence of this process; however, the fossil record is often incomplete both with regard to structure of an individual and in terms of the sequence of evolutionary stages.

The second process is the development from early embryonic and larval stages to an adult (Fig. 1). Since development reflects evolution, gaps in the palaeontological record supposedly can be filled by recourse to developmental data. However, as in the case of the palaeontological approach, there are also limitations in using development as a tool for studying the origin and evolution of anurans. One should not forget that tadpoles, like adults, are adapted to particular environments (e.g., running water, stagnant ponds)

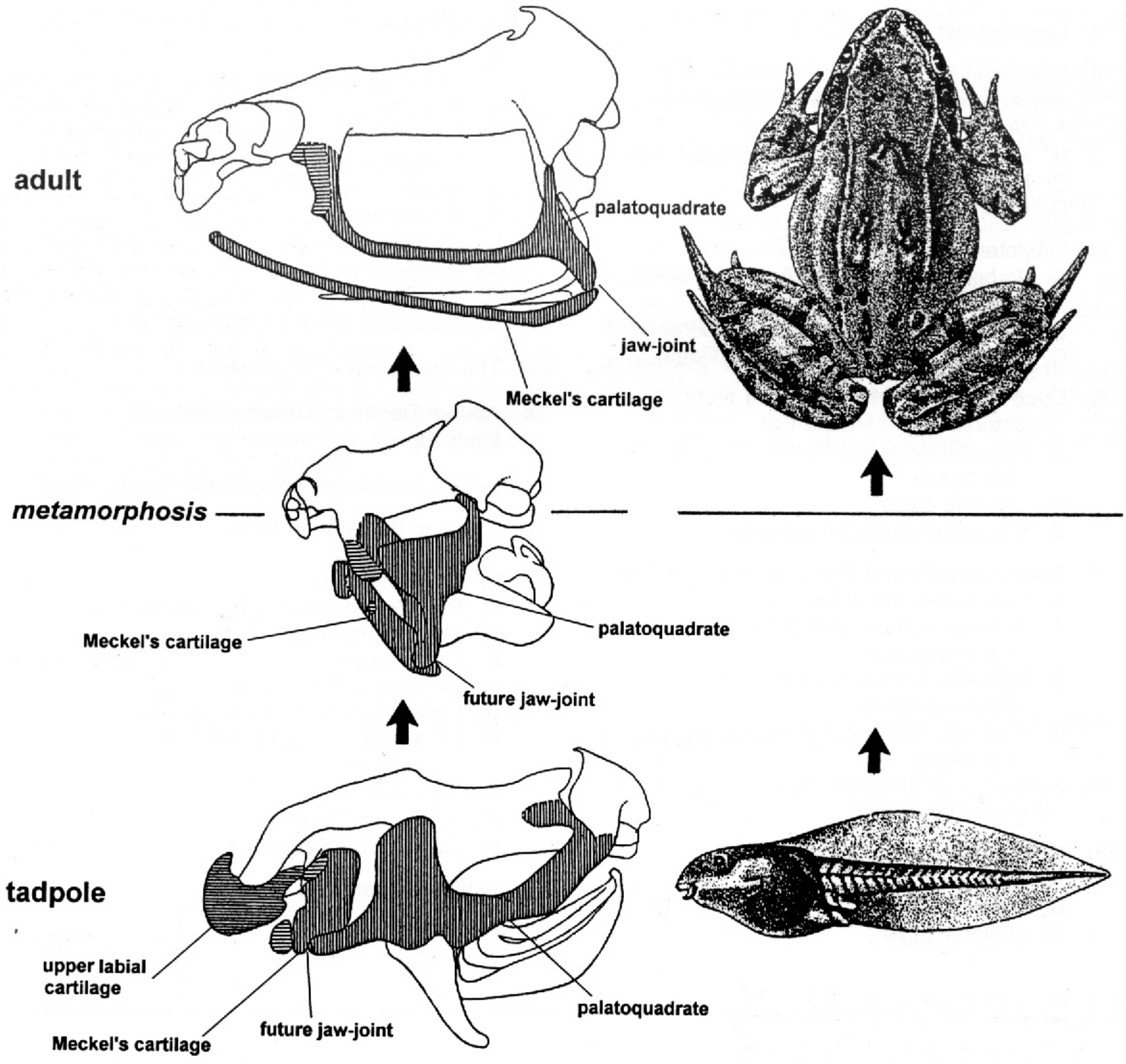


Fig. 1. Developmental changes in the anuran skull, other than the dermal exoskeleton (omitted), as seen in left lateral view. Homologous viscerocranial elements matched by type of hatching. From Roček (1999).

or modes of feeding (e.g., filter-feeding, scraping) that can be reflected in their cranial anatomy. Certain adaptations are associated with various modes of reproduction and may result in some periods of larval development being abbreviated, or entirely suppressed (Fig. 2). An extreme type of such adaptive heterochrony is known as "direct development" in which only advanced larval development is preserved.

Heterochronic changes may be a significant adaptive factor not only in low-level anuran taxa but also in the evolution of the Anura as a whole (Boy 1992; Roček 1995). In amphibians, abbreviation of development is, in an evolutionary context, often associated with neoteny or paedomorphosis. Due to these phenomena, adults correspond to an earlier developmental stage of an ancestral taxon. Undoubtedly, anurans took their origin from ancestral temnospondyls as a result of abbreviated somatogenesis. On the other hand, there is also developmental prolongation that results in structural additions that did not occur in ancestral taxa (see Fig. 61). Both abbreviation and prolongation may be combined so that an individual may correspond in some features to larval morphology but, because of evolutionary novelties, may be quite unique in others.

Retention of ancestral traits and development of new adaptive ones are two processes always involved in organic evolution. It is apparent that in attempting to reconstruct, by means of developmental studies, the evolutionary processes that ultimately led to the skull of contemporary frogs, one must distinguish between inherited ancestral characters and adaptive specializations (Fig. 3). In the course of metamorphosis, larval adaptations are

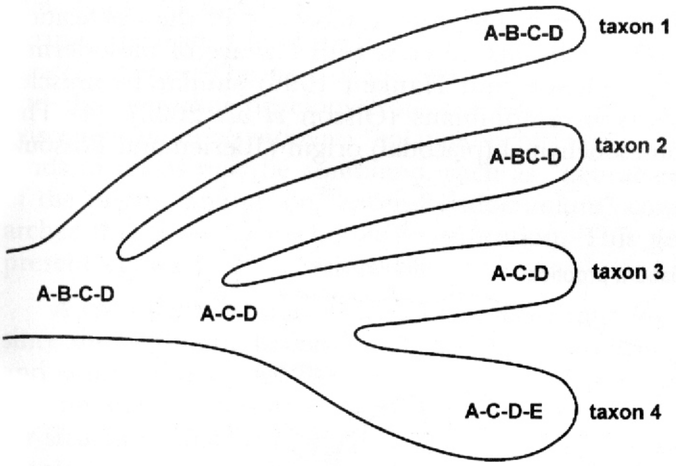


Fig. 2. Hypothetical examples of phylogenetic modification of ontogenies. The ancestral pattern of developmental sequences at the base of the tree goes through stages A-B-C-D. This pattern is preserved in taxon 1 and also in taxon 2 except that stages B and C are shortened. The ontogeny of taxon 3 is abbreviated because stage B has disappeared. By contrast, the ontogeny of taxon 4 is prolonged by the addition of stage E. Modified from Northcutt (1996).

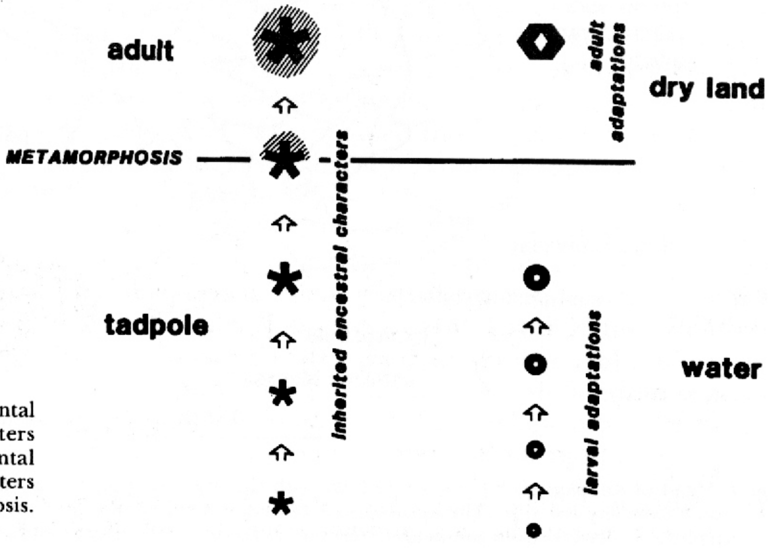


Fig. 3. Scheme contrasting developmental continuity of ancestral characters compared to the developmental discontinuity of adaptive characters during amphibian metamorphosis. From Roček (1993a).

replaced by the terrestrial specializations of adults. In contrast to adaptive specializations, the inherited ancestral characters can be traced through development from an early tadpole to the adult, regardless of metamorphosis, although in the course of metamorphosis such characters can deviate considerably from their early developmental state. Characters that can be traced throughout metamorphosis are inherited from the ancestors of anurans and consequently provide valuable information in evolutionary studies.

Before considering the development of the anuran skull as a tool for understanding its evolutionary origin, it should be mentioned that the skull takes its embryonic origin from several sources, the evolutionary significance of which is still poorly understood because it is associated with such early events as the origin and early evolution of vertebrates (Gans 1993). Basically, the vertebrate skull is of ectodermal and (to a lesser extent) mesodermal origin (Figs 4, 5). The structure of the larval anuran endocranium is portrayed in Figures 6 and 7. It consists of five embryonic components (Fig. 8): (1) The posterior (otic and occipital) region of the braincase takes its origin from the parachordals and the occipital vertebra i.e., from the sclerotomal material of the mesodermal somites. (2) The preotic section of the braincase (arising from the early embryonic cranial *trabeculae* and the visceral skeleton (originally supporting the branchial slits) develop from the neural crest (Olsson and Hanken 1996). Note, however, that Stone (1929) and Reiss (1997) claimed that some preotic structures, such as the dorsal part of the *processus ascendens*, *pila antotica* and posterior part of the *trabeculae* may be of mesodermal or mixed origin (Fig. 4). (3) The median parts of the branchial skeleton (basibranchials, called *copulae* in the amphibians) are possibly primarily ossified muscles in osteolepiforms (Jarvik 1980b) that later, in amphibians, became cartilaginous due to progressive blockade of the ossification process. They do not take their origin from the neural crest cells but are of mesodermal origin (Sadaghiani and Thiébaud 1987; Olsson and Hanken 1996) similar to muscles associated with branchial arch elements in amphibians (Olsson *et al.* 2000). (4) The ethmoidal and otic capsules are of ectomesenchymal (placodal) origin (Toerien and Rossouw

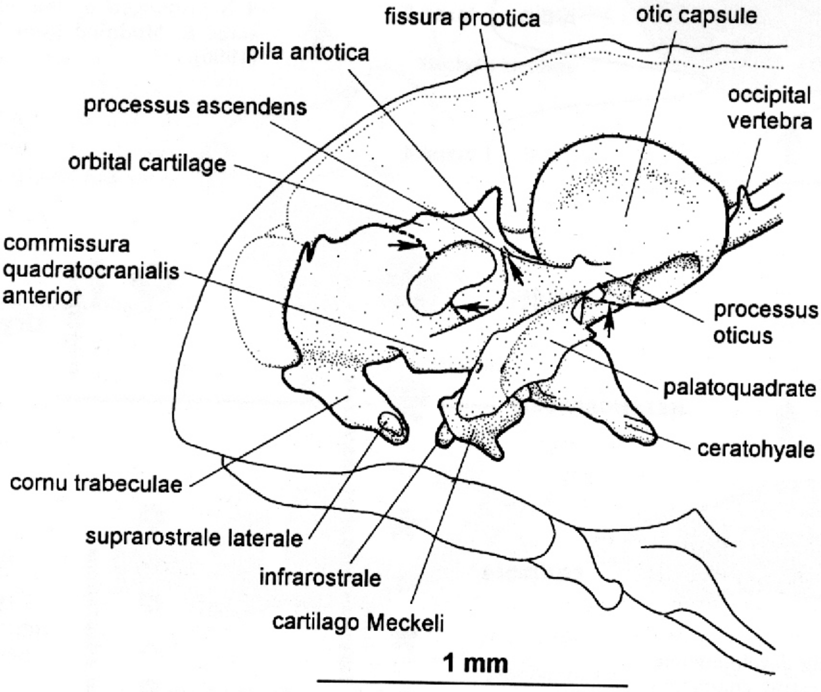


Fig. 4. Head of *Ascaphus truei* (13–15 mm larva with the oral disc protruding ventrally beyond the adhesive organ) as seen from the left side. The approximate boundary between the parts of the skull derived from the mesoderm, and those derived from the neural crest are marked by broken lines and indicated by arrows. From Reiss (1997).

1977). Note, however, that Villy (1890) and Reiss (1997) claimed the otic capsule to be of mesodermal origin. (5) The cranial exoskeleton ossifies in the connective tissue layer of the skin (dermis) which develops from the neural crest cells (unlike the dermis of the postcranial body) (Le Douarin 1982). Moreover, these embryonically different parts of the anuran skull are associated with two different modes of ossification: enchondral (all except for that mentioned earlier under 5) and endesmal (the exoskeleton).

Romer and Parsons (1977) noted that the term "endochondral" can be used for description of an "internal cartilage bone" ("intracartilaginous ossification"; see Williams 1995) whereas formation of bone on the surface of cartilage is described as "perichondral bone". Thus, "endochondral" and "perichondral" both refer to the process of replacement of embryonic cartilaginous primordium by adult bone and are encompassed by the single term "enchondral" as used here and by its synonym "cartilage bone" as used by de Beer (1937).

"Endesmal" "intramembranous", "mesenchymal", "membrane" and "dermal" are synonymous terms in reference to bone that is formed without cartilage as an intermediary.

Method of ossification and the positional relations of elements in the adult skull were principal features used for establishing the general terminology of skull bones as early as the 19th century. The part of the skull that develops by enchondral ossification from mesenchyme through cartilage is called the "endocranium" ("chondrocranium" is a synonym because this structure develops from cartilage). That part of the skull arising by means of endesmal ossification directly from dermal membrane is termed the "exocranium" (synonyms: "desmocranium", "dermatocranium"). Since exocranial bones arise within the dermis, they are found close to the surface of the skull, whereas endocranial bones are located deeper. The part of the skull that protects the brain is called the "neurocranium" and the part that develops from the branchial arches (adjoining pharynx) is called the "viscerocranium" (synonym: "splanchnocranium"). For brief and precise descriptions, both kinds of terms may be combined, such as "neural exocranium" comprising dermal bones of the neurocranium, or "visceral endocranium" comprising all elements of the branchial arches that arise by enchondral ossification. This general terminology is adopted in the present chapter.

A considerable number of anatomical terms for anuran larvae have been introduced since the beginning of the 19th century when Cuvier (1824), Dugès (1834), Reichert (1838) and some others published the first comparative anatomical observations on vertebrates and on the development of the skull in tadpoles. Some authors introduced new names for structures that had already been described and named by earlier workers. For instance, Dugès (1834) used the term "*rostrale supérieure*" when describing the upper jaw of the anuran tadpole, whereas Gaupp (1892, 1893) introduced "*cartilago labialis superior*" for the same structure. Although in that particular case little confusion was generated, other cases (e.g., "*planum ethmoidale*", "*planum internasale*" and "*planum trabeculare anticum*") were complicated by the fact that besides giving different names to supposedly the same structures, very vague definitions, or none at all, accompanied the descriptions. As a result, there is a considerable number of anatomical terms that are synonyms and, on the other hand, there are many homonyms, i.e., the same names designating non-homologous structures. One of the aims of the present chapter is to provide a list of synonyms (although far from complete) and to propose that the earlier of available names be adopted, provided that its first use was accompanied by unequivocal anatomical definition. A second aim is to provide definitions where they have been lacking previously. Latin is the preferred language for anatomical terms because some of those used in human embryology are included in the international code, *Nomina Anatomica* and are precisely defined, in contrast to most vernacular names. Latin terms maintain standardization. When other languages are used, confusion can be avoided if terms are direct translations from the Latin.

Besides differing anatomical terminologies, there is another source of confusion. Development is influenced by heterochrony, so that sometimes tadpoles corresponding in

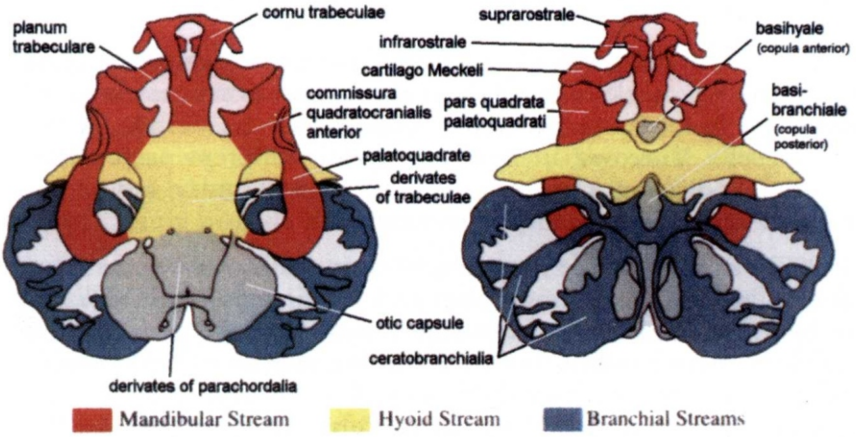


Fig. 5. Contribution of the neural crest to the larval skull of *Bombina orientalis* as seen in dorsal view (left) and ventral view (right). Components derived from the neural crest are coloured according to their migratory stream (see colour key). Mesodermal components are grey. From Olsson and Hanken (1996).

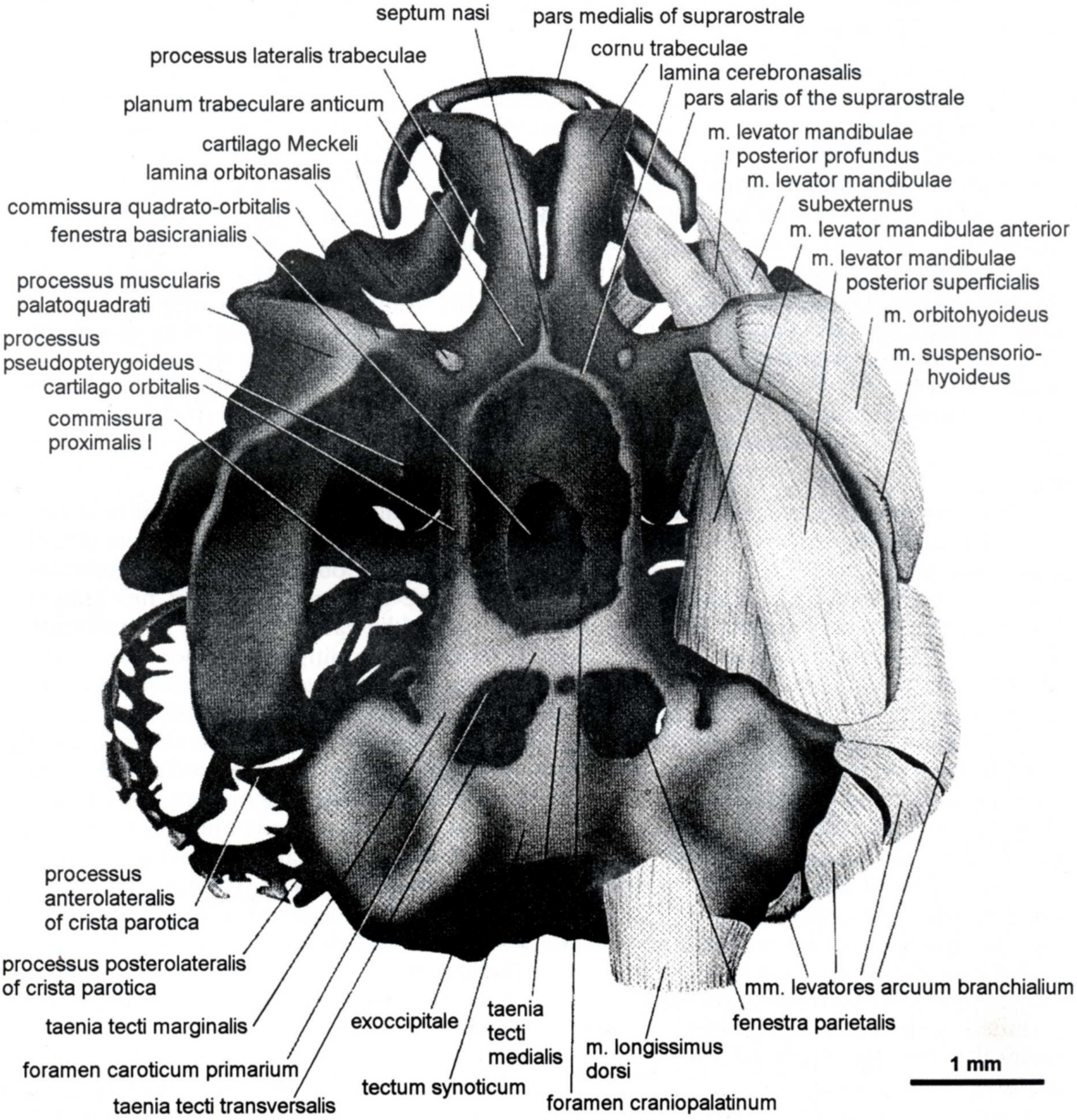
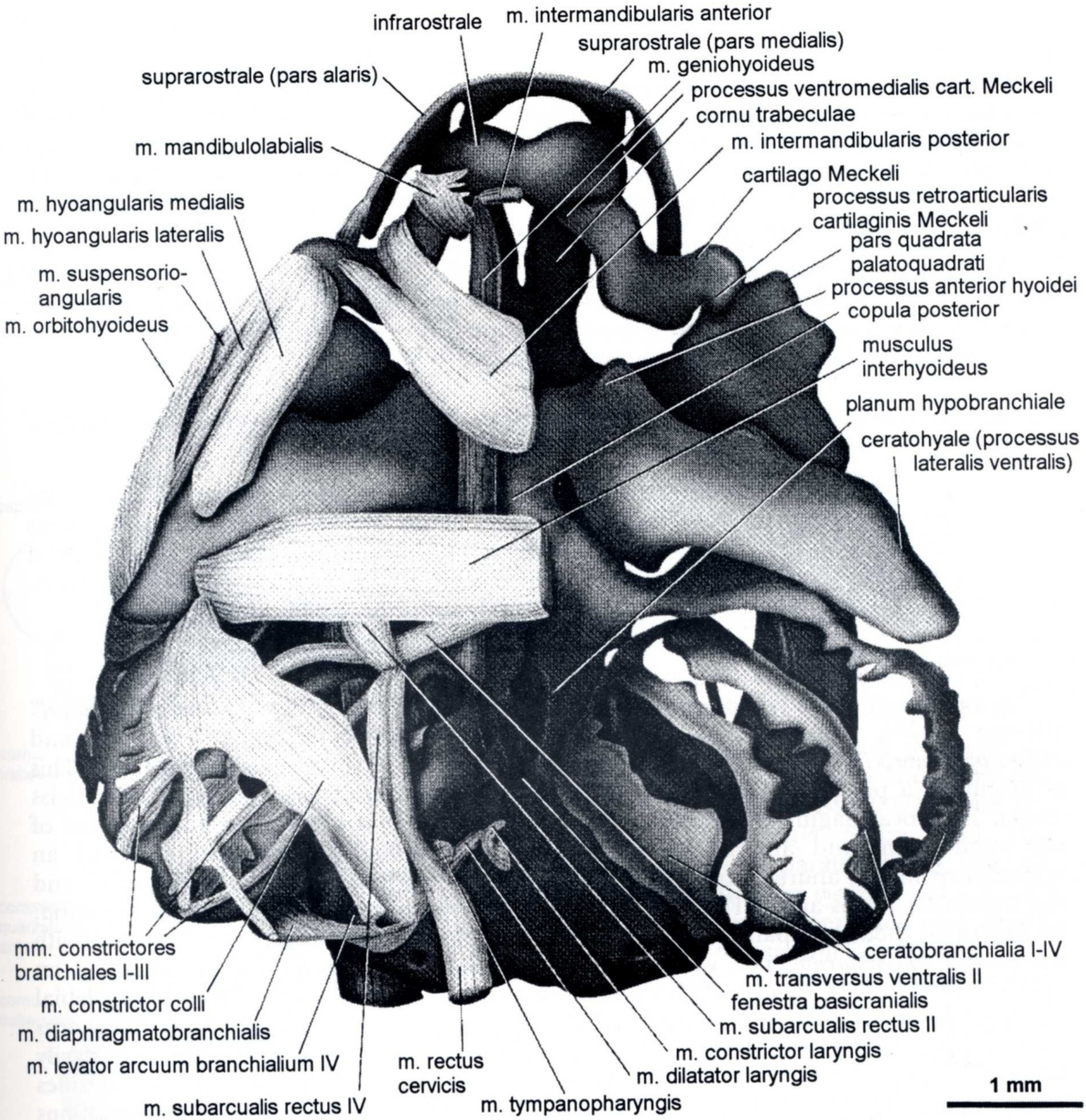


Fig. 6. Dorsal view of the larval endocranium and associated muscles of *Gastrotheca riobambae* at Gosner's (1960) stage 34 to show the general structure of the larval skull. From Haas (1996a).



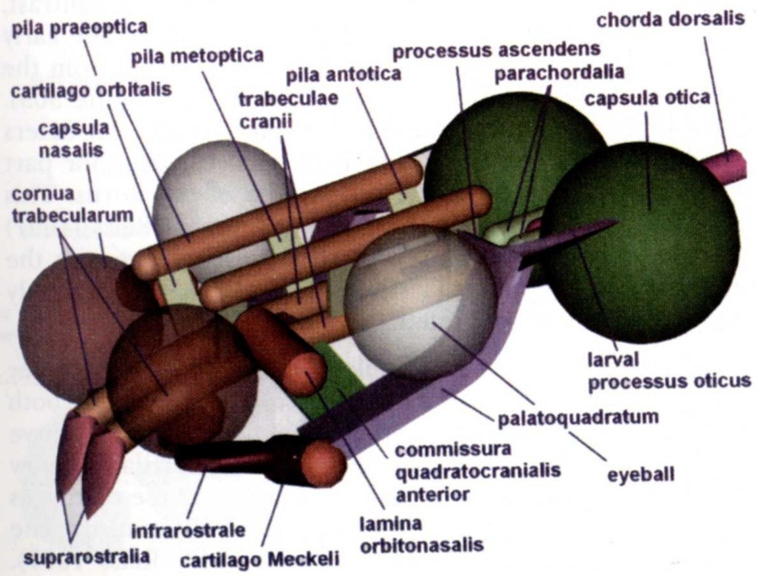


Fig. 8. Antero-dorsal view from the left side of a diagrammatic model showing the principal components of the skull of an anuran pre-metamorphic larva.

external morphology (which is conventionally used as a criterion for staging) differ in their internal anatomical structure. It is somewhat risky to use differences resulting from comparisons of non-corresponding developmental stages (often presented under generalized terms such as "larval chondrocranium"). The development of the anuran skull should be understood as a continuous process, the rate of which may be different in various taxa because of heterochrony.

As indicated by papers published in recent decades, after nearly 150 years of collecting descriptive information on the development of the anuran skull, it is now possible to use these data to elucidate the morphological evolution of the early tetrapods and to construct phylogenies useful in modern taxonomic studies.

II. ETHMOIDAL ENDOCRANIUM, POSTNASAL WALL AND ADJACENT PARTS OF THE PALATOQUADRATE

This part of the skull has different embryonic origins. The upper larval jaws, trabecular horns (and consequently the nasal septum and part of the *solum* of adults), the components of the postnasal wall and the *commissura quadratocranialis* anterior are all viscerocranial elements, and thus neural crest derivatives, whereas the nasal capsule is of placodal origin. Nevertheless, these diverse parts of the skull develop as a functional unit.

A. *Suprarostrale*

Synonyms of the *suprarostrale* are: "*rostrale supérieure*" (Dugès 1834), "*Oberkieferknorpel*" (Goette 1875), "upper labials" (Parker 1876), "*cartilago labialis superior*" and "*Oberlippenknorpel*" (Gaupp 1893), "*praerostrale*" (Petersen 1922 ex Reinbach 1939a). This is originally a paired structure formed exclusively from neural crest mesenchyme (Reiss 1997). Its procartilaginous rudiments occur within a layer of mesenchyme in the roof of the stomodeum and are among the earliest morphological structures to make an appearance in the anuran skull. Their early appearance (before the *trabeculae cranii* and the trabecular horns arise) (Fig. 9) was mentioned by Spemann (1898) for *Rana temporaria*; he described them as a pair of independent procartilaginous structures that later fuse with the *cornua trabecularum*, i.e., with the anterior horns of the *trabeculae cranii*. Based on Spemann's data, de Beer (1937) concluded that the primordia of both upper labial cartilages arise independently of the *trabeculae*. The latter expand anteriorwards, their horns (*cornua trabecularum*; see below) bend outwards and downwards, and only secondarily become continuous with the upper labial cartilages on their side (Spemann 1898). Besides Spemann, van Seters (1922) and Okutomi (1937) also distinguished separate condensations of mesenchyme representing the suprarostrals and the *cornua*, respectively. In contrast, Stöhr (1882) believed (also in *Rana*) that the *trabeculae* expand posteriorly from the early anterior centres of the suprarostrals and only later do the suprarostrals separate from the anterior ends of the trabecular horns (also see Goette 1875, his table 16 and figure 303). Separation of the upper labial cartilages from the cornua led Stöhr (1882), van Seters (1922) and Plasota (1974a) to conclude that these cartilages arise from the anterior part of the trabecular horns and are, in fact, only modified terminal parts of the horns. This may explain the various degrees of continuity between these two structures. Reiss (1997) observed (in *Ascaphus*) that the *trabecula* forms a continuous strip of mesenchyme with the upper labial cartilage. These observations suggest that the *suprarostralia* are probably anterior parts of the *trabeculae* that have become separated.

When chondrification occurs, separate centres are noticeable in the *trabeculae* and upper labial cartilages. In *Rana temporaria* (de Jongh 1968) and *Pelobates fuscus* (Roček 1981), both trabecular horns diverge rostrally from the cranial floor and their anterior sections curve ventrally; their ventrolateral corners articulate with the upper labial cartilages, now separated from the *cornua* (also see Born 1876; Spemann 1898). However, these cartilages and *cornua* may remain interconnected synchondrotically in *Bombina* (Fig. 10) until the late larval stages (Sokol 1981), and the same holds for *Ascaphus* (Pusey 1943; Reiss 1997).

Ramaswami (1940) distinguished between a movable articulation between the *cornua* and the suprarostrals, and a continuous connection of the two (in the microhylid genus *Uperodon*).

The *suprarostralia* are characteristic features of free-living anuran tadpoles. They were not found in *Leiopelma archeyi* (N. G. Stephenson 1951), *Breviceps adspersus*, *Eleutherodactylus coqui*, or *E. nubicola* (Lynn 1942; Hanken *et al.* 1992; Haas 1996a), a condition that, at least in some species, is associated with suppressed larval development. However, since available data report only on cartilaginous structures, it is not known whether or not the upper labial cartilage is formed as a rudiment in the procartilaginous stage. This possibility is suggested by observations on *Breviceps*, in which a rod-like mesenchymatous condensation, considered to be a rudiment of the suprarostral, reaches forward from the tip of a well-chondrified trabecular horn (Swanepoel 1970).

The *suprarostralia* develop in *Discoglossus* (Kraemer 1973, 1974) and some other taxa, including *Ascaphus* (Reiss 1997), *Alytes* (van Seters 1922) and *Bufo* (Sedra 1950; Haas 1996a), from two separate centres (Fig. 10), usually termed the *pars medialis* and *pars alaris* ("*constituant médian du suprarostral*" and "*constituant latéral du suprarostral*" [Kraemer 1973]; "median suprarostral" and "lateral suprarostral" [Reiss 1997]; *pars medialis* and *pars alaris cartilaginis suprarostralis* [d'Heursel and de Sá 1999]). The medial parts may fuse together into a single element called the *pars corporis* (Haas and Richards 1998). In the genus *Litoria* (Haas and Richards 1998, their figures 4b, 4c), the upper labial cartilage may be divided into the *pars alaris* that articulates both with the *cornu trabeculae* and synchondrotically with the *pars corporis* from which it is, however, well distinguishable. Also in some Megophryidae there are two pairs of suprarostrals (Sedra 1950).

Although one would be inclined to consider the *pars alaris* as the *adrostrale* of some other species (also see its synonyms on page 1903 which include the term "lateral suprarostral"), a significant difference is that

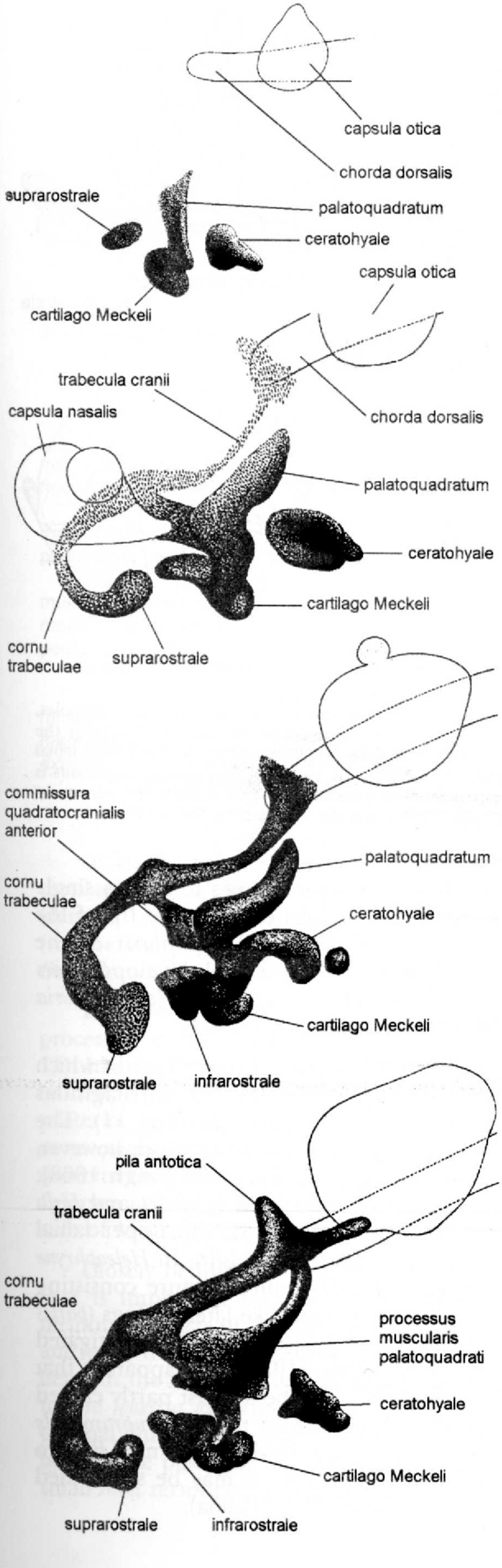


Fig. 9. Early developmental stages of the skull of *Rana temporaria* in left lateral view (larvae are 5, 7.5, 8, and 10 mm total length in descending order from top of page). From Spemann (1898).

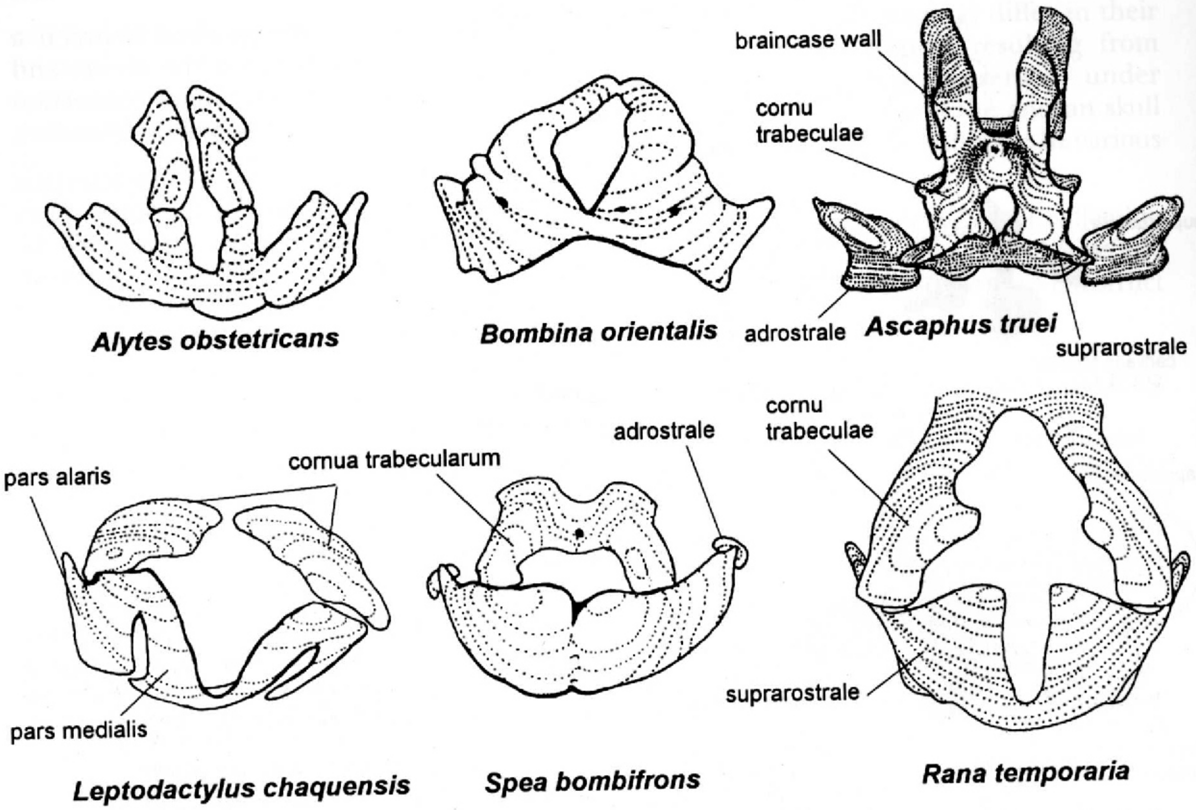


Fig. 10. Anterior view of a contour reconstruction of the upper labial cartilages and trabecular horns of tadpoles, showing the extent of the subdivision of the labial cartilages. The reconstructions are not necessarily of the same developmental stage or drawn to the same scale. Note that the *cornua trabecularum* and the upper labial cartilages are confluent in *Bombina*. The condition is similar in *Ascaphus*, in which the larval labial apparatus is highly specialized (see Fig. 4 for lateral view). The reconstructions of *Ascaphus* and *Spea* include the adrostrals. Drawing of *Ascaphus* from Pusey (1943), *Rana* from de Jongh (1968), and the others from Sokol (1981).

either both parts of the suprarostrals are fused together in various degrees to form a single upper labial cartilage on each side, or both are in contact or located near the tip of the *cornu trabeculae*. Another piece of evidence for differentiating the *pars alaris* of the suprarostral from the *adrostrale* is that in some tadpoles there is a well-developed *pars medialis* and *pars alaris* and, at the same time, a well-developed *adrostrale* (e.g., *Litoria nannotis* [Haas and Richards 1998]) (also see section II D, pages 1903–1904).

The suprarostrals on each side are vertical plates (Fig. 10), the lower edges of which are provided with horny sheaths bearing characteristic denticles; the cartilaginous *suprarostrale* and its horny sheath together serve as the larval upper jaw (Fig. 11). The suprarostrals are still separate from each other at early stages of chondrification; however, they may later fuse with one another across the midline (e.g., in *Rana* [de Jongh 1968]; *Ascaphus* [Reiss 1997]), which is also the case with some individuals of *Pelobates* and *Hyla* (Stöhr 1882) and *Gastrotheca* (Haas 1996a). In *Ascaphus* (Pusey 1943), the upper labial cartilage is unpaired but a V-shaped notch indicates it to be of paired origin. In *Heleophryne* (van der Westhuizen 1961) the *suprarostralia* make up a heavily-built structure consisting of a large median portion (medial parts fused together) and two rod-like lateral wings (*partes alares*). Since the suprarostrals remained paired in the specimens of *Pelobates* investigated by Sewertzow (1891), Plasota (1974a), Roček (1981), and Nikitin (1986), it is apparent that differences in the composition and shapes of these structures may be at least partly caused by comparison of non-equivalent developmental stages. It is obvious that the *suprarostrale* arises as a paired element in early development (see Reinbach 1939a), and may fuse to various extents in different taxa. On the other hand, in some taxa it may be subdivided into a *pars medialis* and *pars alaris* on each side (Plasota 1974a; Haas 1996a).

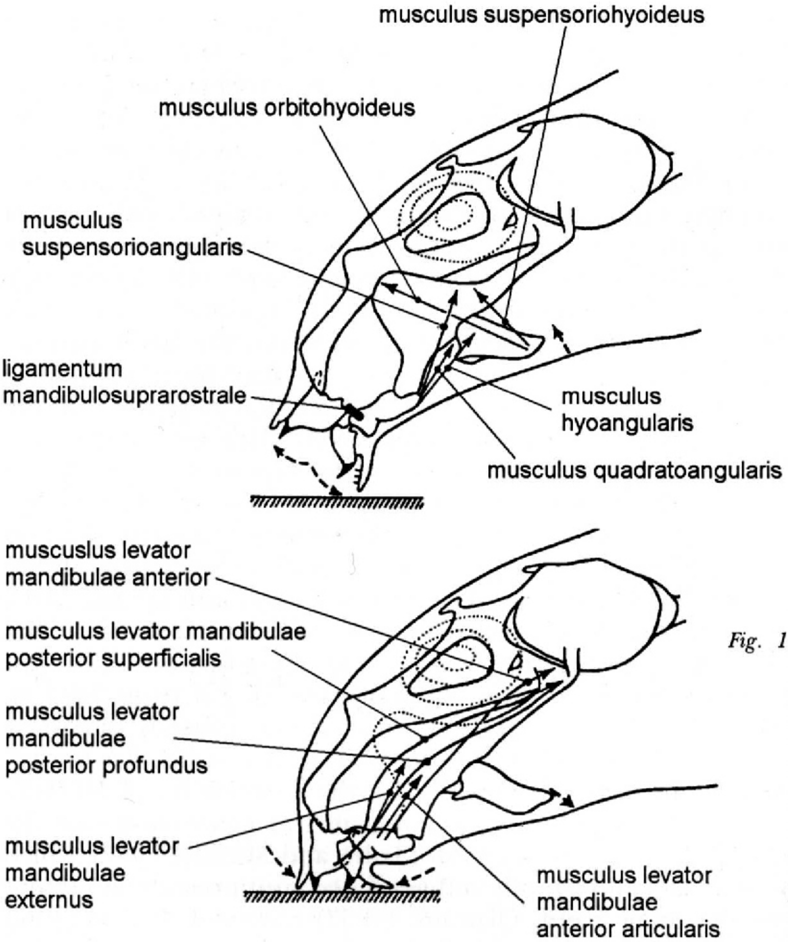


Fig. 11. Lateral views of the head of a tadpole of *Rana temporaria* showing movement of muscles (solid arrows) during feeding. Dashed arrows indicate movement of the jaws.

Upper: Abduction of jaws.

Lower: Adduction of jaws.

Note the function of the *ligamentum mandibulosuprarostrale* and the *musculus levator mandibulae externus*, both of which insert on the *suprarostrale*. From de Jongh (1968).

In *Pelodytes*, both suprarostrals are interconnected by a band of histologically distinct cartilage (Sokol 1981) and in *Hamptophryne* (Microhylidae) by a single, median, connecting element (de Sá and Trueb 1991) similar to the *copula* between the lower labial cartilages (see below, page 1932); similar shapes may be found in *Alytes* (van Seters 1922) and *Discoglossus* (Pusey 1943).

Detailed morphology (such as the presence or absence of the dorsal and ventral posterior processes) may be associated with the function of muscles inserting on the cartilages (Fig. 11). In *Pelobates*, the upper labial cartilage is moved by the *musculus levator mandibulae externus* (*m. temporalis* of Goette [1875]) in the antero-posterior direction. Both upper and lower posterior processes are in contact with the *ligamentum cornu-quadratum anterior* and *ligamentum cornu-quadratum posterior* which guide and support the upper labial cartilage during these movements (Sewertzow 1891). The *ligamentum mandibulosuprarostrale*, first described by Petersen (1922), runs from the posterior dorsal process of the suprarostral to the dorsolateral side of Meckel's cartilage, immediately posterior to its connection with the infrarostral.

Closely behind the medial part of the suprarostrals there is an unpaired median artery that is important for comparison of the suprarostrals among various anurans. It is a terminal branch of the left *arteria carotis interna*, from which the *ramus palatinus* splits off and exits from the braincase through the *foramen cranio-palatinum*. Then, it runs anteriorly beneath the floor of the braincase. That of the side splits into a number of small *rami* close to the *fenestra exonarina* (external naris), but the *ramus palatinus* of the left side keeps its original dimensions, moves medially, closely approaching the *ligamentum intertrabeculare*; closely behind the posterior surface of the medial part of the suprarostrals (in *Alytes*) it splits into small *rami* terminating in the vicinity of the uppermost row of denticles (van Seters 1922).

During metamorphosis, the suprarostrals of various species undergo resorption (if they are medially fused, they split medially), and ultimately disappear (Parker 1871; Born 1876; Gaupp 1893; de Beer 1937; Sedra 1950; van Eeden 1951; van der Westhuizen 1961; de Jongh 1968; Plasota 1974a; Wiens 1989; Haas 1996a; Maglia and Púgener 1998). The vestige of the upper labial cartilage is gradually replaced by a cartilaginous element "*laterale Randleiste*", "*basale Randleiste*", or "*basaler Randknorpel*" of Gaupp [1893]) adjoining the dorsolateral surface of the disintegrating *cornua*. This new element is structurally part of the nasal capsule but developmentally of a non-placodal origin (it is a derivative of the neural crest) (Reiss 1998). Ultimately it gives rise to the *cartilago praenasalis inferior* (see section II C, page 1899). The disintegrating suprarostral may be distinguished histologically from the young cartilage of this new element (Haas 1996a). However, the latter element replaces the former in approximately the same position. This may lead to an alternative interpretation according to which the *cartilago praenasalis inferior* is a derivative of the *suprarostrale* fused to the anterior ends of the *cornua* (Roček 1981). This interpretation is supported by observation of the mesenchymatous rudiment of the suprarostral developing close to the anterior tip of the trabecular horn (partial primordium of the inferior prenasal cartilage) in *Breviceps* (Swanepoel 1970). A close relationship between the suprarostrals and the anterior part of the *cornua* during metamorphosis was observed by Sewertzow (1891) who found the disintegrating upper labial cartilage divided into lateral and medial parts, the medial part being in contact with the *cornu trabeculae*. These observations indicate that the larval suprarostrals, adult *cartilago praenasalis inferior*, and the *solum nasi* (the last developing partly from the *cornua*), have a common developmental origin (Vogt 1842 ex Héron-Royer and van Bambeke 1889), and that the suprarostral may possibly persist as the lower prenasal cartilage on the anterior end of the *solum nasi* (larval trabecular horns), much as the infrarostral persists as the mentomandibular on the anterior tip of Meckel's cartilage (see section V D, page 1932). It may also be noted in this connection that the *cartilago praenasalis inferior* is absent in adult *Xenopus laevis* (Sedra and Michael 1957), which may be associated with the fact that morphologically differentiated suprarostrals are absent in the tadpole (see below). On the other hand, Okutomi (1937) observed disintegrating vestiges of the suprarostrals (however, these might equally have been the adrostrals because of their position in relation to Meckel's cartilage) as well as the previously formed lower prenasal cartilages; this contradicts the view that the suprarostral is preserved in adults as part of the inferior prenasal cartilage.

To complete the range of views on the transformation of the suprarostral during metamorphosis, it is noted that Parker (1876) and Marshall (1893) believed that the upper labial cartilages persist in adults as the cartilages that bound the nostrils anteriorly (the so-called "new upper labials" or "*cartilagines prorhinales*"), and that Reinbach (1939a) maintained that the remnants of the upper labial cartilages are preserved in adults as the *processus praenasales superiores* which, according to him, are evidenced by the *ligamentum suprarostrale*.

The identity of the upper labial cartilage in larval Pipidae and Rhinophrynidae is a matter of discussion (Figs 12, 13). In the earliest stages of *Pipa pipa* (Roček and Veselý 1989, their figures 1A, 3), the ethmoidal region of the skull consists of a thin median horizontal plate, termed the *planum internasale* ("internasal plate" of Parker [1876], "trabecular" or "ethmoid plate" of de Beer [1937]) and not homologous with the *planum trabeculare anticum* (see page 1900). The anterior edge of the plate ("upper labials" of Parker [1876] his plate 56, figures 4, 5]) is extended laterally to form an arch-like protrusion ("*cornu trabeculae*" of Parker [1876]; "ethmoidal flanges" of Sedra and Michael [1957]; "suprarostral plate" and "suprarostral cartilage" of Trueb and Hanken [1992]) that joins a process projecting anteriorly from the orbitonasal wall, so that the ethmoidal region is complete laterally. This connection may not chondrify and can be distinguished as a strip of mesenchymatic tissue ("prenarial ligament" of Parker [1876]; "*ligamentum cornu-quadratum mediale*" of Sedra and Michael [1957]), whereas it consists of cartilage (or diffuse condensation of cartilage) in *Xenopus* (Patterson 1939; Sokol 1977; Trueb and Hanken 1992).

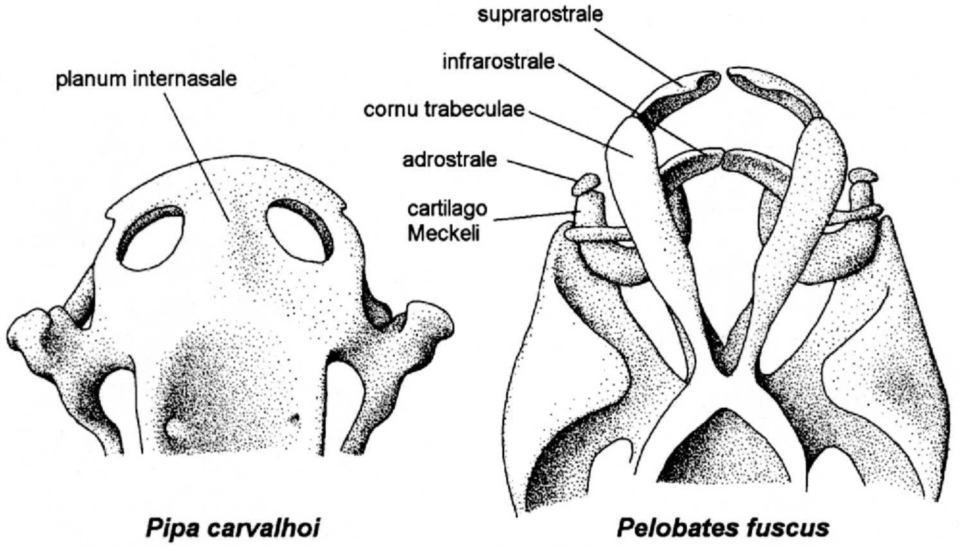


Fig. 12. Dorsal view of a larval ethmoidal endocranium of a pipid *(Pipa carvalhoi)* and a non-pipid *(Pelobates fuscus)* anuran. From Roček (1993a).

The nasal sac is located above the level of the *planum internasale*. It should be noted that Parker considered structures in various taxa and even in different developmental stages to be homologous solely on the basis of their topographic position, as is clear from pages 629 and 631 of his 1876 paper.

The anterior part of the plate with the arch-like margin has no paired precursor, even in the prechondral stages (Föske 1934). Since it serves as a larval upper jaw, it is usually called the *suprarostrale* (e.g., Kotthaus 1933). However, in the illustration reproduced from Kotthaus by de Beer (1937, his plate 79, figure 4) this structure is identified as the *cornu trabeculae*. It has also been known as the "suprarostral" or the "suprarostral plate" (Sokol 1975, 1977; Trueb and Hanken 1992; Swart and de Sá 1999), the "superior labial cartilage" (Paterson 1939), and the "*cornu trabecularum*" (Starrett 1973). Apparently, these authors followed Paterson (1939) who did not label a suprarostral in her figures but did, however, remark that "The Meckel's cartilages are slightly curved rods, which project forwards from the quadrate below the superior labial cartilage formed by the anterior margin of the ethmoidal cartilage". It can be inferred from this statement that she believed that the anterior margin of the internasal plate represented the suprarostral. However, de Beer (1937), in describing the stages of the *Xenopus* chondrocranium, emphasized the "absence of separate suprarostral cartilages, articulated with the trabeculare horns". Without giving any developmental evidence, Weisz (1945), Sokol (1977) and others, have considered the median part of the *planum internasale* to be the *cornua trabecularum*, with the space between the *cornua* being occluded. From this hypothesis, Sokol concluded that the upper labial cartilages of pipids are represented by a semilunar anterior plate entirely confluent with the cornua and fused with one another. He probably based this conclusion on the larva of *Rhinophrynus* in which he found a median fenestra within the anterior part of the internasal plate. Trueb and Hanken (1992) maintained that the anterior part of the internasal plate ("rostral cartilage") of *Xenopus* may be homologous with the upper labial cartilage (suprarostral) in non-pipid anurans, pending the discovery of a tadpole possessing both a flat plate-like anterior extension of the planum internasale and, at the same time, an upper labial cartilage.

It is apparent that Parker's (1876) opinion about the homology of the anterior part of the internasal plate and the suprarostral, was repeated by some later authors without any convincing proof (also see de Beer 1937; Haas 1966a). It is clear only that both structures take their origin from the same region of the neural crest (Sadaghiani and Thiébaud 1987), too vague a foundation for establishing homology between these delicate

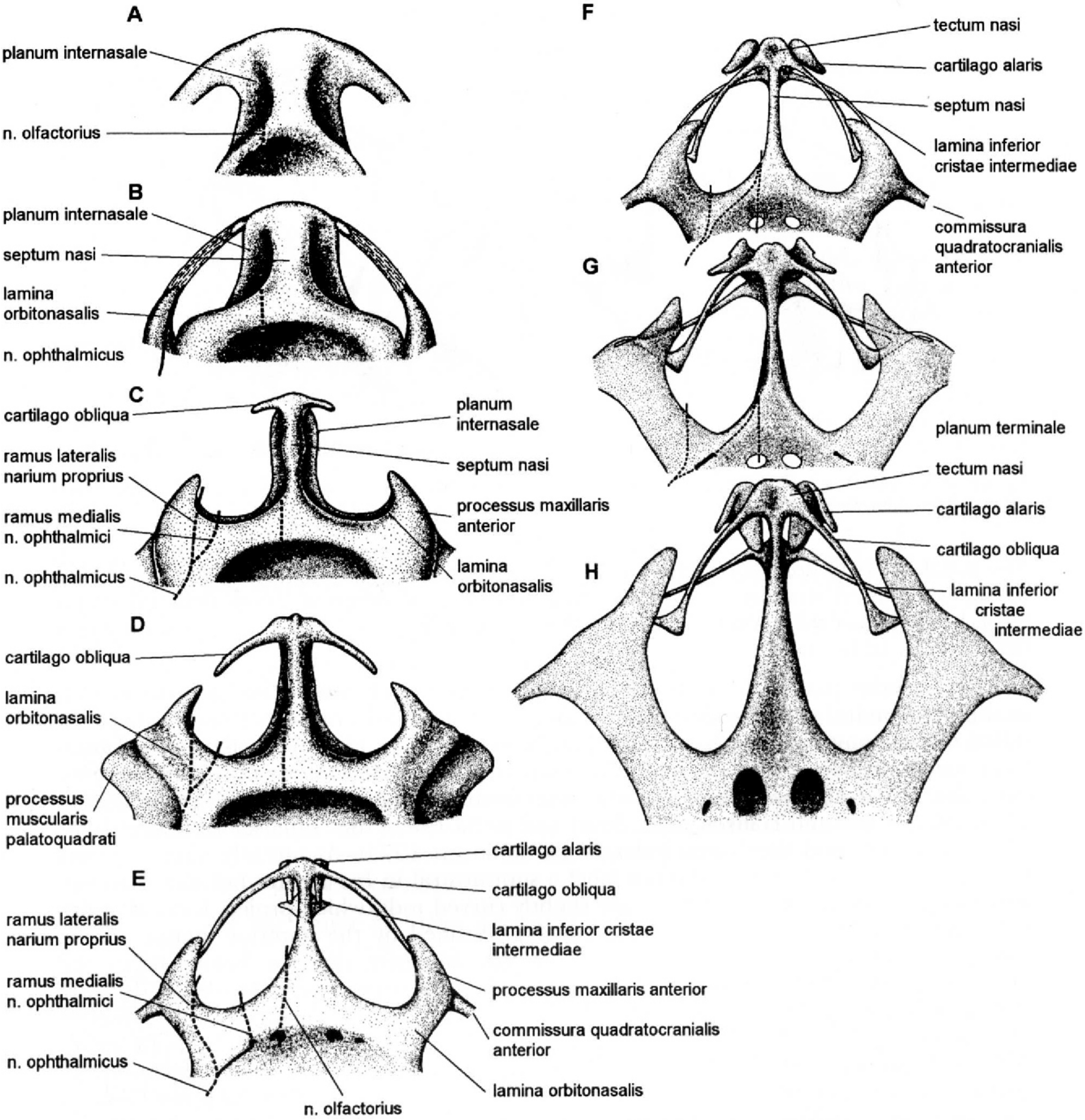


Fig. 13. Dorsal views of the development of the ethmoid region of the skull of *Pipa pipa*. Stages are according to Nieuwkoop and Faber (1967) and drawings are not necessarily to the same scale.

elements. More recently, a description of the larval cranium of *Heleophryne* (Fig. 14) was published in which a structure similar to the *planum internasale* occurred; there is a ligament bordering the lateral margin of the ethmoid region and there is a well-developed suprarostral (van der Westhuizen 1961, his figures 6, 7). The condition in *Heleophryne* does not allow interpretation of the anterior part of the horizontal plate as the upper labial cartilage; most probably this plate is homologous with the *planum internasale* of pipids.

Recently, de Sá and Swart (1999) and Swart and de Sá (1999), in attempting to solve this problem, found two rod-shaped cartilages separate from each other and from the anterior edge of the internasal plate (their "ethmoid" and "ethmoid plate" respectively in larval *Hymenochirus* and *Rhinophrynus*), at the stage when the *septum nasi* is already a

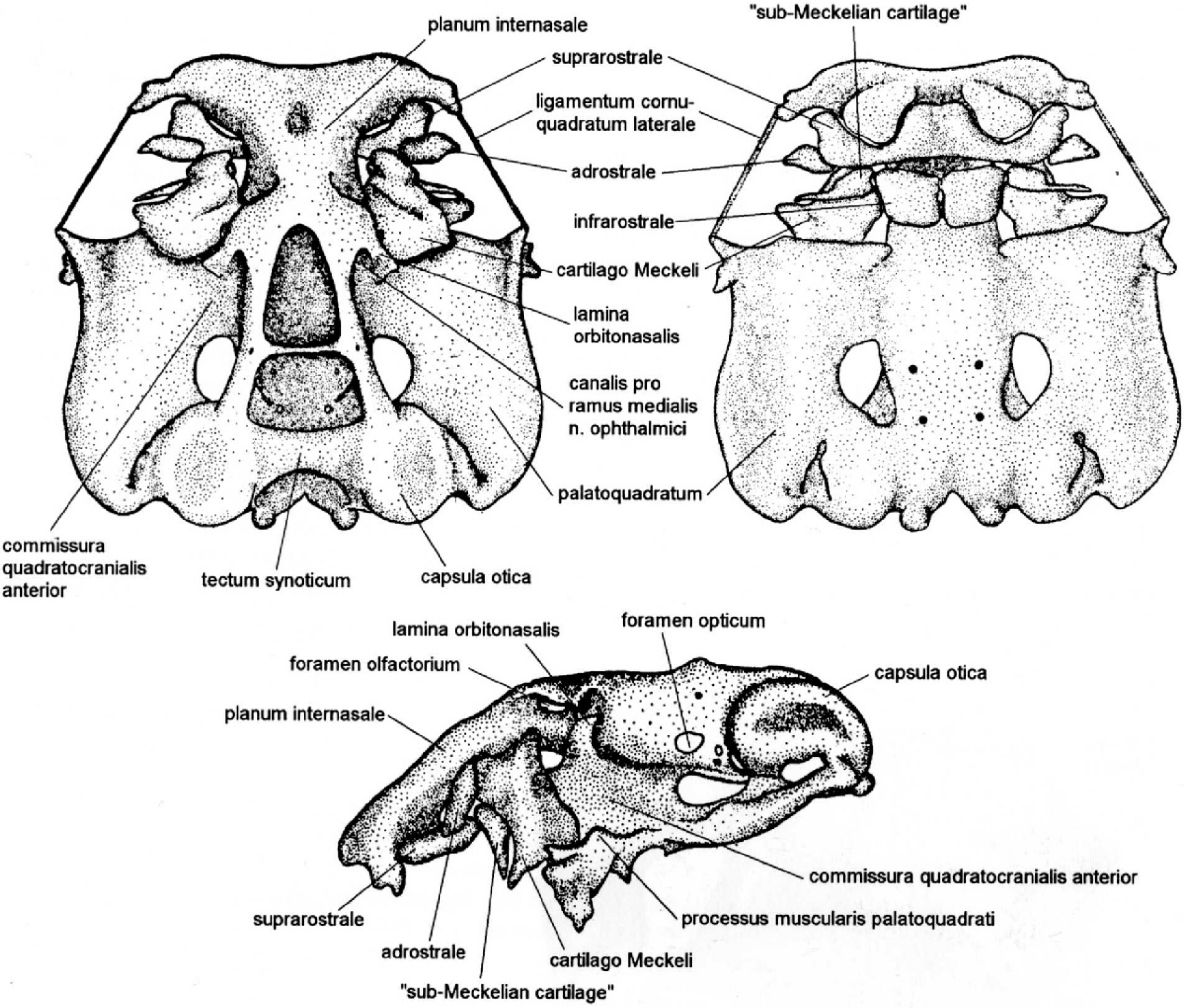


Fig. 14. Larval endocranium of *Heleophryne purcelli* in dorsal (upper left), ventral (upper right) and left lateral (lower) views. From van der Westhuizen (1961).

prominent ridge. In *Hymenochirus*, these cartilages rotate from their originally vertical orientation to a horizontal position and still later they disappear, similar to the larval *septum nasi*. As de Sá and Swart suggested, these two cartilages may be considered as the upper labial cartilages but, as can be judged from their description, they are not incorporated into the anterior part of the internasal plate. In early developmental stages of *Rhinophrynus*, the upper labial cartilages supposedly are only fused to the anterior tips of the trabecular horns (de Sá and Swart 1999; Swart and de Sá 1999); the same occurs in larval *Xenopus*. The separate upper labial cartilages were not observed. It seems that if suprarostrals develop in *Hymenochirus* they are not incorporated into the anterior part of the internasal plate, as Sokol (1977) believed. Until more precise evidence becomes available, it seems inappropriate to apply the term *suprarostrale* to pipids (also see Kotthaus 1933; Paterson 1951, 1955).

B. *Cornua Trabecularum* and *Septum Nasi*

The *cornua trabecularum* ("prorhinal cartilages" of Huxley [1875] ex Parker [1876]; "trabecular flanges" of van Eeden [1951]) are neural crest derivatives (Reiss 1997), as are the *trabeculae cranii*. Experimental studies on various vertebrates, including anurans (*Discoglossus*; Toerien and Rossouw [1977]) have indicated that the nasal septum of adults is formed from the *trabeculae cranii* and that it is not part of the nasal capsule which is of placodal origin.

The origin of the *cornua trabecularum*, their early development and developmental relationship to the upper labial cartilages were mentioned above (also see Reinbach 1939a). It should be emphasized that in the earliest larval stages the forebrain (*prosencephalon*) lies between the nasal sacs, an thus between the *cornua*. Later, however, the *cornua trabecularum* and the nasal sacs extend in a rostral direction so that both project well beyond the anterior end of the *telencephalon*; this leads to the formation of a precerebral rostral region (Swanepoel 1970). The *cornua* arise as part of the *trabeculae*, although somewhat later (Okutomi 1937), and remain continuous with them throughout the whole period of their existence (also see Born 1876). The so-called "hypotrabecular continuations" or "recurrent trabecular cornua" of Parker (1876, figures 3 and 5 of his plate 60 and figure 8 of his plate 62) are either the oblique cartilages (*cartilago obliqua*) or the *lamina inferior cristae intermediae* (Roček and Veselý 1989, their figure 1); both are part of the ethmoid capsules and have nothing in common with the *trabeculae*. The same holds for the "*cornu trabeculae*" of Higgins (1920) and of Paterson (1955), reported in adult *Pipa* (also see Paterson 1945).

In *Rana*, both *cornua* are interconnected dorsally by a *ligamentum intertrabeculare superius* (Gaupp 1893; de Jongh 1968); this ligament continues laterally on to the dorsal side of the nasal sacs. A similar ligamentous connection occurs between the lower parts of the *cornua* (*ligamentum intertrabeculare inferius* of Born [1876]; also see Gaupp [1893]). In *Alytes*, both ligaments develop only after the *cornua* chondrify (van Seters 1922). These ligaments

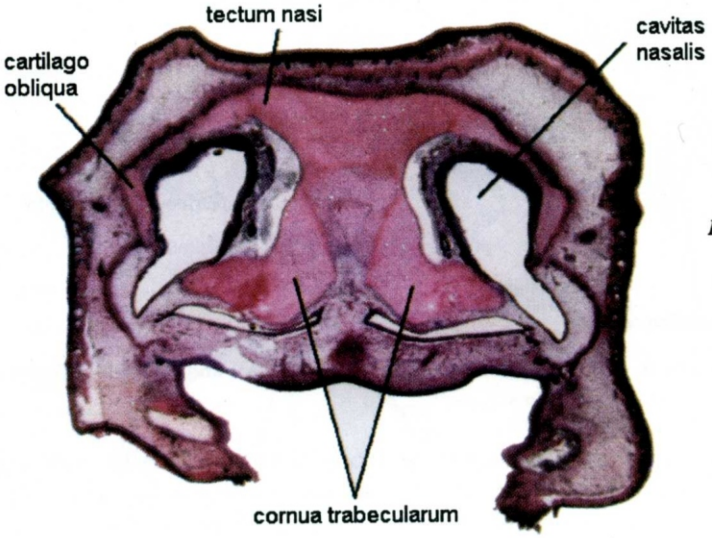


Fig. 15. Frontal section through the posterior part of the ethmoidal region of a metamorphosing *Pelobates fuscus* (stage 64 after Nieuwkoop and Faber [1967]). Between and slightly above the vestigial *cornua trabecularum* is a new cartilage of the nasal capsules. In the anterior part of the ethmoid region the septum is formed only by this new cartilage.

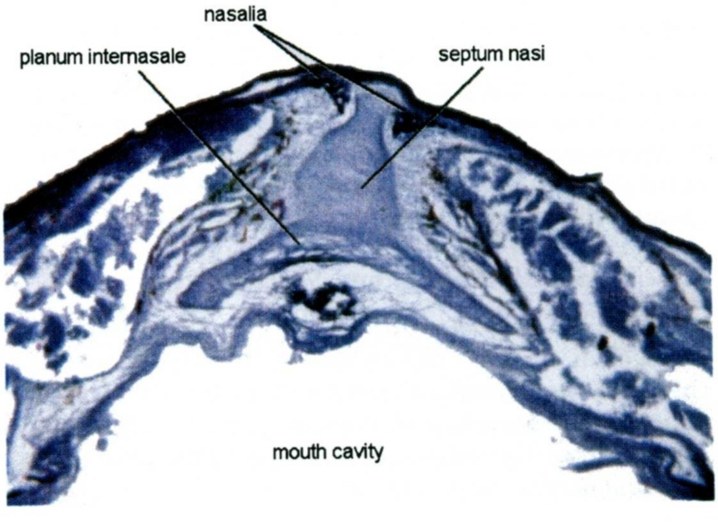


Fig. 16. Frontal section through the ethmoidal region of a larval *Pipa pipa* (stage 52 after Nieuwkoop and Faber [1967]). The nasal septum arises independently of the *planum internasale*. Compare with the illustrations in Roček and Veselý (1989).

are a characteristic feature of free-living tadpoles, and neither one seems to develop in anurans with suppressed larval development (Swanepoel 1970). The *ligamentum intertrabeculare inferius* may be chondrified posteriorly as an horizontal plate ("plan internasal" of van Seters [1922]) from which a median outgrowth may project anteriorly; this chondrified horizontal plate gradually expands anteriorly and encloses the median outgrowth (Reinbach 1939a). Throughout larval development, the *cornua* remain the principal support of the developing olfactory organ and its capsule.

During metamorphosis, a new cartilaginous material begins to fill the space between both *cornua* (Born 1876; Okutomi 1937; Roček 1981) and expands over the dorsal side of the nasal sac, thus forming the medial part of the *tectum nasi*. In *Rana* (Born 1876; de Beer 1937; Plasota 1974a) this scheme is basically similar to that in *Pelobates* (see Fig. 15); however, the septum begins to develop posteriorly as a well-delimited median vertical partition on the dorsal surface of the *planum trabeculare anticum*, within the *fenestra ethmoidalis* (Born 1876; Gaupp 1893), then progresses anteriorly into the intertrabecular space above the chondrified *ligamentum intertrabeculare inferius* and below the *ligamentum intertrabeculare superius*. As noticed by Reinbach (1939a), in *Caudiverbera* the septum expands anteriorly without being in contact with the *ligamentum intertrabeculare*. Basically similar is the early development of the septum in *Eleutherodactylus nubicola*, an anuran with suppressed larval development (Lynn 1942, his figure 28). In *E. coqui*, the *cornua trabecularum* are absent and never form (Hanken *et al.* 1992).

In the course of further development the septum expands dorsally and laterally to form a T-shaped structure (in cross-section) that extends over the dorsal margin of the *cornua* (Fig. 15). This new cartilage is, however, already produced by the developing nasal capsule (see below). In contrast, the septum does not reach ventrally below the *ligamentum intertrabeculare inferius* (Gaupp 1893). The *cornua trabecularum* soon begin to disintegrate at their ends so that the anterior section of the septum (of exclusively capsular origin) arises independently of the *cornua*. Here, the new cartilage of the septum expands anteriorly, over the reduced ends of the *cornua*, thus filling the space between the anterior medial walls of each capsule and forming the *processus praenasalis medius* of the adult. Remarkably, ossification of the cartilage begins in the area between the proximal (i.e., posterior) sections of the *cornua*. This means that the first trace of ossification within the sphenethmoid (called the "presphenoid" by Ramaswami [1942]) occurs while both *cornua* are still detached anteriorly.

Whereas in earlier stages the border between the new cartilage originating from the nasal capsule and the old cartilage of the *cornua* is distinct (Fig. 15) (also see Born 1876; Reinbach 1939a), it later disappears progressively in a posterior to anterior direction so that the extent of the former *cornua* cannot be distinguished. Nevertheless, as can be evidenced by distinct sagittal mounds protruding from the medial part of the ventral surface of the *solum nasi*, the *cornua* become incorporated into the lower part of the septum during its early development, although the thickness of the septum later decreases. Only in the adult, when the septum and *solum* become ossified and comparatively thin, do these mounds disappear. According to Born (1876), Gaupp (1893), Okutomi (1937), Reinbach (1939a), Lynn (1942), de Jongh (1968), Roček (1981), de Sá and Trueb (1991) and Maglia and Púgener (1998), unresorbed remnants of the *cornua trabecularum* are incorporated into the medial part of the *solum nasi*.

During its anterior expansion, the septum reaches the medial surface of the *cornua trabecularum* and the lower part of the septum becomes connected with the medial part of both trabecular horns (Stadtmüller 1936). Then, the *cornua* undergo partial resorption. In *Pelobates*, they are resorbed in their anterior section, up to the level where the *cartilago praenasalis inferior* joins the *solum nasi* (also see Born 1876). In their proximal (= posterior) section, the *cornua* are resorbed only from their lateral surfaces, the medial ones being preserved and incorporated into that part of the adult nasal capsule where the septum merges with the *solum nasi*.

The fact that in *Pelobates* the septum arises from intertrabecular material and only later extends dorsally, whereas in *Rana* it arises above the *cornua trabecularum* and separate from them, only later extending ventrally into the intertrabecular space, may be explained by differences in position of the nasal sacs. These are located underneath the *cornua* in the early development of *Pelobates*, so that the *cornua* separate them from each other. In *Rana*, they are located above the *cornua* (Fig. 9), which requires a new partition early in development (Born 1876). Also in the Pipidae, in which the nasal sac is located dorsal to the internasal plate, a median and rather broad, elevated part is present in the earliest stages of chondrification. This is the first rudiment of the *septum nasi* (Figs 13A, 16); however, a substantial part of the septum (and a great majority of the nasal skeleton, including its *solum*) arises above the internasal plate ("supraethmoidal plate"); this plate later disappears completely (Parker 1876; Roček and Veselý 1989). As the nasal sac grows bigger, the septum becomes higher and thin (similar to non-pipid anurans in which the septum extends anteriorly above the level of eroding trabecular horns) and it extends over the eroding anterior part of the internasal plate (Trueb and Hanken 1992). The situation in *Heleophryne* (van der Westhuizen 1961) recalls in some respects the condition in the Pipidae, i.e., the *septum nasi* develops above the internasal plate (also see Trueb and Hanken 1992). However, *Heleophryne* is unique in that the *tectum nasi* develops in isolation from the septum. In *Hymenochirus*, the larval *septum nasi* projects dorsally from the internasal plate, but this septum is eroded away and replaced by a newly formed adult *septum nasi* (de Sá and Swart 1999).

Whether the vestiges of the thin lateral parts of the internasal plate medially adjoining the choana in metamorphosing pipids (Fig. 13D) are homologous with the vestigial *cornua trabecularum* incorporated into the *septum/solum nasi* of non-pipid anurans (Fig. 15) remains questionable but not excluded. The situation is complicated by the fact that in non-pipid anurans the *solum nasi* develops from several independent parts (the *cornua* being only one of them; see page 1898), whereas in *Pipa* it is only a temporary structure, extremely limited in extent and arising from a single element. Recent investigation by de Sá and Swart (1999) on *Hymenochirus* suggests that there is a single, median, rod-shaped element (termed the "anterior process of the ethmoid plate" or "APE") in the early development of the ethmoid cranium which is later paralleled ventrally by anteriorly expanding structures called the trabecular horns. The APE and the *cornua* later form a continuous cartilaginous plate that grows dorsally to form the larval *septum nasi* (a similar process was found in *Rhinophrynus*). This septum is later eroded and replaced by a newly formed adult *septum nasi* (which is undoubtedly of capsular origin). It is obvious that in *Hymenochirus* there is a different developmental timing of the APE (which is a larval structure producing a septum that later disappears). The adult *septum nasi* develops as a new structure between the *cornua trabecularum* (see page 1893).

The fact that the *ligamentum intertrabeculare inferius*, interconnecting the lower parts of the *cornua trabecularum*, may chondrify posteriorly as an horizontal plate (called the "plan internasal" by van Seters [1922]) and that this plate disintegrates completely during late premetamorphic stages (Reinbach 1939a) may suggest that this ligament (and the horizontal cartilaginous plate, if the ligament is chondrified) may be homologous with the medial part of the *planum internasale* of pipids; the *septum nasi* arises dorsal to both structures (Fig. 16) and both disappear in the course of development. If this is true, then judging by the condition in temnospondyls in which the ethmoidal endocranium is a shallow horizontal plate (Roček 1991a, his figure 5), it is highly probable that the trabecular horns evolved from the internasal plate by suppressed chondrification along the midline. This process may be similar to that in which the *ligamentum cornu-quadratum laterale* evolved from the anterolateral margin of the plate, and which is still observable in the development of *Pipa* (Fig. 13 A–C). Such a trend would be quite opposite to that whereby both *cornua* coalesce to form the internasal plate (Higgins 1920). This also would explain the fact that no trabecular horns were found in temnospondyls, despite expectations to the contrary (Säve-Söderbergh [1936], his text-figure 8).

It should be added that in the late intracapsular embryo of *Leiopelma*, both trabecular horns are curved ventrally (Fig. 17) and the cranial cavity is open anteriorly (N. G. Stephenson [1951], his figure 5). With progressive development, a block of cartilage forms the broad anterior wall of the cranial cavity. Since both ethmoidal capsules are located ventrolateral to the anterior part of the cranial cavity, lateral to both cornua, an extensive *cavum internasale* arises. This thick, broad wall of the cranial cavity extends ventrally and anteriorly, in front of the more posteriorly directed trabecular horns (N. G. Stephenson 1951). Anteriorly, it is terminated by the *processus praenasalis medius*.

Disregarding specialized deviation from the common scheme, it is likely that the vestiges of the *cornua trabecularum* take part in the formation of the *septum nasi* (and partly also of the floor of the nasal capsule; see page 1898). However, this holds true only for the posterior part of the septum. In contrast, the anterior part of the septum arises as a result of the fusion of the medial walls of the nasal capsules (see discussion by Gaupp [1893]).

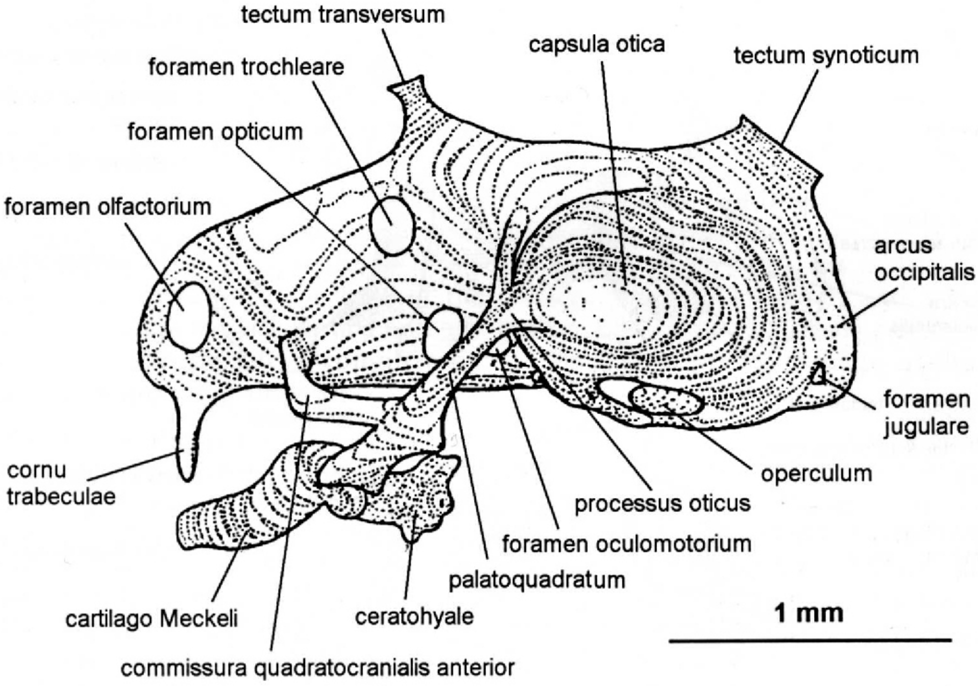


Fig. 17. Left lateral view of a reconstruction of the skull of the late intracapsular embryo of *Leiopelma* (ethmoidal capsule omitted). Note the position of the trabecular horns and the absence of labial cartilages. From N. G. Stephenson (1951).

C. Nasal Capsule

The nasal capsules develop from the nasal placodes and are thus of ectomesenchymal origin (Toerien and Rossouw 1977; Reiss 1990, 1998). However, some of their parts (e.g., the *septum nasi* and the postnasal wall) develop from visceral elements and are thus neural crest derivatives.

To understand properly the development of the nasal capsule, i.e., which parts develop from placodal material and which are added from the neural crest, it is convenient first to describe the ultimate structure of the nasal capsule in the adult (Fig. 18). Basically, the capsule consists of the *septum nasi*, which is a median partition separating the cavity (*cavitas nasalis* or *cavitas capsulae nasalis*) on one side from that of the other. Laterally, the nasal cavity is enclosed by an incomplete wall composed of several elements. The *cartilago obliqua* ("*lamina obliqua*" of Jarvik [1942]; "*plica obliqua*" of E. M. Stephenson [1951]) runs

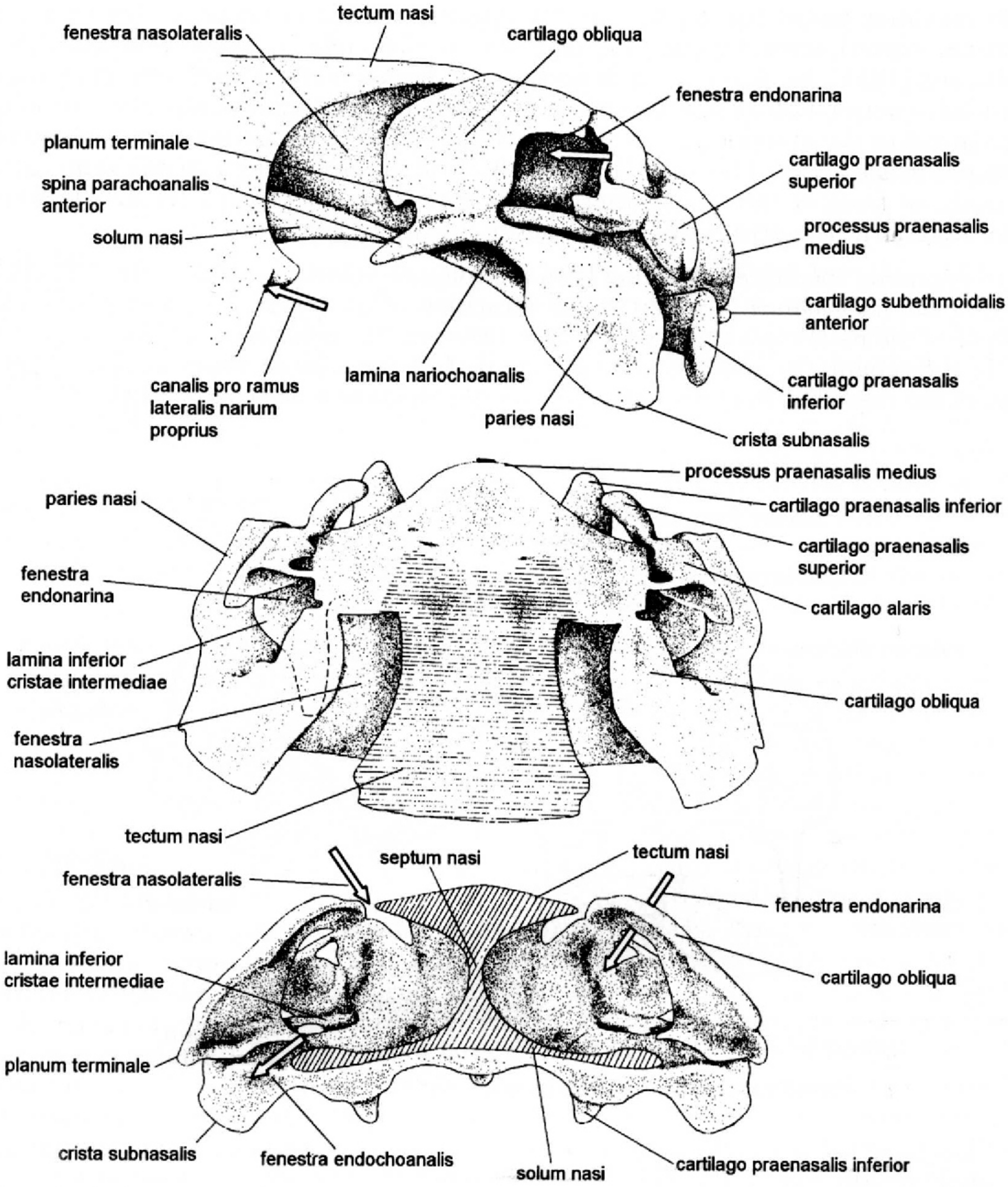


Fig. 18. Ethmoidal endocranium of an adult *Pelobates* in right lateral (above), dorsal (centre), and posterior (below) views. Hatching indicates cartilaginous parts. Broken lines indicate outlines of the *lamina inferior cristae intermediae*. From Roček (1981).

posterolaterally across the dorsal and lateral part of the capsule; it is absent in *Leiopelma* (Wagner 1934a; but see E. M. Stephenson 1951). Laterally, the *cartilago obliqua* is connected by the *planum terminale* ("*pars terminalis*" of Jarvik 1942) to an horizontal lamina. Since this lamina separates the *recessus inferior* from the *recessus medius* of the nasal cavity (see page 1897), it may also be considered as the *lamina inferior cristae intermediae* (Stadtmüller 1936, his figure 415d). Because it also separates the *fenestra endonarina* from the *fenestra endochoanalis*, it may be interpreted (and termed) as the *lamina nariochonalis* (Jarvik 1942; Jurgens 1971). This lamina terminates anteriorly in a slanting plate called the *paries nasi*. The anterior part of the capsule consists of a vertical wall that is confluent with the *septum nasi*. The roof of the capsule (*tectum nasi*) is complete only along the posterior wall of the capsule and the septum. The floor of the capsule (*solum nasi*) is complete, anteriorly and medially, along the lower part of the septum.

It follows from the description of the capsular walls that they are far from being complete. The elongated gap between the *tectum nasi* and the *cartilago obliqua* (*fenestra nasolateralis*) reaches up to the ventrolateral margin of the capsule and continues into the floor of the capsule as the *fenestra endochoanalis*. The *fenestra nasolateralis* is not developed in *Leiopelma* (Wagner 1934a). Anterior to the *cartilago obliqua* is the *fenestra endonarina* ("*apertura nasalis externa*" of Born [1876]) through which the *naris externa* of the nasal sac opens on to the surface of the head. The fenestra is rimmed by the oblique cartilage posteromedially, by the *tectum nasi* dorsally, the *lamina nariochoanalis* ventrally, the anterior wall of the capsule anteromedially, and anterolaterally by a well-delimited cartilaginous structure called the *cartilago alaris* ("*Naseflügelknorpel*" of Born [1876]; "2nd upper labial" of Parker [1876, his plate 54, figures 3, 5 and plate 61, figures 4, 5]). In contrast to other anurans, it may ossify in aging *Xenopus* (Bernasconi 1951; Smirnov 1994a). Anteriorly, the *cartilago alaris* is joined by the *cartilago praenasalis superior* ("Born's cartilage" of Gaupp [1893]; "1st upper labial" of Parker [1876, his plate 54, figures 3, 5]) protruding anteriorly from the wall of the capsule. However, it is connected with the capsule only by a connective tissue in *Breviceps* (de Villiers 1931a). A similar process, also protruding anteriorly and called the *cartilago praenasalis inferior*, was first described by Wiedersheim (1876) ("Wiedersheim's cartilage" of Born [1876]; "rhinal process" of Huxley [1875, his figure 9]; "trabecular cornua" and "*cornua trabecularum*" of Parker [1876, his plate 55, figures 4, 5]). It runs from the ventral surface of the *solum nasi* anteriorly.

The *solum nasi* is pierced by a large *fenestra endochoanalis* in the posterior part of the capsule, and by a much smaller *fenestra nasobasalis* ("*foramen apicale*" and "*foramen epiphaniale*" of Gaupp [1896]) which may be doubled in some species (Born 1876, his table 39/2). The latter is located medially to the base of the *cartilago praenasalis inferior*, and serves as a passage for the *ramus medialis narium* and *arteria orbitonasalis* into the *cavum praenasale*. The posterior wall of the capsule is complete except for canals for the passage of the *nervus olfactorius* and some other nerves.

The cavity of the nasal capsule contains the olfactory sac which is subdivided into several diverticles (e.g., Bancroft 1895; Föske 1934; Trahms 1936; Helling 1938; Paterson 1951). This subdivision is reflected also on the inner surface of the capsule, especially in its anterior part where horizontal ledges protruding from the inner surface of the capsular wall insert between the diverticles. The medial ledge is called the *crista intermedia* which bifurcates laterally into the *lamina superior* and *lamina inferior* (also see Reinbach 1939a). The *lamina superior cristae intermediae* delimits the *recessus superior* of the nasal cavity from the *diverticulum principale* and *diverticulum sacciformis* of the olfactory organ. The *recessus medius* is that part of the cavity situated between the *lamina superior* and *lamina inferior*; it contains the *diverticulum medium*. Between the *solum nasi* and the *lamina inferior* is the *diverticulum inferius*.

In general, the nasal capsules take their origin independently of the trabecular horns, although later the horns are partly incorporated into the structure of the capsulae. In the early larvae of *Pelobates*, the small nasal sacs are located below the level of the *cornua*, being connected with the mouth cavity by a long choanal canal, whereas in the larvae of *Rana* they are located above the level of the *cornua* (Born 1876). The capsules develop on the surface of the nasal sacs only after the *cornua* and suprarostrals are already chondrified.

The origin of the ventral part of the septum and the medial part of the *solum* were described above in connection with the development of the *cornua trabecularum*. They take their origin from the neural crest. The remaining parts of the septum, i.e., the posterior section of the dorsal part adjacent to the *tectum nasi* and anterior to the resorbed tips of the *cornua* throughout its depth, are of capsular origin. The septum as a whole is either among the earliest developing parts of the capsule, the tectum being formed afterwards as a derivative of the septum (the same holds for pipids [Trueb and Hanken 1992]), or the septum may be retarded in its development with the tectum arising independently as a pair of primordia above the posterior part of the nasal sacs (Gaupp 1893). It seems that the tectum arises as a result of expansion from the cartilaginous material at the level of the posterior portion of the capsule because Born (1876) mentioned, when describing his observations on *Pelobates*, that this expansion is above both trabecular horns, over their upper margin, and on to the dorsal surface of the nasal sac. However, at the level of the anterior portion of the capsule the septum arises separately from the horizontal nasal *tecta*, which first fuse with one another and only later are joined in the midline by the dorsal extension of the septum. Similarly, the anterior wall of the nasal capsule (and also the anteriormost section of the median partition between both capsules) arises independently of the septum and both structures fuse with each other only later (Born 1876; Gaupp 1893). An independent origin of the tectum has also been documented in *Heleophryne* (van der Westhuizen 1961).

The *lamina inferior cristae intermediae* appears simultaneously with the *tectum nasi* and separates the medial and lower diverticles of the nasal sac. Later, the *cartilago alaris* arises as an independent rudiment next to the *apertura nasalis externa* of the nasal sac. In *Xenopus*, however, the alary cartilage is said to arise from the posterior margin of what Trueb and Hanken (1992, their figure 5) called the "suprarostral cartilage". This contradicts information gained from wax models of *Xenopus* constructed from serial histological sections, according to which the alary cartilage arises as an independent element, similar to the condition in non-pipid anurans (personal observations; also see Föske 1934). Also, the *cartilago obliqua* arises as an independent chondrification, which may later come into contact with the *tectum nasi* to varying extents.

Finally, the floor of the capsule develops from several elements that either derive from the *cornua* (posteriorly) or arise independently. Some of them develop in a horizontal membranous layer enclosing the *cornu trabeculae* (disintegrated and progressively resorbed in this part). Lateral to each trabecular horn is a separate cartilaginous bar termed the "*basale Randleiste*" or "*laterale Randleiste*" by Gaupp (1893, his plate 14, figure 22). Posteriorly, this cartilage borders the *fenestra endochoanalis* as a thin horizontal ledge on the lateral surface of the trabecular horn, forming a narrow *solum nasi* medial to the choana. Anteriorly, however, it comes on to the dorsal surface of the vestigial trabecular horn. Medially, the membranous layer stretches to the lower edge of the *septum nasi*. It should be remembered that the septum arises independently of the trabecular horns in this anterior part of the ethmoidal region. Within this part of the membrane another cartilage develops, called the "*septale Knorpelleiste*" by Gaupp (1893) and "*mediale*" or "*paraseptale Randleiste*" by Stadtmüller (1936). Also, this cartilage goes on to the dorsal surface of the vestigial trabecular horns, where it fuses with the "*laterale Randleiste*", thus giving rise to a new floor of the capsule which, in this anterior part, arises above the level of the *cornua* ("*supratrabeculär Boden*" of Gaupp [1893]). In *Bombina*, the anterior part of the *solum nasi* (adjoining the anterior wall of the capsule) fails to chondrify and remains membranous, due to paedomorphosis; a similar situation may be found in *Ascaphus* and *Leiopelma* (Slabbert 1945). In *Heleophryne* (van der Westhuizen 1961) the *solum nasi* develops as an horizontally-situated, lateral cartilaginous plate on the outer surface of the internasal plate.

The *solum nasi* also may form lateral to the choana as a narrow temporary bridge connecting the lateral part of the *cartilago obliqua* with the *processus maxillaris anterior*, and protruding anteriorly from the lateral part of the developing postnasal wall. This connection is interrupted in adult *Pelobates*; however, it persists at least in young animals of *Bombina* (Born 1876) (also see the *spina parachoanalis anterior* in Roček [1981, his figure 7]. The connection also seems to be present in *Eleutherodactylus nubicola* (Lynn 1942).

In *Pipa pipa*, the faint vestiges of the internasal plate represent the narrow, temporary, medial *solum*; however, these vestiges later disappear completely so that in adults the floor of the nasal capsule is lacking (Roček and Veselý 1989, their figure 1H). In *Xenopus*, on the other hand, the *solum* of metamorphosing individuals consists of a band of cartilage that extends from the medial part of the postnasal wall forward along the medial portion of the choana; it is broadly separated from the *septum nasi* medially. The lateral part of the *solum* consists of a strip of cartilage that is attached to the lower inner part of the oblique cartilage. The anterior part of the *solum* is represented "by a cartilaginous process that grows forward toward the premaxilla"; later it "extends dorsad to unite with the alary cartilage" (Trueb and Hanken 1992). This looped connection between the *cartilago alaris* and the *solum nasi* has been homologized with the *cartilago praenasalis superior* by Paterson (1939) and Sedra and Michael (1957). Trueb and Hanken (1992), following Paterson (1939) expressed the view that in *Xenopus* the prenasal cartilage may represent both superior and inferior prenasal cartilages fused together. Nevertheless, the floor of the nasal capsule becomes progressively restricted even in *Xenopus*.

The *cartilago praenasalis inferior* develops close to the anterior end of the vestigial trabecular horn (Born 1876; Gaupp 1893) at the same sagittal level as the more posteriorly situated *solum*. However, the fusion between these two elements only comes later, simultaneously with the resorption of the anterior section of the trabecular horns. The base of the *cartilago praenasalis inferior* designates the anteriormost extent of the resorbed trabecular horns. In the context of the development of the anterior section of the *solum nasi*, it is obvious why this cartilage protrudes below the floor of the anterior part of the capsule.

It should be noted that Parker (1876, his plate 54, figures 1–5) was convinced that the *cartilago praenasalis inferior* is actually the preserved anterior portion of the *cornu trabeculae* (also see Reinbach 1939a; N. G. Stephenson 1951; Swanepoel 1970). N. G. Stephenson (1951, his figures 2, 8A) explicitly stated that in *Leiopelma* the trabecular horns persist from before the formation of the nasal capsules in the intracapsular embryo to the adult frog (here they support the *praemaxillae*). Possible developmental relations between this cartilage and the larval suprarostral were discussed in section II A, page 1888. It should be noted that this cartilage is absent in the Pipidae (Paterson 1939; Sedra and Michael 1957), which may be important in regard to possible homologies of the ethmoidal structures of pipid and non-pipid tadpoles. One should, however, recall that Paterson (1939) and Trueb and Hanken (1992) maintained that in *Xenopus* the prenasal cartilage may represent a fusion of the superior and inferior prenasal cartilages.

The posterior wall of the nasal capsule arises from several elements that are described below, but it should be emphasized that they do not belong developmentally to the nasal capsule.

As the described elements grow in size, they partially fuse with each other and give rise to the complex structure of the adult nasal capsule. It seems that in some taxa various parts of the nasal capsule may be considerably delayed in their development (e.g., *Pseudophryne, Crinia*; Jacobson [1968]). However, in most anurans the *crista subnasalis* and the interior of the nasal cavity are among the last developing structures of the nasal capsule. The nasal cavity becomes partly divided by incomplete horizontal *laminae* protruding from the inner surface of the anterior wall, thereby separating diverticles of the nasal sac.

To complete the description of the *septum nasi* and nasal capsule it may be added that in *Bufo regularis* and *Atelopus moreirae* a median cartilage develops between the ventromedial edges of the two *premaxillae*. This structure was called the "intermaxillary cartilage" by Sedra (1950). Similar cartilage was also found in adult *Leiopelma* (E. M. Stephenson 1951) and *Pelobates* ("*cartilago subethmoidalis anterior*" of Roček [1981, his figures 4, 6]) (also see Fig. 18).

D. Postnasal Wall

Experimental studies by Toerien and Rossouw (1977) suggest that the postnasal wall (including the *lamina orbitonasalis* and *processus maxillaris posterior* is not part of the nasal capsule and thus not of placodal origin, but rather develops from the neural crest as a part of the visceral skeleton that becomes incorporated into the nasal capsule. This is in agreement with the results of experimental extirpations of the nasal placodes (Reiss 1998).

During the development of the anuran postnasal wall (i.e., of the partition separating the nasal and orbitotemporal regions of the skull), some independent cartilaginous elements may be observed that either later disappear or fuse with others. In early larvae, the olfactory nerves run uncovered over the dorsal surface of the horizontal plate, connecting both *trabeculae* at the base of the trabecular horns (Figs 19, 20). This plate is the *planum trabeculare anticum* (*sensu* Gaupp 1893, his plate 13, figure 1). Parker (1876) gave the definition of the term internasal plate as "the coalesced *trabeculae* in the ethmoidal region" but in his plate 55, figure 3, he designated by this term Gaupp's *planum trabeculare anticum*. The *planum trabeculare anticum* has also been called the "ethmoidal wall" and "trabecular commissure" by Parker (1876), "*Stammplatte*" by Goette (1875), "*Ethmoidalwand*" and "*Basalplatte*" by Born (1876), "*Internasalplatte*" by Stöhr (1882), "*Ethmo-Vomerinplatte*" and "*vordere Trabecularplatte*" by Gaupp (1893), "ethmoid plate" by Winslow (1898), "*Internasalplatte*", "*planum internasale*", "*ethmoidalplatte*" and "*Ethmo-Vomerin-Platte*" by Okutomi (1937), "*planum praecerebrale*" and "*septum praecerebrale*" by Stadtmüller (1936), "intertrabecular plate", "ethmoid plate", "trabecular plate" and "internasal plate" by de Beer (1937, his plate 76/1), but is probably not the "*plan internasal*" of van Seters (1922). One of the possible sources of controversy may be that two different structures are included under the term "ethmoidal plate": (1) the *planum trabeculare anticum* between the anterior ends of both *trabeculae cranii*, at the base of the *cornua trabecularum* (i.e., an early larval structure) (Fig. 20), and (2) the anterior trabecular plate of advanced pre-metamorphic larvae (e.g., Hall and Larsen 1998, their figure 2A) which is the anterior part of the newly-formed cartilage between the *cornua trabecularum*, i.e., the anterior part of the developing *septum nasi*.

There is no partition between the ethmoidal endocranium and the braincase in early stages (also see Jacobson 1968). This partition arises later, first from a distinct mesenchymatous (later cartilaginous) horizontal layer covering the olfactory nerves from above (see Roček 1993a, his figure 4). It is probably paired in origin, as evidenced by Plasota (1974a, his figures 17–19) for *Pelobates*. It was clearly considered part of the orbital cartilage by van der Westhuizen (1961).

Shortly after formation of the horizontal layer its two sides fuse (Born 1876) and the walls of the olfactory canals grow downwards from them, ultimately reaching the *planum trabeculare anticum* ("*Produkte der Trabekel*" of Born [1876]). The horizontal elements may be termed the *laminae cerebronasales* ("*Ethmoidalplatte*" of Gaupp [1893], "*planum praecerebrale*"

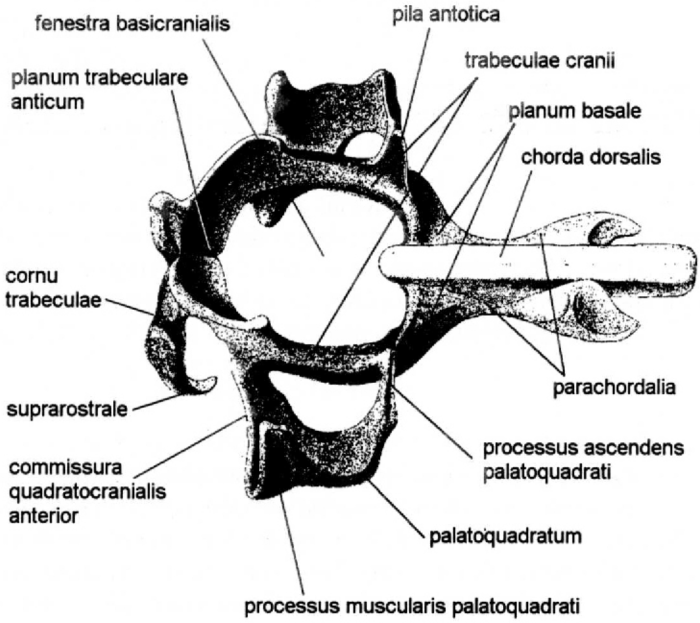


Fig. 19. Dorsal view of an early developmental stage of the chondrocranium of *Rana* (total length of embryo about 7.5 mm) omitting Meckel's cartilages and the ceratohyals. From Stöhr (1882).

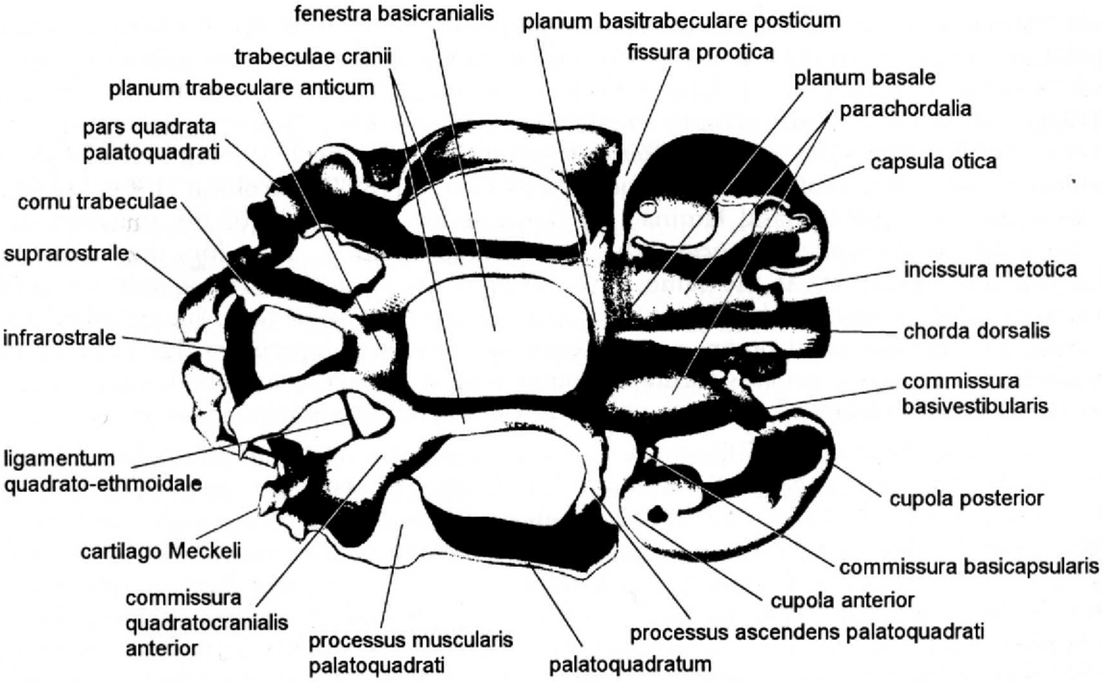


Fig. 20. Dorsal view of the chondrocranium of an embryonic *Rana temporaria* after disappearance of the external gills (embryo 14 mm in total length). From Gaupp (1893).

and *"Präcerebralplatte"* of Gaupp [1906], "bars of cartilage joining the dorsal ends of the preoptic roots of the orbital cartilages and the *pila ethmoidalis*" and "sphenoseptal commissure" of de Beer [1937], "*pila ethmoidalis*" of N. G. Stephenson [1951], "*tectum anterius*" of Sedra and Michael [1957, their figures 3, 7], "ethmoidal plate" of de Jongh [1968, his plates 6, 7], "Cl" and "Cp" of Plasota [1974a, his figures 17-19], "*taenia ethmoidalis*" of Haas [1966a, his figure 4], "anterior roof (tectum)" of Hall and Larsen [1998]). It should be noted that the "sphenoseptal commissure" of Ramaswami (1940) is probably not homologous with the structure de Beer (1937) called by that name because Ramaswami stated (his page 32) that "the preoptic root and the *pila ethmoidalis* are roofed over by the sphenoseptal cartilage".

The downward extensions of the *laminae cerebronasales* are called *columnae ethmoidales* (*sensu* Gaupp 1893, his figure 12) but have also gone by the names "*Ethmoidal-Pfeiler*" (Born 1876), "*pilae ethmoidales* (de Beer 1937), "*pila praecerebralis*" (Reinbach 1939a) and "lateral tectal process" (Panchen 1970). Born (1876) believed these lateral columns to be produced by the *trabeculae*. In *Rana*, the *lamina cerebronasalis* is formed in a similar way, then both *columnae ethmoidales* enclose a space between them, called the *fenestra ethmoidalis sensu* Gaupp (1892) "*Ethmoidalschlitz*" (Born 1876) and shortly afterwards a median partition is formed that starts to grow from the *planum* dorsally, ultimately reaching the *lamina* and filling the ethmoidal fenestra (Born 1876; Gaupp 1892). This is the first rudiment of the septum. Later, the lateral walls of the olfactory canals are added (Born 1876).

Development of the lateral part of the postnasal wall (*"pars plana"* of Gaupp [1893]) is more complicated, and occurs later than that of the medial part. In the early developmental stages, the *commissura quadratocranialis anterior* (see Section V B, page 1923) serves exclusively as a functional partition between the future nasal capsule and the orbital area. On the dorsal surface of the *commissura*, the *nervus ophthalmicus* runs anteriorly. Later, new material (also see Haas 1996b, his figure 2) added anterolaterally to the *commissura* encloses the ophthalmicus nerve ("*ramus primus quinti*" of Born [1876] or *nervus profundus V*) in a slot and later in a canal between the braincase wall and this new horizontal cartilage (Born 1876; Reinbach 1939a; Swanepoel 1970; Reiss 1998) that separates the nasal sac from the orbit. This well-defined material is generally termed the *lamina orbitonasalis* ("palatine wings" in adults [Parker 1876]; "*Knorpelspange*" [Stöhr 1882]; "*cartilago palatina*" and "*processus antorbitalis*" [Gaupp 1892]; "*Antorbitalfortsatz*" [Gaupp 1893]; "palatine cartilage" [Winslow 1898]; "*planum antorbitale*" [Gaupp 1906]; "*processus antorbitalis*" [van Seters 1922, his figure 8]; "*planum antorbitale primarium*" [Reinbach 1939a]; "*larvales planum antorbitale*" [Reinbach 1950b]; also see footnote by Gaupp [1893]). Jacobson (1968, his figure 1) used the term "orbitonasal lamina" for the anterior connection of the palatoquadrate to the *planum trabeculare anticum* (his "trabecular plate"), i.e., for the *commissura quadratocranialis anterior*. At the same time, he used the term "anterior quadratocranialis commissure" for the *lamina orbitonasalis*. His statements are not reliable (e.g., among other errors he indicated that the nasal organs are posterior to the *fenestra hypophyseos* [his page 2], that the posterior maxillary process forms the outer wall of the nasal organs [his page 3] and that the "*foramen rotundum*" is in the centre of the ascending process [his page 4]).

The passage for the ophthalmicus nerve is called the *canalis orbitonasalis* or *foramen orbitonasale* ("*canalis orbitonasalis medialis*" of Reinbach [1939a]). Moreover, van der Westhuizen (1961) termed the contact between the *lamina orbitonasalis* and *lamina cerebronasalis* as the "sphenethmoid commissure" (note statement above about this term). The fusion of these two structures in *Rana* is not completed before the end of metamorphosis (Gaupp 1893). In *Leiopelma* the *lamina orbitonasalis* becomes continuous with the front end of the *commissura quadratocranialis anterior*, but these two structures are distinguishable through their different degrees of chondrification (N. G. Stephenson 1951), as in the case of the border between the orbitonasal lamina and the braincase wall (Fig. 21) (also see Roček 1993a, his figure 5).

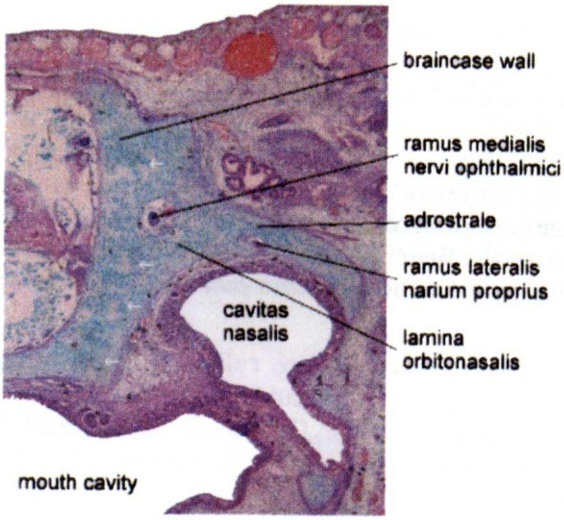


Fig. 21. Frontal section through the right postnasal wall of *Ascaphus truei* (stage 64 after Nieuwkoop and Faber [1967]). White arrows mark the line of coalescence between the wall of the braincase and the *lamina orbitonasalis*. Compare with Roček (1993a).

The *commissura quadratocranialis anterior* does not contribute to the formation of the canal because it already had become detached from the braincase wall (see Section V B, page 1925; also see Fig. 60); its anterior end either shifts on to the posterior or posterolateral surface of the *lamina orbitonasalis* (Reinbach 1950b; N. G. Stephenson 1951; Swanepoel 1970, his figure 33), terminates freely (van Eeden 1951, his figures 15, 16; Plasota 1974a), or is related in other ways to the *lamina orbitonasalis* (van Seters 1922, his figure 8). Consequently, the course of the *canalis orbitonasalis* may be used as an indicator of the medial extent of the *lamina orbitonasalis* (Stadtmüller 1936; de Beer 1937). Although, as mentioned above, descriptions by Jacobson (1968) are inaccurate, it seems from his graphic reconstructions (his figures 1, 19) that in *Pseudophryne* the *lamina orbitonasalis* (his "anterior quadratocranialis commissure") develops within the ligament stretched between the *processus muscularis palatoquadrati* and the braincase wall.

The most lateral part of the *lamina orbitonasalis* is demarcated by the *processus maxillaris anterior* (Fig. 22) (also see Gaupp [1893]; "*lamina cribrosa*" of Winslow [1898, his figures 20, 21]) and by the course of the *ramus communicans* between the *ramus maxillaris V* and the *ramus palatinus VII* (Fig. 23D). In the majority of species this thin, but constant, nerve is enclosed within a canal that marks the border between the *lamina orbitonasalis* and the *processus maxillaris posterior* (e.g., van Eeden 1951]).

In later developmental stages, the ophthalmicus nerve splits into a medial branch (the *ramus medialis nervi ophthalmici*) directed toward the anterior aperture of the *canalis olfactorius*, and a lateral one (the *ramus lateralis narium proprius*) crossing the dorsal surface of the *lamina orbitonasalis*. The *ramus lateralis narium proprius* is enclosed within a canal (*canalis orbitonasalis lateralis*) (Reinbach 1939a) by a distinct ovoid or rod-like cartilage called the *adrostrale* (*sensu* Dugès [1834, his figure 71]; "x" of Plasota [1947a]; "*epipraemandibulare*" of Roček [1981, his figure 22]). In those anurans in which the lateral part of the upper labial cartilage and the adrostral occur at the same time it is difficult to decide whether terms like "second pair of suprarostrals" (de Beer 1937) or "suprarostral 2" (Ramaswami 1943, his figures 1, 2), or "dorsal rostral" (Ramaswami 1944, his plate 1) are homologous with the adrostrals. The adrostral arises in non-pipid anurans simultaneously with the upper labial cartilage (or begins to chondrify slightly later), closely associated (or articulated) with its posterolateral portion (e.g., Schulze 1892). Plasota (1974a) even believed that it originates from the posterior part. It is cartilaginous in *Pelobates*, *Bombina*, *Megophrys*, *Heleophryne*, and *Hyla squirella* (Born 1876; Ramaswami 1943; Plasota 1974a; Sokol 1981;

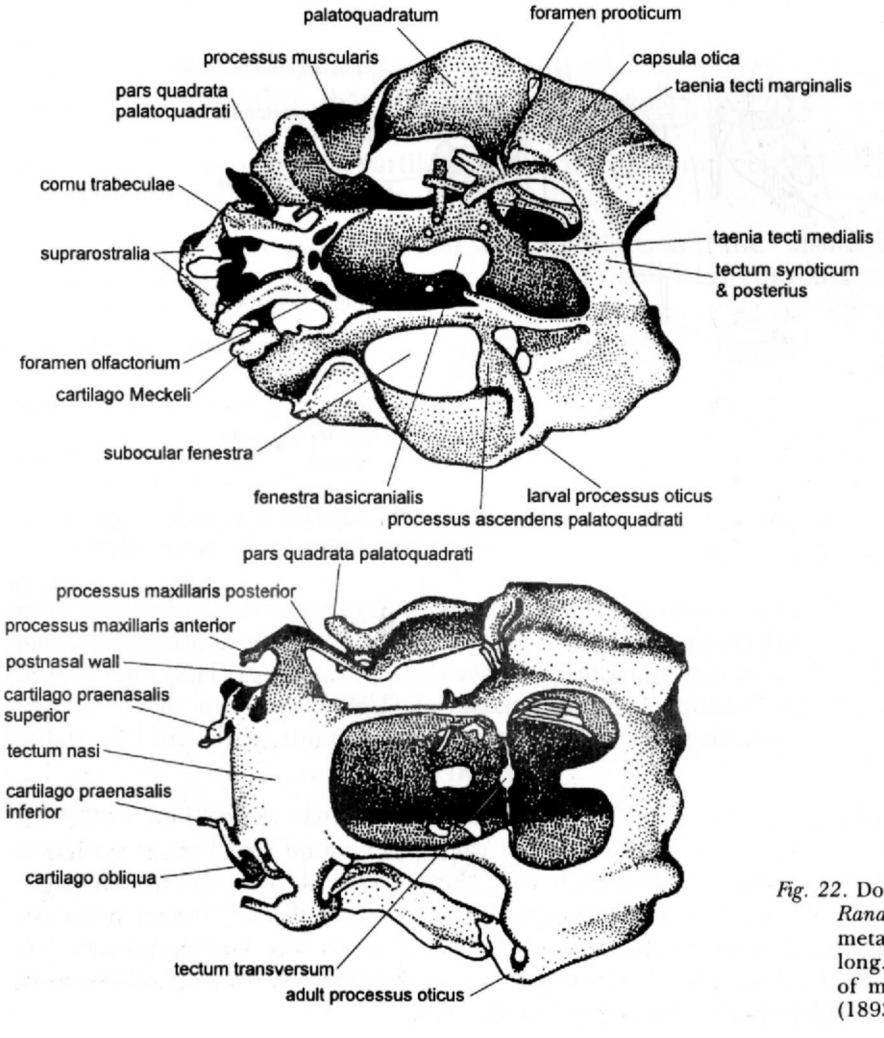


Fig. 22. Dorsal view of chondrocrania of *Rana temporaria*. Upper: Before metamorphosis; tadpole 29 mm long. Lower: Close to completion of metamorphosis. After Gaupp (1893) from Jarvik (1980b).

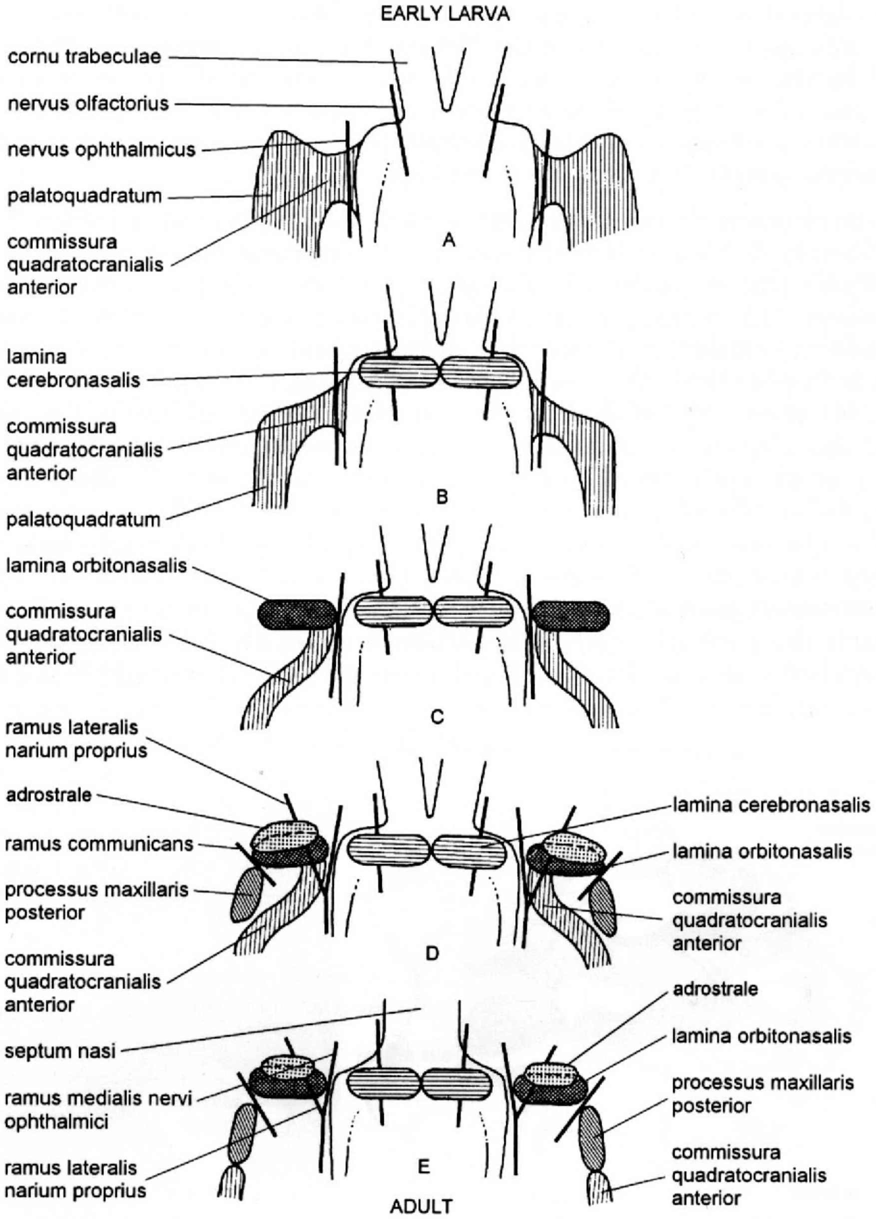


Fig. 23. Dorsal view of developmental stages of the anuran postnasal wall. Diagrams A through D represent a progression from an early larva to the adult. From Roček (1993a); also see figures 1A–1C in Reiss (1998).

cf. However, Maglia and Púgener 1998) whereas in *Pelodytes*, *Scaphiopus bombifrons* and *Hyla regilla* it occurs as a small condensation of mesenchyme (Sokol 1981). It is absent in *Rana* (Born 1876) and not found in advanced larvae of *Scaphiopus intermontanus* (Hall and Larsen 1998). It was also reported by Nikitin (1986). Ramaswami (1944) observed that its lower end softened during metamorphosis in *Heleophryne* and "the remains of it could be made out only with difficulty".

In some larval anurans, e.g., *Litoria nannotis* (Haas and Richards 1998, their figures 8, 9), the presence of the well-separated lateral part of the upper labial cartilage (*pars alaris*) and of the adrostral may be taken as evidence that these elements are not homologous (Fig. 24). It is, however, difficult to decide if structures described in the literature under the above-mentioned synonyms are in fact the adrostral, or only the lateral part of the suprarostrale. Dugès (1834, his plate 12, figures 71, 73) considered the adrostral as an appendix of the suprarostral with a high degree of mobility.

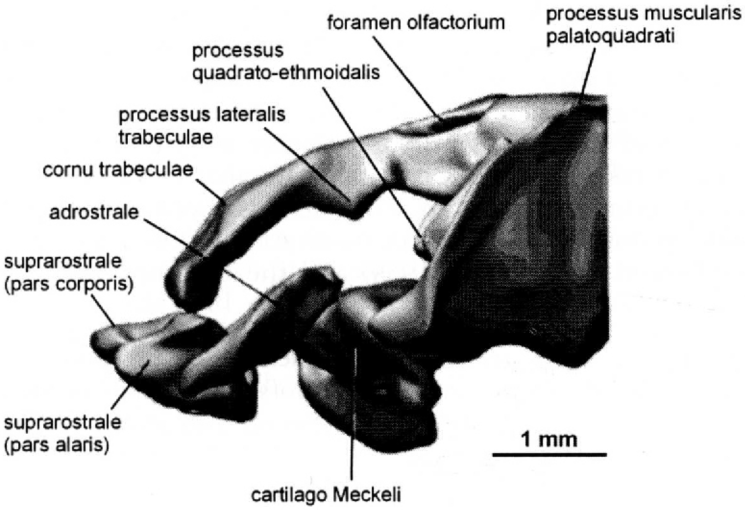


Fig. 24. Left lateral view of the ethmoidal region of the skull of *Litoria nanotis*, showing the *adrostrale* and both parts (*pars corporis* and *pars alaris*) of the suprarostral cartilage. From Haas and Richards (1998).

The area termed in various adult anurans as the "bulge" or "anterior process on postnasal wall" by Jurgens (1971, his figures 1, 10, 11, 13) and the "*processus antorbitaire*" by Kraemer (1974, his figure 10) has a characteristic morphology. Its structure and the fact that dorsally it encloses the canal for the *ramus lateralis narium proprius* indicates distinct origins for this part of the postnasal wall and the *lamina orbitonasalis* and that the former represents the larval adrostral. Swanepoel (1970) suggested that the *planum triangulare* (the dorsolateral part of the postnasal wall in the adult) develops independently of the medial part of the postnasal wall (= *lamina orbitonasalis*). Judging from a comparison of this structure in *Breviceps* (Swanepoel 1970) and *Pelobates* (Roček 1981), however, one cannot exclude the possibility that the early larval *planum triangulare* in *Breviceps* might be homologous with the adrostral. In pipids, the adrostral does not pre-exist as a separate element, but arises as new cartilaginous material, ultimately enclosing the *ramus lateralis narium proprius* as in non-pipids.

It is obvious that the "postnasal wall" of adults and the "*lamina orbitonasalis*" of larvae do not represent the same structure. It also should be emphasized that the *commissura quadratocranialis anterior* does not contribute to the adult postnasal wall (Gaupp 1906) although Reinbach (1939a, 1950b) maintained that the adult postnasal wall (his *planum antorbitale secundarium seu definitivum*) involves the remnant of the *commissura quadratocranialis anterior* in its upper part.

The ossification extends over a considerable part of the postnasal wall in adults, and also includes various parts of the *septum nasi* and the anterior part of the braincase, usually up to the region in front of the optic foramen; it may also enclose the prootic foramen dorsally in *Xenopus* (Trueb and Hanken 1992). This enchondral ossification (cf. however, Trueb *et al*. 2000) is usually called the sphenethmoid, *sensu* Parker and Bettany (1877) ("*os en ceinture*" of Cuvier [1824]; "*os substitiens*" of de Villiers [1930]; "*sphenoidale*", "*ethmoidale*", and "orbitosphenoid" of Stadtmüller [1936]) and its extent may vary according to its degree of development (age); it may even co-ossify with the prootics in hyperossified forms such as *Pipa pipa*. In contrast, there is no ethmoidal ossification whatsoever in *Ascaphus* (de Villiers 1934) or *Breviceps* (Swanepoel 1970). The sphenethmoid usually ossifies as a paired structure within the postnasal wall. In *Hyla regilla* the ossification is within the paired *lamina cerebronasalis* (Gaudin 1973) and a similar condition is found in *Caudiverbera* (Reinbach 1939a) and *Bombina orientalis* (Smirnov 1997, his figure 2). De Villiers (1934, his figure 6) and Sedra and Michael (1957) called the part of the sphenethmoid in front of the otic foramen the orbitosphenoid.

In *Xenopus*, the lateral wall of the braincase between the postnasal wall and the prootic is so ossified that the posterior boundary of the sphenethmoid cannot be recognized. However, this demarcation is conventionally considered to occur at the level of the optic foramen. That part of the sphenethmoid in *Xenopus* that forms the lateral wall of the braincase anterior to the optic foramen is very thin, with no cavities. It ossifies directly from the membrane and consequently Trueb and Hanken (1992) suggested that the ossification of the sphenethmoid might be membranous, i.e., the bone is not preformed in cartilage owing either to regression of the cartilage or to a change in growth pattern. This ossification, therefore, cannot be taken to be homologous with that of the dermal exocranial bones in which ossification occurs in the dermis. The lateral wall of the braincase between the optic foramen and the prootic is evidently an ossification of the larval *pila antotica*; it was called the pleurosphenoid by Paterson (1939) and the orbitosphenoid by Sedra and Michael (1957).

Hall and Larsen (1998) considered an additional centre of ossification on the posterior portion of the dorsal surface of the nasal septum and nasal roofs to be the "dermal sphenethmoid". This later fuses with the endochondral sphenethmoid and might be the "supraethmoid" of Gilchrist and von Bonde (1919) (also see section VII F, page 1946).

III. ORBITOTEMPORAL REGION

A. *Trabeculae Cranii* and Anterior Part of the Braincase

The *trabeculae cranii* arise from neural crest cells (Olsson and Hanken 1996, their figure 5), a fact that may be taken as evidence they originally were part of the premandibular visceral skeleton (also see Kuratani *et al.* 1997), in contrast to the posterior (otic) section of the braincase which is of mesodermal origin. In contrast, Reiss (1997) distinguished a pair of anterior (ectomesenchymal) and posterior (mesodermal) *trabeculae* underlying the prosencephalon in early larval *Ascaphus*. The ectodermal origin of the *trabeculae* in the Anura was recognized already by Lundborg (1899, his plate 12, figures 7–9), who derived them from the dorsal wall of the stomodeum.

The *trabeculae cranii* (*sensu* Rathke [1832]; "*Spangen*" or "*Balken*" of Stöhr [1882, his plate 3, figure 18]; "anterior cranial trabeculae" of Hall and Larsen [1998]) are two separate parallel bars (Figs 19, 20) extending back as far as slightly behind the tip of the notochord (Stöhr 1882; Spemann 1898; N. G. Stephenson 1951). The *trabeculae* originate as posteriorly expanding procartilaginous structures, after the appearance of the primordia of the visceral skeleton (also see Okutomi 1937). The *trabeculae* connect at the base of the *cornua trabecularum* by fusing with one another as a horizontal plate termed the *planum trabeculare anticum* (see page 1900). In *Alytes*, this occurs comparatively late (van Seters 1922, his plate 8, figure 1). Both *trabeculae* separate again throughout the whole extent of the orbital region, except for the most posterior part at the level of the anterior end of the notochord, where they are interconnected by a similar plate termed the *planum trabeculare posticum* ("*Trabecularplatte*" and "*Balkenplatte*" of Stöhr [1882, his plate 3, figure 18]; "anterior parachordals" of de Beer [1937]; "anterior *Anlage* of the parachordal" of Smit [1953, his figure 6]; "rudimentary basal plate" and "hypochordal commissure" of Hanken *et al.* [1992], but not the "posterior trabecular plate" of Hall and Larsen [1998] because they included in this term the part of the braincase floor arising earlier in ontogeny by obliteration of the basicranial fenestra). In the majority of anurans, the *trabeculae* are confluent with the *planum basale* of the otic region throughout the entire development of the prochondral and cartilaginous stages (Figs 19, 20; also see observations by van Seters [1922] on *Alytes*, N. G. Stephenson [1951] on *Leiopelma*, and Swanepoel [1970] on *Breviceps*). In *Polypedates* (Okutomi 1937), the rudiments of the *trabeculae cranii* and those of the basal plate are discontinuous. From the above, it is apparent that some authors have not distinguished the *planum trabeculare posticum* (a derivative of the posterior part of the cranial *trabeculae*) from the *planum basale* (a derivative of the anterior part of the parachordals), undoubtedly because the *trabeculae* and parachordals fuse with each other in early larval development and become continuous.

In the orbitotemporal region of *Ascaphus*, Reiss (1997) distinguished two pairs of *trabeculae*, an anterior pair originating from ectomesenchyme, and a posterior pair of mesodermal origin. Prochondral condensation begins in the posterior *trabeculae* which at this stage are already continuous with the parachordals and extend from the posterior border of the eye and along the side of the infundibulum. The anterior *trabeculae* begin to condense later and, as can be judged from Reiss' illustrations (1997, his figures 1, 2), are not continuous with the posterior *trabeculae*. Only later (still in the procartilaginous stage) do the posterior ends of the anterior *trabeculae* establish contact with the posterior *trabeculae*. Chondrification spreads in a postero-anterior direction, i.e., it begins in the parachordals and spreads forward into the anterior *trabeculae*. Posterior to anterior chondrification has also been confirmed in other anuran species (e.g., see Swanepoel 1970).

In the floor of the future braincase between the *trabeculae* of the left and right sides, there is a large *fenestra basicranialis* ("*fenestra hypophyseos*" of de Beer [1937]; "basi-cranial fontanelle" of Parker [1876]), through which the *arteriae carotides internae* enter the *cavum cranii*. In later development, the *fenestra basicranialis* becomes progressively obliterated so that the floor of the braincase ("*solum interorbitale*" of Gaupp [1893]; probably the "trabecular plate" of Reiss [1997]) arises. From the former *fenestra basicranialis*, only two pairs of foramina persist. The anterior pair is termed the *foramina craniopalatina* (*sensu* Gaupp 1893) which are the openings for the *arteriae palatinae*. The *arteriae palatinae* are branches of the *arteriae carotides internae* and split from the *arteriae carotides* within the braincase in the majority of anurans. In *Breviceps* the split occurs before the *arteriae palatinae* enter the braincase (Swanepoel 1970). Through the posterior pair of openings, called the *foramina carotica primaria* (*sensu* Gaupp 1893), the *arteriae carotides internae* pass into the braincase. The *foramina craniopalatina* become obliterated in later larval or metamorphic stages (Reinbach 1939a). Also the *arteriae carotides internae* enter the braincase of the adult via different openings, the reason why the larval foramina are called "*primaria*".

The *planum trabeculare posticum* bears an upwardly pointing, rudimentary process called the *pila antotica* ("*crista trabeculae posterior*" of Okutomi [1937]; "*pila prootica*" of Reinbach [1939a]) to which the *processus ascendens palatoquadrati* is attached. De Beer (1937) erroneously described the *pila antotica* as being attached to the *parachordalia* in the anterolateral corners of the basal plate. The *pila antotica* are among the earliest parts of the braincase walls (Fig. 9), and this also holds true for those anurans in which larval development is suppressed and in which the ascending process never develops (Lynn 1942, his figures 25, 27). However, it may be absent in those anurans, e.g., Microhylidae (Ramaswami 1940) in which the *processus ascendens* is extraordinarily large. Except for the *pila antotica* (and the developing medial part of the postnasal wall; see section II D), the braincase walls are still membranous, so that the optic, oculomotor, and trochlear nerves pass freely through this membrane above the *trabeculae*.

Soon after the development of the *pila antotica*, another column, the *pila metoptica* ("metoptic pillar" of Hall and Larsen [1998]) arises dorsally from the *trabeculae*, thereby separating the common foramen for the *nervus oculomotorius* and *arteria ophthalmica magna* from the *foramen opticum* (de Beer 1937; Reinbach 1939a; van der Westhuizen 1961). There are variants, however, as both the nerve and vessel may pass through separate foramina in some anurans (van der Westhuizen 1961) and, as in the case of the *pila antotica*, the *pila metoptica* is absent in at least some microhylids (Ramaswami 1940). The *pila metoptica* may be less distinct in later developmental stages in some taxa, e.g., *Scaphiopus* (Hall and Larsen 1998), so that a separate oculomotor foramen is hard to distinguish.

Anterior to the *foramen opticum* is still another column, the *pila antoptica* ("preoptic pillar" or "preoptic pila" of Reiss [1997]; "preoptic root" of Cannatella [1999]; also see section II D, page 1901). It should be noted that some authors (e.g., Hall and Larsen [1998, their figure 3a]) apparently used the term "preoptic pillar" for the whole preoptic part of the braincase wall, not just for the early larval column extending dorsally from the *trabecula cranii*.

The extent and time of occurrence of cartilage in the braincase varies among anurans. In *Rana*, the floor of the braincase becomes completely cartilaginous only after metamorphosis, whereas in *Heleophryne*, it is cartilaginous in pre-metamorphic larvae (van der Westhuizen 1961). The floor may remain highly fenestrated in some anuran larvae, e.g., *Pseudis minuta* (Lavilla and de Sá 1999). It is obvious that the *trabeculae* persist in the floor of the braincase except for a short section between the *foramen caroticum primarium* (the opening for the *arteria carotis interna*) and the *foramen oculomotorium*; see page 1909).

In premetamorphic tadpoles of *Megophrys* there is a tongue-like median projection ("subethmoidal process" of Ramaswami [1943, his figure 2a,b]) from the roof of the buccal cavity in the orbitotemporal region, slightly posterior to the "ethmoid plate" (undoubtedly the *planum trabeculare anticum*). This projection is supported by a cartilage that has no connection with any other cartilage.

At metamorphosis (e.g., in *Rana*) or in an earlier developmental stage (e.g., in *Alytes*) an horizontal cartilaginous bar, called the *cartilago orbitalis* ("*dorsale Randspange*" of Gaupp 1893), arises above each *trabecula*. These orbital cartilages connect the postnasal wall with the *pila antotica* and thus dorsally enclose the optic and trochlear nerves in their respective foramina. The orbital cartilage is the early larval structure connecting the *pila antotica* with the *pila metoptica* and early structures of the postnasal wall, and in no case can it be synonymized with the *taenia* (*tecti*) *marginalis* which is a structure occurring in adults (cf. Hall and Larsen 1998). The orbital cartilage may be vestigial, e.g., in *Pseudis minuta* (Lavilla and de Sá 1999, their figure 1C). In contrast, the foramen for the *arteria carotis interna* (originally passing through the floor of the braincase between the *trabeculae*), becomes confluent with the foramen for the *nervus oculomotorius*, thereby passing through the wall of the braincase above the *trabeculae*, i.e., the *trabeculae* become interrupted at this site (Gaupp 1893; van der Westhuizen 1961). The two *pilae antoticae* may be connected by a transverse bar, the *tectum transversum*, (the "*taenia tecti transversalis*" of Gaupp [1893]; possibly the "epiphysial bar" of N. G. Stephenson [1951] and E. M. Stephenson [1951, her figure 2a]), to which the *taenia tecti medialis* may become attached (e.g., in *Rana*) (Fig. 22). Apparently, the "epiphysial bar" of *Leiopelma* is located more anteriorly than the *taenia tecti transversalis* of *Rana*, casting some doubt as to the homology of this structure in these two anurans.

The roof of the braincase never becomes complete in anurans, leaving various vacuities between the *taeniae* and *tecta*. The *tectum synoticum* and the *tectum transversum* may be connected to each other via the *taenia tecti medialis* in the midline (e.g., in *Rana*), or the transverse tectum and the medial taenia may be only rudimentary (e.g., in *Pelobates*), thus leaving an extensive *fenestra frontoparietalis* between the postnasal wall anteriorly and the *tectum synoticum* posteriorly. The medial section of the postnasal wall may therefore be termed the *tectum anterius* (Sedra and Michael 1957, their figures 3, 7). This pattern is reflected in the morphology of the ventral surface of the frontoparietal as incrassations fitting into the vacuities of the endocranial roof of the braincase (Jarošová and Roček 1982). The *fenestra frontoparietalis* may be subdivided by the *taeniae* into an anterior part called the *fenestra frontalis* (Reinbach 1939a) and one or two posterior parts (*fenestra parietalis dextra* and *fenestra parietalis sinistra*). It is difficult to know what was meant by the term "*tectum medium*" by Ramaswami (1940) because he only mentioned (in a section dealing with the occipito-auditory region) that the *tectum synoticum* "anteriorly continues into the *tectum medium*".

In *Alytes* and *Phyllomedusa*, in addition to the orbital cartilage, a large independent supraorbital cartilage (*cartilago supraorbitalis*) develops dorsal to the eye during late metamorphosis (Parker 1882, his plate 24 I, II; Stadtmüller 1931a). This cartilage remains isolated from the braincase wall throughout development. Stadtmüller (1931a) homologized it with the supraorbital ledge of osteolepiforms and *Polypterus* but Reinbach (1939a) denied its homology with the *crista* (= *lamina*) *supraorbitalis* that stretches over the anteromedial corner of the orbit of adult anurans (see Roček 1981, his figures 1–3).

At the end of metamorphosis, the braincase walls are formed completely of cartilage, pierced only by the *foramen opticum* (opening for the optic nerve), by a small foramen above the *foramen opticum* called the *foramen trochlearis* (for the trochlear nerve) and behind it by a pair of foramina, of which the dorsal is the medium-sized *foramen oculomotorium* ("metoptic foramen" of N. G. Stephenson 1951), and the ventral is the larger *foramen caroticum* (opening for the internal carotid artery). The oculomotor nerve and the carotid artery may sometimes pass through a single foramen; also the optic and oculomotor nerves often pass through a single foramen when the *pila metoptica* is resorbed and the two foramina become confluent. The trigeminal and facial nerves pass through the *fissura prootica*. In adult *Pipa pipa*, however, the oculomotor nerve leaves the braincase through the same foramen as the trigeminal nerve, i.e., through the *foramen prooticum* (Arnold 1898). Perhaps in this case the *pila antotica* is resorbed (as seen for the *pila metoptica*) with both foramina becoming confluent.

According to Reiss (1997), the *foramina craniopalatina* mark the border between the neural crest and the mesodermal parts of the floor of the braincase. In the lateral wall of the braincase, the boundary passes through the rear of the *foramen opticum*. The *pila metoptica* is predominantly mesodermal in origin, but contains some neural crest cells in its anteroventral part. The mesodermal mesenchyme gives rise to the caudal end of the orbital cartilage. Probably the *pila antotica* is also of mesodermal origin.

It was already mentioned in connection with the ossification of the sphenethmoid that the walls of the braincase in adult pipids completely ossify and fuse with the prootics. Trueb *et al.* (2000) reported on a diffuse centre of ossification in the connective tissue forming the neurocranial wall medial to each eye and enclosing the *foramen orbitonasalis* in the postmetamorphic young (12.5 mm snout to vent) of *Pipa pipa*. This ossification is preceded by chondrocranial cartilage that disappears and is replaced by connective tissue in which ossification later forms. This structure is interpreted as a membranous ossification (sometimes erroneously called the "dermal sphenethmoid") and occurs only in recent pipids (Trueb 2000, pers. comm.).

B. *Fissura Prootica* and *Foramen Prooticum*

In the orbitotemporal region of the braincase of larval anurans, the lateral wall is separated from the otic capsule by a fissure called the *fissura prootica* (Fig. 20; also see Roček [1981, his figure 15]; Haas 1996b, his figure 2). The trigeminofacial ganglion is located within this fissure and the trigeminal, facial, and abducens nerves pass through it. Anterior to the fissure are the *processus ascendens palatoquadrati* and *pila antotica*. The fissure itself extends to the floor of the braincase and remains quite distinct until the last stages of metamorphosis.

Later in development, when the wall of the braincase is entirely cartilaginous, the posterior end of the orbital cartilage and the dorsal end of the *pila antotica* become connected to the roof of the otic capsule by the *taenia tecti marginalis* ("*taenia tecti longitudinalis*" of N. G. Stephenson [1951]) (Fig. 22). This new cartilage ("*Orbitalflügel-Knorpel*" of Goette [1875]) obliterates the former fissure between the *processus ascendens* and the otic capsule, dorsal to the trigeminofacial ganglion. The wall of the braincase becomes confluent with the otic capsule, except for the *foramen prooticum* ("*foramen ossis prootici*" of Gaupp [1899]) which is a common passage for the trigeminal, facial, and abducens nerves. Because this foramen is covered by a membrane, it is often called the "*fontanella prootica*". In some primitive anurans such as *Ascaphus*, *Leiopelma*, *Discoglossus*, and *Bombina*, it may be subdivided by a strip of cartilage, called the prefacial commissure, into the dorsal prootic foramen (for the trigeminal nerve) and the posteroventral palatine foramen (for the facial nerve and the internal jugular vein); this is the vestige of an original separation between the trigeminal and facial ganglia (de Villiers 1934; N. G. Stephenson 1951; Sokol 1975; Cannatella 1999). In the larval chondrocranium of *Dendrobates auratus*, the fusion between the orbital cartilages and the otic capsules is lacking (de Sá and Hill 1998).

In larval *Xenopus*, the prootic fissure is even better developed (see section XI D, page 1968) because a previously firm connection between the orbitotemporal part of the braincase and the otic capsules becomes interrupted due to a considerable reduction of the walls of the braincase (also see Trueb and Hanken 1992). The floor of the braincase immediately anterior to the tip of the notochord is thin and membranous. Because the palatoquadrate lacks any connection either with the braincase or the otic capsule, the larval *processus oticus palatoquadrati* having disappeared completely (see section V C, page 1929), the orbitotemporal and otic sections of the braincase are entirely separate except for narrow strips of membrane in the floor of the braincase. These endocranial divisions would be movable, unless their movements were prevented by the developing exocranial bones (especially the parasphenoid and frontoparietal). At the end of metamorphosis the connection of the orbitotemporal part of the braincase with the otic capsule is reconstituted and soon begins to ossify (pers. obs.; Trueb and Hanken 1992).

In those anurans in which the larval stages are suppressed (e.g., *Eleutherodactylus nubicola*), there is a large slot between the otic capsule and the *pila antotica* in the earliest cartilaginous stages (Lynn 1942, his figure 25). This slot is undoubtedly the prootic fissure since it serves as a passage for the trigeminal nerve at a stage corresponding to the metamorphic stages of other anurans (judging by the degree of development of the palatoquadrate and of Meckel's cartilage). Later the fissure is closed dorsally by the *taenia tecti marginalis*, as in other anurans, but the large prootic fontanelle persists even in adults (Fig. 25).

C. *Capsula Optica* (Sclerotic Cartilage)

At metamorphosis in most species, but prior to metamorphosis in *Rana tigrina* (Ramaswami 1940), the eyeball becomes protected on its medial side by a sclerotic cartilage ("*sclera bulbi oculi*" of Reinbach [1939a]). It consists of two layers, the cartilaginous capsule itself and an outer fibrous layer. The sclerotic cartilage persists in adult *Xenopus*, and is unique in possessing a cartilaginous process to which the *musculus rectus inferior* is attached (Stadtmüller 1929). This capsule is also found in adult *Leiopelma* (E. M. Stephenson 1951) and *Bombina* (Slabbert 1945).

The cartilaginous optic capsule is homologous with the ossified sclerotic ring in primitive amphibians and with the membranous sclera of mammals. It is probably of mesodermal origin (Bjerring 1977; his figure 13).

IV. OTICO-OCCIPITAL PART OF THE SKULL AND STRUCTURES OF THE MIDDLE EAR

This part of the skull, also called the otico-occipital region, is a natural unit delimited anteriorly by the tip of the notochord and/or *parachordalia*, by the posterior extent of the infundibulum, and by the position of the *chiasma opticum* (also see Okutomi 1937).

A. *Parachordalia* and Posterior Part of the Braincase

According to Villy (1890) and Reiss (1997), the *parachordalia* and otic capsules are of mesodermal origin. However, Toerien and Rossouw (1997) claimed that the ethmoidal and the otic capsules are both of ectomesenchymal, i.e., placodal, origin. In *Xenopus*, the otic region of the braincase develops at least from three metameres (manifested as myotomes), but four metameres are present in early development (Smit 1953, his figures 1, 3). Chiarugi (1891) and Sewertzow (1895) recognized three myotomes in *Bufo*. In *Microhyla*, only two (possibly three) metameres were identified (van der Steen 1930, ex Smit 1953). During further development, myotomes are reduced, the most anterior being the first to disappear. Due to this, in early development there is some forward shifting of the remaining myotomes in relation to the position of the otic vesicle (Sewertzow 1895 [1949]; van Seters 1922). The *parachordalia* presumably develop from the corresponding sclerotomic material. Although it has been suggested that the "*Balkenplatte*", "*mesotischer* (*periphärer*) *Knorpel*" and

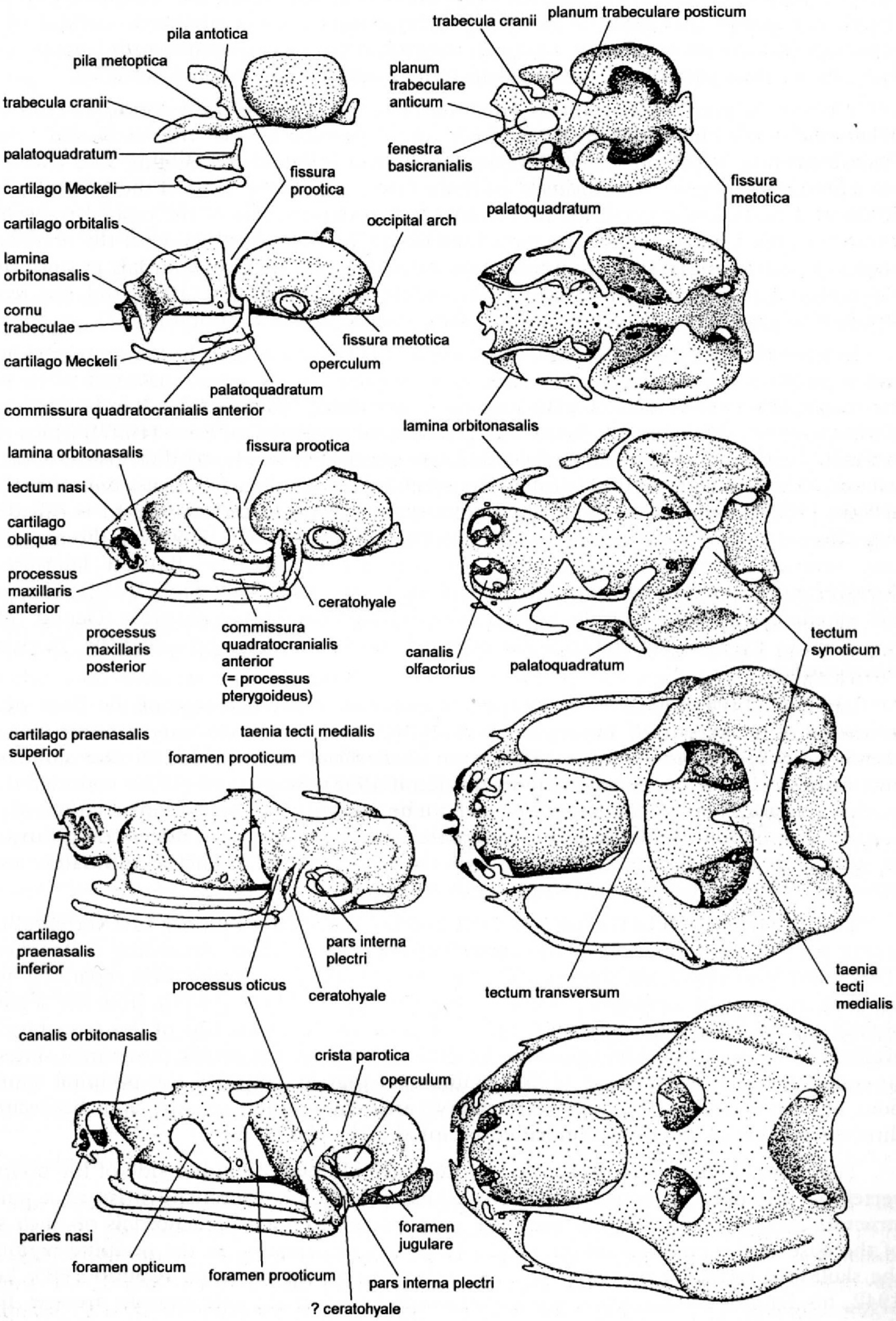


Fig. 25. Development of the chondrocranium in an anuran with suppressed larval development (*Eleutherodactylus nubicola*). Drawings are of progressively older stages from the top of the page downward. The left column shows left lateral views; the right column depicts dorsal views. From Lynn (1942).

"*Occipitalplatte*" represent the original segmentation (Stöhr 1882 and Gaupp 1893), Smit (1953) concluded that there is no ontogenetic evidence for a metameric origin of the *parachordalia* (also see van Seters 1922). In contrast, there was agreement with Gaupp (1906) that the occipital part of the anuran skull represented one postcranial vertebra.

The otic region originates only after the principal parts of the visceral skeleton have developed, and chronologically follows the appearance of the *trabeculae cranii*. Chondrification of the otic region begins as a pair of gradually elongating rods called the parachordal cartilages ("*Balkenplatten*" of Stöhr [1882]), from the level of the posterior edge of the *planum trabeculare posticum* (interconnected posterior ends of the cranial trabeculae; see section III A, page 1906). The parachordals are located on each side of the notochord, medial to the auditory sac. Chondrification extends along the parachordals posteriorly to the occipital region (Gaupp 1893). Stöhr (1882) and van Seters (1922) did not record separate origins of the parachordals and the *trabecule*, as did Okutomi (1937).

In front of the level of the *foramen acusticum*, the tip of the notochord becomes reduced and both parachordal cartilages progressively become fused across the midline to form the basal plate ("*vordere Parachordalplatte*" of Stöhr [1882]; "*planum basale*" and "*Basalplatte*" of Gaupp [1893, his plate 13, figure 1]; "acrochordal cartilage" of Reiss [1997]) which then extends posteriorly. When the *parachordalia* are connected by chondrified tissue dorsal to the notochord, the connection is called the epichordal commissure ("*commissura epichordalis*" of Smit [1953]), whereas a chondrified connection ventral to the notochord is called the hypochordal commissure ("*commissura hypochordalis*" of Smit [1953]). However, the notochord may remain exposed either dorsally of ventrally or may be flanked laterally by dorsoventrally flattened parachordals, depending on the family (see Stöhr 1882). The space still remaining open between the parachordals is called the *incisura occipitalis* (Gaupp 1893). It is filled by material derived from the occipital vertebra that Gaupp called the "*tuberculum interglenoidale*".

Ultimately, the notochord is completely enclosed in the cartilage of the floor of the braincase. The extent of notochordal chondrification seems to vary among taxa. In metamorphosed *Rana* (Gaupp 1893) and in *Bombina* (Goette 1875), the notochord chondrifies, whereas in *Xenopus* it does not (Smit 1953). Swanepoel (1970) considered the gradual disappearance of the notochord to be caused, not by chondrification of the notochord itself, but rather by its being replaced by the expansion of surrounding cartilage. In adult *Caudiverbera* the notochord and the floor of the braincase ultimately ossify (Reinbach 1939a); this ossification proceeds anteriorly.

The posterior ends of the parachordals become articulated with the first vertebra, thus taking part in the formation of the cranio-vertebral articulation. According to Mookerjee (1931) and Smit (1953, his figures 13D, 14, 15), the *condyli occipitales* arise separately from the skull as a pair of cartilages ("intervertebral cartilages" of Smit [1953]), from the segment behind the occipital arch, and only later fuse with the posterior tips of the parachordals. Hence, the occipital condyles appear to be derived from the embryonic postcranial skeleton. In contrast, N. G. Stephenson (1951) maintained that in *Leiopelma* the occipital condyle does not arise from a separate "intercalary" arch, but rather appears as a backwardly-directed process of the well-chondrified occipital arch.

The neural arches ("*Okzipitalpfeiler*" of Reinbach [1939a]) on either side of the occipital vertebra ("proatlas" of some authors, see Smit [1953] for references) arise as a paired structure growing dorsally from the most posterior part of the parachordals on each side of the base of the cranium (Stöhr 1882). They become involved in the occipital region of the skull and form the posterior section of the wall of the braincase (Gaupp 1893; Lynn 1942, his figures 27–32). Since the posteromedial part of the otic capsule diverges from the parachordal and is thus separate, there is a space between the capsular wall and the arch forming the wall of the braincase; this space (Fig. 25) is called the *fissura metotica* (de Beer 1937, his plate 77, figures 1–3) ("*foramen metoticum*" of Reinbach [1939a]). The glossopharygeal and vagus nerves exit the larval braincase through it. Later, it is bridged over by a thin *crista occipitalis lateralis* (Gaupp 1893) that is continuous medially with the *tectum synoticum* (to the *tectum posterius* according to Reinbach [1939a]). However, in spite of the *fissura metotica* being closed dorsally, a faint groove ("*sulcus occipitalis*" of Reinbach [1939a]) marks the border between the *tectum posterius* and the roof of the otic capsule. Through this groove the *arteria occipitalis* runs anteriorly to reach the posteromedial corner of the orbit. In subadult *Caudiverbera* the groove may be bridged over by cartilage so that the *canalis arteriae occipitalis* pierces the endocranium (Reinbach 1939a). In the majority of other taxa the groove remains open, or the artery may be enclosed in dermal bone (e.g., *Pelobates*), or may run in a groove on the dorsal surface of the dermal bone (e.g., *Bufo*) (see treatment of the frontoparietal, page 1943).

Due to further expansion of the cartilages surrounding it, the *fissura metotica* becomes obliterated so that only a small *foramen jugulare* persists, through which the glossopharyngeal and vagus nerves leave the braincase (also see Smit 1953). Thus, the combined trunk of these two nerves never actually pierces the cartilaginous wall of the otic capsule but remains outside the capsular cavity. A crista develops between the base of the posterior part of the capsule and the floor of the braincase and temporarily separates the *foramen jugulare* from a second opening, the *foramen perilymphaticum accessorium* (Gaupp 1893), through which the *ductus perilymphaticus anastomoticus* passes. Later (during metamorphosis), the crista disappears (Gaupp 1893) and the two openings fuse with one another again, to form a single *foramen jugulare*. The *ductus perilymphaticus anastomoticus* runs through the anterior portion of this combined opening and the glossopharyngeal and vagus nerves pass through its posterior part.

The roofs of both otic capsules become connected above the posterior part of the braincase by a *tectum synoticum* ("synotic roof" of Hall and Larsen [1998]) that chondrifies independently of the capsules and of the *taeniae tecti marginales*. The tectum is confluent with the *crista occipitalis lateralis*, which is derived from the occipital arch (see above). A median bar of cartilage called the *taenia tecti medialis* projects anteriorwards in *Rana* and in some other genera (Fig. 22). The upper lateral margins of the walls of the braincase arise independently of the otic capsule and are termed the *taeniae tecti marginales* (Gaupp 1893, his plate 14, figure 12); they usually arise later than the *tectum synoticum*. Since the occipital arches are included in the formation of the posterior part of the skull (see above) it is probable that the *tectum synoticum* is confluent with the *tectum posterius* of the occipital segment (de Beer 1937). The *tectum posterius* may be absent in some genera, such as *Breviceps* (Swanepoel 1970). Van Seters (1922) apparently considered the *tectum posterius* and *tectum synoticum* to be synonyms. Gaupp (1893) indicated that the *tectum synoticum* extended posteriorly to the level of the *foramen perilymphaticum superius* and anteriorly to the *foramen endolymphaticum*. The tectum may be absent in some anurans, e.g., *Heleophryne* (Ramaswami 1944).

The region of the *foramen jugulare* begins to ossify as the *occipitale laterale* or *exooccipitale* ("*pleurooccipitale*" of Reinbach [1939a]), the ossification then spreading across the borders of such developmentally separate units as the posterior part of the otic capsule, the parachordal, and the occipital arch (Gaupp 1893).

B. *Capsula Otica*

The *capsula otica* ("*capsula auditiva*" of Gaupp [1893]) arises independently of the parachordals (Reichert 1838 ex Okutomi 1937; Goette 1875; van Seters 1922; Smit 1953) and chondrifies either from a single centre on the outer surface of the lateral semicircular canal (Stöhr 1882), or from both an anterior and a posterior centre (e.g., in *Alytes*; van Seters [1922]). Nevertheless, even in those forms in which chondrification begins in a single centre it occurs separately in the anterior and posterior walls of the capsule (the "*cupola anterior*" and "*cupola posterior*" respectively of Gaupp [1893]); in the posterior wall it spreads anteriorwards in contrast to the general trend of ossification in the otic region. In general, chondrification spreads across the capsule, leaving a large opening ("*fenestra basicapsularis*" of de Beer [1937]; "*foramen ovale primarium*" and "*primäres Foramen ovale*" of Gaupp [1893, his plate 13, figure 1]) in the floor of the capsule between the two commissures (see below). The definitive *foramen ovale* arises either directly by the gradual obliteration of this fenestra, or secondarily as a new foramen ("*fenestra vestibuli sekundär*" of Okutomi [1937]).

There has been some discussion on the origin of the floor of the otic capsule. Peeters (1910 ex van Seters 1922) believed the cartilaginous floor of the otic capsule (at least the part delimiting the *foramen ovale* medially) to be formed by a posterior expansion of the parachordal cartilage. However, van Seters (1922) was convinced that all margins of the floor of the otic capsule (including the medial ones) are formed from capsular material and not from the *planum basale* of the embryonic *parachordalia*. Okutomi (1937) claimed that the parachordals extend laterally to bound the otic capsule from below. He called these lateral extensions "*metotischer Knorpel*".

At this time the medial wall partitioning the capsule from the braincase is not yet chondrified. In *Ascaphus*, a sheet of mesenchyme (which soon does chondrify) extends from the parachordal beneath the future *sacculus*; this structure was called the basiotic lamina by Reiss (1997) ("basal otic lamina" of Hall and Larsen [1998]). It is separated from other parts of the capsule by the *fenestra basicapsularis*. Posteriorly, the basiotic lamina is separated from the parachordal by what Reiss (1997) termed the mesotic fissure (note: "*fissura mesotica*", not "*fissura metotica*", see above, page 1912). Later when the basiotic lamina chondrifies, the fissure is closed posteriorly by the posterior mesotic commissure, thereby giving rise to the mesotic fenestra.

When the basiotic lamina cannot be recognized, the capsule is connected directly with the parachordals by the *commissura basicapsularis* (*sensu* de Beer [1937]; "*commissura basicapsularis anterior*" of Gaupp [1893, his plate 13, figure 1]) at the level of the anterior part of the capsule, closely posterior to the *ramus hyomandibularis*, and beside the *commissura basivestibularis* (*sensu* de Beer 1937; "*commissura basicapsularis posterior*" of Gaupp [1893, his plate 13, figure 1]) anterior to the *nervus glossopharyngeus* (Fig. 20). Finally, the *fenestra basicapsularis* becomes progressively obliterated from the parachordal cartilage, leaving only a small *fenestra ovalis* covered by a membrane ("*membrana opercularis*" of Gaupp [1893]; also see van der Westhuizen [1961]). In *Leiopelma* there is no basicapsular fenestra and the area of the *fenestra ovalis* becomes closed by cartilage in early (intracapsular) development (N. G. Stephenson 1951).

Reiss (1997) noted three commissures associated with the otic capsule of *Ascaphus*. One is the prefacial commissure, a chondrified bar between the parachordal and the *cupola anterior* that connects the braincase with the otic capsule in front of the root of the facial nerve. The second is the palatobasal connection ("*processus basalis*"; see section V C, page 1930), joining the palatoquadrate to the basiotic lamina. The third is the anterior mesotic commissure linking the basiotic lamina and the parachordal. Anteriorly, the basiotic lamina is continuous with the prefacial commissure and with the *cupola anterior* (anterior basicapsular commissure). Posteriorly, it is in contact with the *cupola posterior* (posterior mesotic commissure).

The partition between the posterior part of the braincase and the otic capsule is the last part of the capsule to develop. When the medial wall of the capsule arises it leaves a large anterior fenestra. This fenestra, however, becomes completely obliterated in further development. Behind and below this fenestra is the *foramen endolymphaticum*, through which the *ductus endolymphaticus* courses. Close beneath this duct, there arises the elongated *foramen acusticum*, through which both branches of the acoustic nerve (*ramus vestibularis* and *ramus cochlearis*) pass into the capsule. Posteriorly, but close to the floor, is a passage of the *ductus perilymphaticus superior*, called the *foramen perilymphaticum superius* (Gaupp 1893); "*foramen rotundum*" of Hasse [1873]). This foramen opens into the *fissura metotica*. During metamorphosis (or earlier in some genera) the single *foramen acusticum* divides into an anterior foramen (*foramen acusticum anterius*) for the vestibular branch of the vestibulocochlearis nerve, and a posterior one (*foramen acusticum posterius*) for the cochlear branch (Gaupp 1893). Sometimes the *foramen acusticum anterius* is subdivided into the *foramen acusticum maius* and *foramen acusticum minus* (Reinbach 1939a). The *foramen perilymphaticum* becomes separated into the *foramen perilymphaticum superius* and *foramen perilymphaticum inferius* ("*foramen pro aquaeducto cochleae*" of Hasse [1873]) and, in some cases (e.g., *Polypedates*; Okutomi 1937) also into the foramen *perilymphaticum accessorium* for the *ductus perilymphatici*.

While the capsular walls are still incomplete, cartilaginous septa begin to separate the three semicircular canals from each other inside the otic capsule, first laterally, and then medially (*canalis semicircularis anterior* and *canalis semicircularis posterior* from the anterior and posterior walls of the capsule respectively). The *utriculus* and *sacculus* still occupy a common space called the *cavum utriculosacculare*; later, the interior of the capsule becomes completely divided by septa (Gaupp 1893).

On the external surface of the capsule, the lateral semicircular canal forms an horizontal ridge-like bulge, the *crista parotica* ("*tegmen tympani*" of Parker [1876]; "*processus squamosus*" of Gaupp [1893]; "*processus muscularis capsulae auditivae*" of Sedra and Michael [1957]) that roofs the *fenestra ovalis* dorsally. This occurs rather late in metamorphosis in *Rana*, but obviously earlier in *Heleophryne* (see van der Westhuizen 1961). In adult *Rana*, as well as in *Chiromantis* (Swanepoel 1966, his figure 14) and *Scaphiopus* (Hall and Larsen 1998) the anterior part of the *crista parotica* is continuous with the *processus oticus palatoquadrati* and its posterior part (in *Rana*) with the *annulus tympanicus* (Gaupp 1893). Van der Westhuizen (1961) confirmed that cartilaginous edge of the *crista parotica* is formed by cartilage cells from the destroyed hind end of the larval palatoquadrate. De Villiers (1934) noted that in adult *Ascaphus* the *crista parotica* preserves its identity as a palatoquadrate derivative and is histologically distinguishable from the capsule (also see Swanepoel 1970). These observations suggest that the *crista parotica* is not derived from the otic capsule (Fig. 26). In contrast, Barry (1956) maintained that the *crista parotica* in *Bufo* is derived exclusively from the otic capsule. Also, Kruijtzer (1931) concluded that the *crista parotica* is partly derived from the otic capsule and partly from the dorsal part of the hyoid arch. It seems that the *crista parotica* is a complex structure perhaps derived from several sources, its basal part from the capsular wall and its anterior part from the palatoquadrate; its posterior part develops in close association with the *pars interna plectri* and thus from the dorsal end of the hyoid arch (Swanepoel 1970).

In larval *Hamptophryne* (Microhylidae) the *crista parotica* forms an extensive, fenestrate, and irregularly margined sheet of cartilage associated with the otic capsule and the palatoquadrate. This sheet of cartilage is connected by a slim strip of cartilage called the subpalatoquadrate cartilage (de Sá and Trueb 1991, their figures 6, 7A) to the *pars quadrata palatoquadrati*. This sheet of cartilage and the subpalatoquadrate cartilage both undergo reduction and finally disappear before metamorphosis. Their identity is

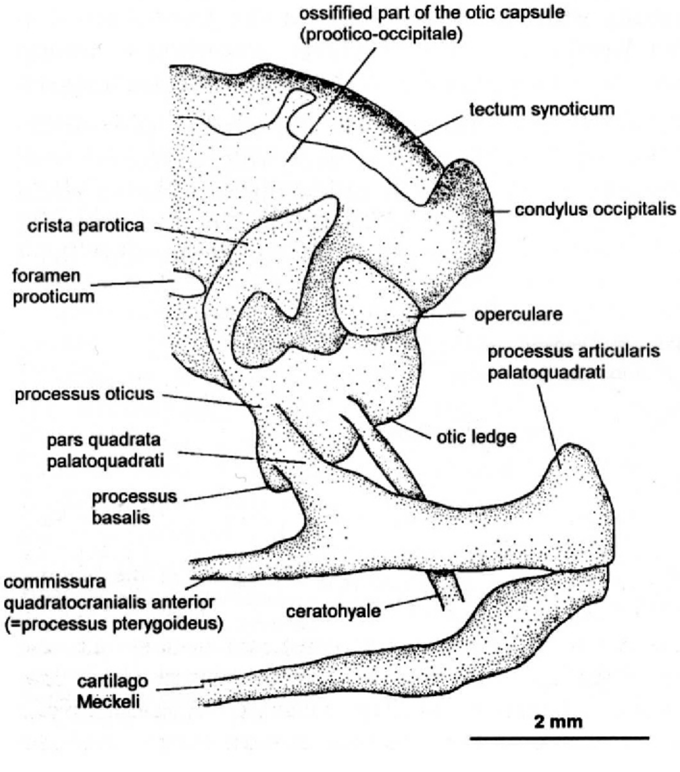


Fig. 26. Left lateral view of the posterior part of the skull of an adult male *Chiromantis xerampelina* showing the *crista parotica* and the attachments of the palatoquadrate and ceratohyal to the otic capsule. From Swanepoel (1966).

unclear, but a structure similar to the former was also found in larval *Rhinophrynus* in which the most posterior connection of the palatoquadrate with the otic capsule was called the "larval *crista parotica*" by Swart and de Sá (1999, their figure 1).

Ultimately, the otic capsule ossifies from two separate parts, the *prooticum* anteriorly and the *opisthoticum* ("*exoocipitale*" of Sewertzow [1891] and van der Westhuizen [1961] posteriorly. The posterior perichondral ossification also includes the *tectum synoticum* and part of the basal plate. Later, these ossifications expand so that only narrow median strips of cartilage ("*cartilago prootico-occipitalis*" of Ecke [1935]) may remain in adults (e.g., in *Bufo* [Ecke 1935] and *Hyla* [Gaudin 1973]). Eventually, even these cartilages may disappear and the capsule, including the roof and floor of the braincase, becomes entirely ossified. The ossified *tectum synoticum* was called the *supraoccipitale* by Parker (1871). However, Sokol (1977) used the same name (supraoccipital) for a different ossification in the dorsal part of the occipital arch of *Pipa carvalhoi*.

Occasionally, some independent, stick-like structures arise in the ossified medial wall of the otic capsule and protrude into braincase; these were reported in *Caudiverbera* as "*corpusculum metoticum*" by Reinbach (1939a).

C. Sound-conducting Apparatus

Two structures arise within the *fenestra ovalis* ("*fenestra vestibuli*" of Stadtmüller [1936]). In *Rana* (Gaupp 1893), a plate of cartilage arises within the *membrana opercularis* in the posterior part of the fenestra, independently of the wall of the capsule (also see Eiselt 1941). This is generally termed the *operculum fenestrae ovalis* or *operculum auris* ("stapes" of Parker [1976, his plate 54, figures 7, 8]). According to van Seters (1922), van Eeden (1951), van der Westhuizen (1961, his figure 13), and Swanepoel (1970), the cells of the developing *operculum* arise and migrate from the edges (mainly the ventral one) of the *fenestra ovalis* in *Alytes*, *Ascaphus*, *Heleophryne*, and *Breviceps*. As Kingsbury and Reed (1909) suggested, the operculum is probably a derivative of the otic capsule. According to de Villiers (1934), a small muscle deriving from the *musculus levator scapulae superior* and originating on the suprascapular cartilage of the shoulder girdle, inserts on to the posterior part of the operculum (Fig. 27). This muscle was called the *musculus opercularis* by Gaupp (1893). The operculum acquires cartilaginous continuity with the dorsal edge of the *fenestra ovalis* as early as during metamorphosis (van der Westhuizen 1961); however, according to Gaupp (1893) this connection is temporary and is interrupted again at the end of metamorphosis.

An independent horizontal bar of cartilage (Fig. 28) arises in the anterior part of the fenestra in front of the operculum in metamorphosing larvae with well-developed hind legs in *Rana*, and in similar stages in *Heleophryne*. This bar is called the *pars interna plectri* or "footplate"("*interstapediale*" of Parker [1871]; "stapes" of Parker [1876, his plate 59, figure 7]; "*pseudooperculum*" of Gaupp [1892]; "fenestral plate" of Kingsbury and Reed

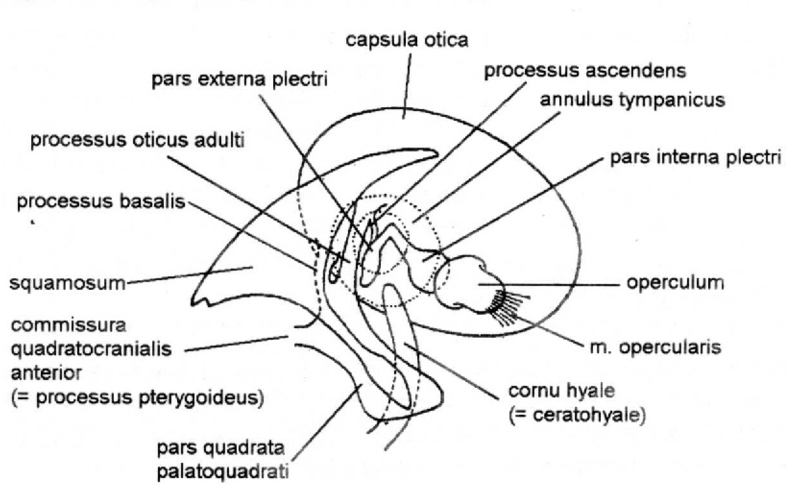


Fig. 27. Diagram of the left otic capsule of an adult *Rana*, showing the sound-conducting apparatus and the posterior connections of the palatoquadrate. Anterior is towards the left. From Stadtmüller (1936).

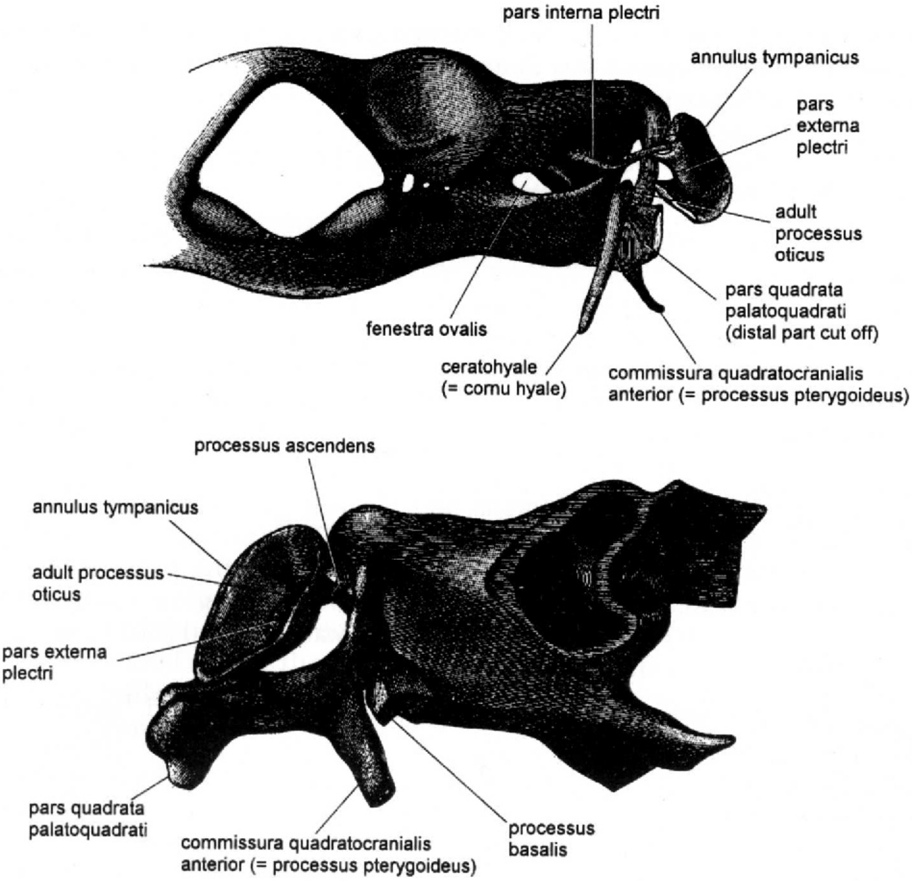


Fig. 28. Posterior (upper) and anterior (lower) views of the right otic capsule of a young metamorphosed *Rana temporaria* (2.5 cm in total length), showing the topographic relationships of the sound-conducting apparatus and the posterior connections of the palatoquadrate. The operculum, *pars quadrata*, and part of the *annulus tympanicus* have been removed in the upper picture; similarly, the *processus basalis* and the anterior part of the otic capsule (*prominentia canalis semicircularis anterior*) have been cut off in the lower picture. From Gaupp (1896).

[1909]; "*pars otica columellae*" of Reinbach [1950a]; "otostapes" of Tumarkin [1955]). In *Rana* it soon acquires cartilaginous continuity with the ventral edge of the fenestra. This connection, called the *crista praeopercularis* by Gaupp (1893), may become synostotic in adults of some taxa (e.g., *Heleophryne*; van der Westhuizen [1961]). Its posterior end is connected by a ligament to the operculum and is continuous with the cartilaginous hind end of the *crista parotica* in *Breviceps*. This led Swanepoel (1970) to the conclusion that the *pars interna*, and the posterior part of the *crista parotica* are both derivatives of the hyoid arch (see page 1970). The anterior end of the bar is connected by another ligament ("*ligamentum suspensorio-columellare*" of Gaupp [1893]; "*ligamentum suspensorio-stapediale*" of Huxley [1874]; "*ligamentum stapedo-extracolumellare*" and "*ligamentum intermedium*" of Reinbach [1939a]) to the palatoquadrate. The bar arises within the ligament. Above this ligament runs the hyomandibular branch of the facial nerve and the communicans branch of the glossopharyngeal nerve. This topographic situation is important in terms of the origin of the *columella auris*. The ligament is interrupted at the completion of metamorphosis (in small froglets without tails), because the entire posterior part of the palatoquadrate (the larval *processus oticus*) is resorbed and replaced by another connection (adult *processus oticus*) with the anterior part of the *crista parotica* (Fig. 26; also see Hall and Larsen 1998). Also, the primordium of the *annulus tympanicus* (see page 1918) becomes attached to the palatoquadrate.

The *pars interna plectri* turns at a right angle to the site of formation of the tympanum and fuses synchondrotically with another cartilaginous element, the *pars externa plectri* ("*extrastapediale*" of Parker [1871]; "medio-stapedial" of Parker [1876]; "*extracolumellare*" of Versluys [1898] ex Stadtmüller [1936]; "extraplectral" of de Villiers [1930]; "hyostapes" of

Salvadori [1928]; "*pars quadrata columellae*" of Reinbach [1950a]; "extrastapes" of Bolt and Lombard [1985]). The *pars externa* was thought to develop in a transient ligament connected to the *ceratohyale* (Salvadori 1928 ex de Beer 1937); however, it was later proven to develop from disintegrated cells originating in the hind margin of the palatoquadrate (Reinbach 1939a; van der Westhuizen 1961) when this part of the palatoquodrate attains a vertical position beneath the otic capsule.

The *pars externa* connects vertically to the lower surface of the *crista parotica* by way of the *processus ascendens plectri* ("*suprastapediale*" of Parker [1871]; "*processus dorsalis columellae*" of Gaupp [1892]; "*processus superior columellae*" of Gaupp [1893]; "*laterohyale*" of Salvadori [1928]; "*processus ascendens columellae*" of Reinbach [1939a]). This connection is cartilaginous at first but later the attachment may be only by a ligament. It should be noted that the *processus ascendens* is absent in the Aglossa (de Villiers 1932); Ecke (1935) mentioned its absence in *Bufo bufo*. In *Caudiverbera*, the lateral part of the *pars externa plectri* is fused to the inner surface of the tympanic membrane (Reinbach 1939a).

The connection between the columella and the edge of the *fenestra ovalis* transforms into a ligament. It should be emphasized that the first cartilaginous rudiment of the columella appears while the ceratohyal is still articulated with the palatoquadrate, at some distance away in the anterior part of the orbitotemporal region (Gaupp 1893). Also noteworthy is that in *Bombina*, Litzelmann (1923 ex Stadtmüller 1936) found a secondary fusion of the *ceratohyale* with the columella.

The *columella auris* was called "stapes" by Versluys (1898) and "*stelidium*" by Fuchs (1905). However, according to Schmalhausen (1953), the term "stapes" should be restricted only to the *pars interna* and *pars media*. The *columella auris* arises apart from the operculum from two separate chondrifications that in the adult may later ossify in the central part, generally called the "shaft" ("*mediostapediale*" of Parker [1871]; "*interstapediale*" of Parker [1876, his plate 54, figures 7, 8]; "*pars media*" of Gaupp [1893]; "*stilus columellare*" of Okutomi [1937]; "*columellare*", "stapes", "*mesostapediale*", "*os columellare*", and "*os intermedium*" of Reinbach [1939a]). The *pars interna* and the *pars media* develop as a single morphological unit and consequently they are distinguished only on the basis of ossification of the distal part (also see Tatarinov 1962). Two ossifications were reported in the columella of *Hyla regilla* (Gaudin 1973), *Xenopus*, *Pelobates*, and *Bufo* (de Villiers 1932); the conclusions of de Villiers were, however, doubted by Stadtmüller (1936). Only one ossification centre was found in *Scaphiopus* (Hall and Larsen 1998). In *Alytes* (Kruijtzer 1931, his figure 11; de Beer 1937), there is no subdivision between the internal and external parts of the plectrum, i.e., there is no ossified *pars interna* even in adults (Stadtmüller 1936), and the dorsal end of the *ceratohyale*, after becoming detached from the posterior surface of the palatoquadrate, becomes attached to the plectrum. By contrast, in anurans with a well-developed *pars media* and *pars externa*, a distinct border occurs between these two elements (Reinbach 1939a). Medially to the anterior free end of the plectrum in *Alytes* the cartilage giving rise to the basal connection (see page 1930) develops as an independent chondrification; however, it is attached to the plectrum by mesenchyme.

In adult *Bombina*, Stadtmüller (1931c, his figure 6) and Slabbert (1945, his figure 1) found an oval, somewhat cylindrical structure, called the *cartilago paraarticularis*, attached by connective tissue to the *pars quadrata palatoquadrati*. According to Stadtmüller (1931c) and Smirnov (1990, his figure 3B), the *cartilago paraarticularis* is a vestige of the *pars externa plectri*.

The cartilaginous tympanic ring (*annulus tympanicus*), which is a characteristic feature of some Anura, is no doubt a derivative of that part of the palatoquadrate at the base of the anterior margin of the *processus muscularis* (Parker and Bettany 1877 ex Winslow 1898; Cope 1888; Villy 1890; Gaupp 1893; Spemann 1898; later confirmed by many other authors, e.g., Reinbach 1939a; van der Westhuizen 1961; Swanepoel 1970). The *annulus tympanicus* chondrifies only after metamorphosis and remains separate but closely associated with the palatoquadrate. It should be noted in this regard that the Eustachian tube of the larva is located below the *commissura quadratocranialis anterior*, i.e., below the anterior part of the eye, and only during metamorphosis does it move backwards (Villy 1890). Finally, the annulus fuses dorsally to the *crista parotica*. On the outer margin of the annulus is stretched the tympanic membrane. The *tuba Eustachii* and the *pars externa plectri* run through the inner opening of the annulus. In *Xenopus* (Kotthaus 1933), the *annulus tympanicus* ("*processus basilaris*" of Kotthaus [1933]) arises from the ventral side of the otic process and almost joins the anterior corner of the *crista parotica*. The annulus may ossify (although incompletely) in some hyperossified anurans, e.g., *Pipa pipa* (Trueb *et al.* 2000).

It is difficult to say whether data provided by Ramaswami (1935) on the timing of the appearance of the plectral apparatus in *Scaphiopus* and *Megophrys* are reliable. He indicated the *pars media plectri* to be the first part of the apparatus to make its appearance, which is not in agreement with relevant data on other anurans. He also found, ventral to the *pars media*, a peculiar small cartilaginous nodule, which takes its origin from the lower part of the otic capsule and extends as far as the *pars externa plectri*, with which it fuses. He interpreted this connection to be a cartilaginous commissure between the *pars externa plectri* and the lower part of the otic capsule, and different from the *processus ascendens plectri*. He also mentioned that in both these genera there is an *annulus tympanicus* (but lacking in *Megophrys major*).

In summary, the sound-conducting apparatus in adult anurans consists of two morphologically and functionally distinguishable parts: (1) the opercular system, involving the operculum, located within the *fenestra ovalis* and connected by the *musculus opercularis* to the shoulder girdle, and (2) the tympanal system, involving the plectrum (= columella) (Fig. 29), and consisting of three parts, the *pars interna* (adjoining the operculum), the *pars media* (= *pars ossea*), and the *pars externa* (= extracolumella). The *pars externa* is involved in the tympanum and produces the tympanum's dorsal process (*processus ascendens*).

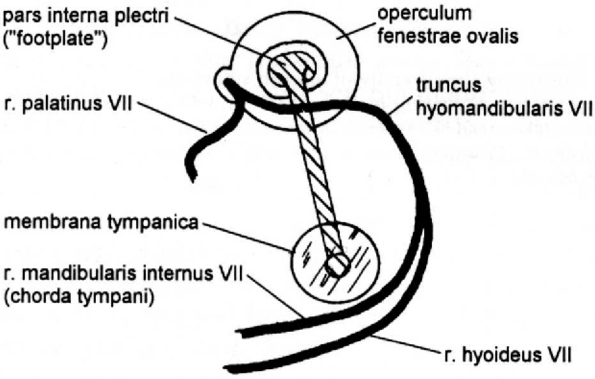


Fig. 29. Diagram of the topographic relationship of the anuran left columella to the *chorda tympani*. From Lombard and Bolt (1979).

These elements develop from various sources: the operculum is undoubtedly a derivative of the otic capsule (e.g., see Gazagnaire 1932). Some authors, e.g., Fuchs (1907), Kingsbury and Reed (1909), Litzelmann (1923), Stadtmüller (1931b), and Reinbach (1950a) also regarded the *pars interna plectri* as a derivative of the capsule (although separate from the operculum); van der Westhuizen (1961) included the *pars media plectri* among the derivatives of the capsule. By contrast, the *pars externa plectri* and the *annulus tympanicus* develop from the *pars quadrata* of the palatoquadrate (van der Westhuizen 1961). According to van der Westhuizen, the *processus ascendens* is also of dual origin; its dorsal part arises as a cartilaginous process given off by the *crista parotica*, whereas its lower portion develops as a dorsally directed procartilaginous process of the *pars externa plectri*. It should also be emphasized that in the Anura, the operculum always arises earlier than the plectrum (de Villiers 1934; Plasota 1974b), whereas in the Caudata the reverse occurs.

Developmental and morphological differences are associated with functional ones. According to Lombard and Straughan (1974), the opercular system enhances the perception of air-borne sounds below 1 kHz and monitors environmental sounds in terrestrial situations, whereas the tympanal system is capable of perceiving sounds above 1 kHz and is thus involved in reproductive communication. Smirnov and Vorobyeva (1988) suggested that these morpho-functional differences are correlated with developmental timing, the opercular system arising earlier than the tympanal one.

The opercular system is more conservative than the tympanal one. The tympanal system also displays a large extent of diversification (Fig. 30). It does not develop in normal adults of some burrowing or aquatic Anura like *Pelobates*, but is present in *Scaphiopus*, *Spea*, and *Megophrys* (Ramaswami 1935; Wiens 1989); it is not present in *Hemisus*, *Brachycephalus*, *Pseudophryne*, *Crinia*, primitive taxa like *Ascaphus* and *Leiopelma* (de Villiers 1934; Wagner 1934b; de Beer 1937; E. M. Stephenson 1951; N. G. Stephenson 1951; van Eeden 1951; van der Westhuizen 1961; Jacobson 1968), some *Microhyla*, *Bombina* (Stadtmüller 1931b, 1936; Ecke 1935; Slabbert 1945; Hanken and Hall 1984), and some others. However, a rudimentary plectrum may be present in *Bombina* (Litzelmann 1923), at least in some old individuals (Smirnov 1984, 1989, 1990 his figure 3; also see Stadtmüller 1931b).

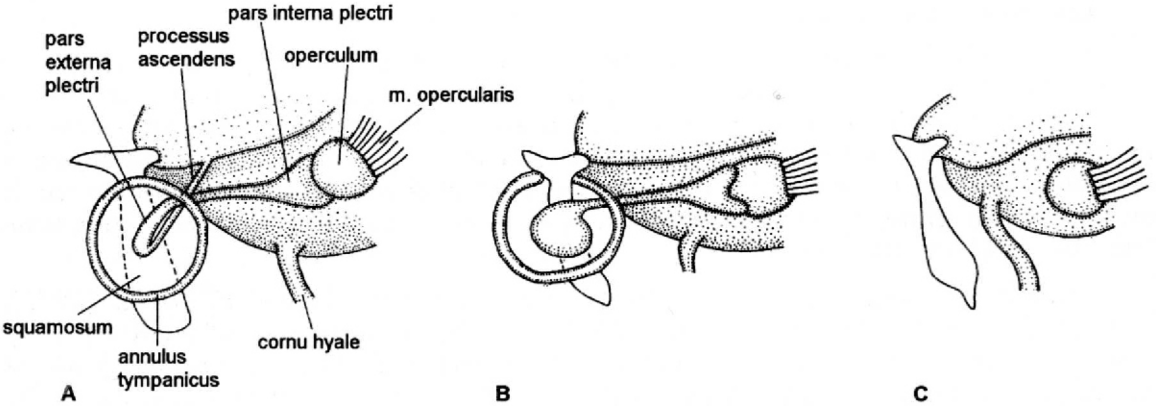


Fig. 30. Diagrams of lateral views of the left otic capsule, illustrating the diversity of anuran sound-conducting systems. A. Opercular and tympanal systems complete; documented as occurring in *Rana*, *Bufo*, and *Rhacophorus* (compare Fig. 27). B. Tympanal system partly reduced (*processus ascendens* absent; *annulus tympanicus* not developed dorsally); documented as occurring in some *Microhyla*. C. Tympanal system completely absent; documented as occurring in *Bombina*, *Pelobates*, *Ascaphus*, and some *Microhyla*. From Smirnov and Vorobyeva (1988).

In pipids, the opercular system is reduced or lost but the tympanal system is preserved. In adult *Xenopus*, the columella consists of the *pars interna* and *pars externa plectri*, united by an ossified *pars media*. Only a small operculum is preserved behind the *pars interna* (de Villiers 1934; Paterson 1939, 1955; Sedra and Michael 1957). Trueb and Hanken (1992) did not find an operculum in *Xenopus* but did observe a delicate disk of cartilage filling the *fenestra ovalis*. This structure is lacking in *Pipa* and *Hymenochirus* (de Villiers 1932; Paterson 1945; Sokol 1962). In contrast to the condition in the Pipidae, the opercular system is preserved and well developed in *Rhinophrynus* but the plectral apparatus is lacking (Trueb and Cannatella 1982, their figure 2C).

One might expect the sound-conducting apparatus to be well developed in primitive anurans. This is true for *Discoglossus*, *Alytes* and probably *Barbourula* which possess a complete sound-conducting apparatus similar to that of *Rana*, the only exception being that in the discoglossoids the *processus ascendens partis externae plectri* is absent (Ramaswami 1942; Slabbert and Maree 1945). However, in *Rana* and other derived anurans the complete sound-conducting apparatus is not expected and should therefore be explained by other than evolutionary reasons.

There is considerable variation in the structure of the sound-conducting apparatus. For instance, although *Pelobates* has an operculum and a rudimentary *pars interna plectri*, these undergo reduction during development (Plasota 1974a; Roček 1981). Consequently, the condition of the sound-conducting apparatus in adults may reflect various degrees of morphogenesis. In *Pelobates* it develops from a rather large element which, however, degenerates into a small vestigial structure attached to the *crista praeopercularis*. Note, however, that individuals with a completely-developed plectrum, although devoid of the *processus ascendens*, have been described (see Gadow 1889). Variation in the sound-conducting apparatus has been interpreted in many different ways (Schmalhausen 1968; Smirnov and Vorobyeva 1988), although nearly all authors have concluded that variability is more closely related to ecological conditions than to evolutionary history.

Well before their middle-ear elements are functional, anuran larvae possess a peculiar hearing organ similar to the Weber's organ of teleostean fishes (Beaumont and Gaudin 1962). This organ is represented by a string of connective-tissue fibres that originate from the alimentary canal and connect the lungs (that develop later) with the labyrinth. This structure disappears at metamorphosis in anurans.

V. PALATOQUADRATE AND ENDOCRANIAL LOWER JAW

A. Palatoquadrate of Larvae

That the palatoquadrate is an ectodermal derivative has long been recognized (Lundborg 1899). In *Ascaphus* (Reiss 1997), the whole palatoquadrate is ectomesenchymal in origin, except for the dorsal end of the ascending process which is of mesodermal origin; the latter might be a vestige from the early larval connection of the ascending process to the orbital cartilage and *pila antotica*. In *Bombina*, the situation is different in that the whole palatoquadrate, including its ascending process, is derived from the neural crest (see Olsson and Hanken [1996, their figure 5]).

The earliest rudiment of the palatoquadrate ("pterygopalatine" of Parker [1876]; "*quadratum*" and "Quadratbeinknorpel" of Stöhr [1882]; "*suspensorium*" of Huxley [1875]; "pterygoquadrate" of Ramaswami [1938]) is observable in *Rana* as a continuous bar of procartilaginous tissue located perpendicular to the notochord. It develops prior to the appearance of the *trabeculae cranii* but simultaneously with the first primordium of the *suprarostrale* (Fig. 9; also see Spemann 1898). Noteworthy is its anterior position in front of the eye. The bar is nearly vertical and continuous with the rudiments of Meckel's cartilage and the infrarostral cartilage (Goette 1875, his figure 319; van Seters 1922; Reiss 1997); these rudiments extend horizontally and forward from its lower end. The dorsal end of the bar remains free even after the *trabeculae* are distinguishable. A similar condition exists in *Xenopus* (de Beer 1937).

There has been some confusion of terminology about this region. In some of his illustrations, Parker (1876, his plate 55, figure 1 and plate 56, figure 5) used the term "pterygo-palatine bar" to designate the *commissura quadratocranialis anterior*, rather than the palatoquadrate because he used the term "pedicle" or "mandibular pedicle" for the palatoquadrate in his cursorial descriptions. Also, Huxley (1875a) used the term "*suspensorium*" for the mode of attachment of the palatoquadrate to the neurocranium (autostyly). This was later described as the "*suspensorium* of the lower jaw" and still later extended to the palatoquadrate (see Stadtmüller 1936). A few later authors (e.g., Sokol 1977) have used this term in its original sense of a mode of attachment of the posterior end of the larval palatoquadrate to the otic capsule and the neurocranium.

The first connection of the palatoquadrate with the trabecula is by means of the *commissura quadratocranialis anterior* (page 1923). It should be noted that in *Rana*, the development of the *commissura* precedes that of the trabecula so that the former may be distinguished as an anteriorly directed process on the palatoquadrate (which is still in the vertical position), well before the *trabeculae* arise (to which it will later attach) (Spemann 1898). At about this stage the palatoquadrate begins to chondrify and Meckel's cartilage and the lower labial cartilage separate from the palatoquadrate to form a movable articulation with it (Stöhr 1882). Curiously, the ceratohyal, which arises separately from the palatoquadrate, becomes connected to it by a ligament, and later by a temporary cartilaginous connection. Later, the latter connection is interrupted and becomes a movable joint between the palatoquadrate and the ceratohyal. The palatoquadrate gradually rotates anteriorly and thus attains a more horizontal position, except for its posteromedial part which remains nearly vertical; this part turns at a right angle medially and becomes attached to the *pila antotica* (Stöhr 1882). This posteromedial part of the palatoquadrate is termed the *processus ascendens* (page 1928). Because of the horizontal position of the palatoquadrate in this developmental stage, the articulation with Meckel's cartilage is far forward, anterior to the level of the *commissura quadratocranialis anterior*.

At approximately this stage, on the lateral edge of the palatoquadrate there arises the *processus muscularis* (*sensu* Gaupp [1893]; "*Orbitalfortsatz*" and "*processus orbitalis*" of Reichert [1838]; "*Jochfortsatz*" of Goette [1875]; "orbitar process" of Parker [1876]). In *Hymenochirus*, the muscular process, as well as the subocular part of the palatoquadrate, are absent (Sokol 1962). The muscular process is also absent in *Leiopelma* (N. G. Stephenson 1951). This process later becomes connected to the lateral wall of the braincase or to the terminal part of the *commissura quadratocranialis anterior* by a ligament, called the *ligamentum tectum* (also see Sokol 1975; Haas 1996b), so that it encloses the jaw musculature dorsally and forms a tunnel called the *fenestra muscularis* (*sensu* Reinbach 1939a; also see Okutomi 1937, his figure 15). Stöhr (1882), Sewertzow (1891) and Reinbach (1939a) found a small cartilage within this ligament. Also Sedra (1950, his plate 1, figure 2) found an horizontal bridge of cartilage chondrifying from a special centre and extending medially from the upper edge of the *processus muscularis*; he termed this structure the *commissura quadrato-orbitalis* (Fig. 6). The *ligamentum tectum* may sometimes ossify; it is probably homologous with the *ligamentum tecti* of Cannatella (1999) that stretches between the *processus muscularis* and the *processus antorbitalis*. Alternatively, the *ligamentum tectum* may become chondrified ("*cartilago tecti*" of Cannatella [1999]). It may consist of two parts, the *ligamentum tecti superius* and *ligamentum tecti inferius* (Cannatella 1999). Gradwell (1972) illustrated it in *Rana catesbeiana* as a composite of the *ligamentum supraorbitale cranii* and *ligamentum supraorbitale ethmoidale*. The chondrified ligament disappears in later development (Reinbach 1939a).

In order to emphasize its homology with the corresponding portion of the palatoquadrate in osteolepiform fishes, the part of the palatoquadrate that articulates with Meckel's cartilage is termed the *pars quadrata* or *pars pterygoquadrata* ("*cartilago quadrata*" of Parker [1877]; "*pars articularis*" of Gaupp [1893]; "*processus articularis quadrati*" of Wiens [1989, his figure 1]) and its joint is called the *articulatio quadrato-mandibularis* (*sensu* Reinbach 1939a). The ventral surface of the larval *pars quadrata* that articulates with the *ceratohyale* is termed the *processus hyoquadratus*; the joint was called the *articulatio quadrato-hyalis* by Reinbach (1939a).

The part of the larval palatoquadrate posterior to the *processus muscularis* was termed the *pars metapterygoidea* by Okutomi (1937); earlier authors (e.g., Parker 1876) called it the "pedicle" or "mandibular pier". There is some confusion over the term "pedicle". Judging from Parker's figures 1–3 of plate 55, the medial part of what he called the "pedicle" is in fact the *processus ascendens*. However, entirely different structures are designated by the same name in adults; these are mainly associated with the suspensorial function of the palatoquadrate (see Parker's plate 54, figure 5) and are only seemingly identical with the larval structure.

Parker (1876) and others maintained that in adult *Rana* the *pars metapterygoidea* may be ossified by a bony plate called the "metapterygoid". However, most other observations contradict this view and confirm that the palatoquadrate does not ossify. Even in the largest individuals of hyperossified taxa, e.g., *Pipa pipa* (Trueb *et al.* 2000), the palatoquadrate shows no indication of calcification. The only exception is the *pars quadrata palatoquadrati* that may rarely ossify as the *os quadratum* in *Xenopus* (Parker 1876), *Ascaphus* (de Villiers 1934), *Leiopelma* (E. M. Stephenson 1951), *Scaphiopus holbrooki* (Ramaswami 1935), *Brachycephalus*, and *Hemisus* (McLachlan 1943). Also, the ossified *pars quadrata* may fuse with the quadratojugal that in turn ossifies in the tissue connecting the *pars quadrata* with the posterior end of the maxilla (see section VII C, page 1941).

The morphology of the early larval palatoquadrate, with its anteriorly directed quadrate portion, is obviously related to the highly specialized feeding adaptations of the mouth and does not reflect any evolutionary sequence (Shishkin 1973).

B. Anterior Connections of the Palatoquadrate

As mentioned above, the anterior section of the larval palatoquadrate is attached to the *trabecula* by the *commissura quadratocranialis anterior* (*sensu* Gaupp [1893, his plate 13, figure 1]; "ethmovomerine cartilage" of Huxley [1858]; "pterygopalatine" of Parker [1871]; "*Flügelgaumenplatte*" of Goette [1875]; "conjugational plate" of Parker [1876, his plate 57, figure 3]; "*querer Gaumenbalken*" of Born [1876]; "*processus pterygopalatinus*" of Stöhr [1882] "palatopterygoid bar" of Villy [1890]; "*processus palatopterygoideus*" of Sewertzow [1891]; "*vordere suspensorio-trabeculare Verbindung*" of Stadtmüller [1936]; "anterior basal process" of Pusey [1943]; "pterygoid process" of N. G. Stephenson [1951]; "antorbital plate" of Toerien and Rossouw [1977, their figure 1d]; "*lamina orbitonasalis*" of Toerien and Rossouw [1977]; "larval pterygoid process" and "adult pterygoid process" of Reiss [1997]). It arises as a process directed anteriorly from the vertical palatoquadrate, even before the *trabeculae* may be discerned (also see Okutomi 1937; Swanepoel 1970). It represents the first connection of the palatoquadrate to the neurocranium. As soon as the *trabeculae* appear, the *commissura* joins the *trabecula* from its own side at the level of the *planum trabeculare anticum*. At this period of development, the posterior part of the palatoquadrate may still be free in some anurans (e.g., in *Breviceps*; Swanepoel 1970). Some authors (e.g., Reinbach 1939a) considered the commissure as only that part lying medially to the *processus pseudopterygoideus* (if present) and the *processus quadratoethmoidalis*.

The development of the *commissura quadratocranialis anterior* indicates that it is part of the palatoquadrate. The *commissura* may not form in some anurans with suppressed free-living larval stages (e.g., *Eleutherodactylus coqui*), except for a posterior section called the *processus pterygoideus* (Hanken *et al.* 1992, their figures 3D, 4F).

The attachment of the palatoquadrate has been studied in *Ascaphus* (Pusey 1943; van Eeden 1951) as well as in *Rana*; the comparison is rendered less precise by the fact that the *Ascaphus* involved were at a somewhat later developmental stage than were the *Rana*. In contrast to *Rana*, in the earliest developmental stages available for *Ascaphus*, the palatoquadrate is attached ventrally to the wall of the braincase along the former *trabecula cranii*. This attachment extends from the posterior margin of the choana to a position directly in front of the anterior wall of the otic capsule. The *nervus ophthalmicus* is enclosed in a canal ("profundus tunnel" of Pusey [1943, his plate 12, figure 17 and plate 13, figure 20]) that follows the line of attachment. The canal arose earlier in ontogeny by fusion of the palatoquadrate with the *trabecula*. The flattened anterior part of the palatoquadrate lies nearly vertically, but proceeding backwards it gradually slants sideways. Its *pars quadrata* (marking the position of the future jaw joint) is situated directly behind the level of the anteriormost extent of the palatoquadrate. Kraemer (1974) may have recorded an earlier stage of the development of the palatoquadrate in *Discoglossus*; in developmental stage 27, characterized by the beginning of chondrification of the *trabeculae*, the palatoquadrate had not yet entirely coalesced with the *trabecula*, and was still free in its anterior portion. This suggests that the fusion of these two structures in ontogeny proceeds in an antero-posterior direction, exactly as in *Ascaphus* (van Eeden 1951; also see Gaupp 1906); Ramaswami (1938) recorded the palatoquadrate as still being free posteriorly in large larvae of *Philautus variabilis*.

In some species there is a small forwardly-pointing process approximately in the middle of the anterior edge of the *commissura quadratocranialis anterior*. This process is called the *processus quadrato-ethmoidalis* or *processus pterygoideus* (*sensu* Gaupp [1893]; "*processus cornu-quadratus medialis*" of Sedra and Michael [1957]; also see Okutomi [1937, his figure 20]) and from it the *ligamentum cornu-quadratum posterior* ("prepalatine ligament" of Parker [1871, 1882]; "*ligamentum quadrato-ethmoidale*" of Gaupp [1893]; "*ligamentum cornu-quadratum mediale*" of van der Westhuizen [1961]) runs to the *cornu trabeculae* just in front of the *fenestra* *endochoanalis*. This ligament inserts on to the *processus lateralis trabeculae* (*sensu* van Seters 1922) directly in front of the *planum trabeculae anticum*. According to Pusey (1943) and van Eeden (1951), a similar ligament in *Ascaphus* stretches from the lower edge of the *commissura quadratocranialis anterior* to the line of fusion of the trabecular horn with the median suprarostral plate. The *processus quadrato-ethmoidalis* may be absent in *Megalophrys montana* according to Kruijtzer (1931 *ex* Ramaswami 1943), but is reported as being present by Ramaswami (1943). The connection between the *processus quadrato-ethmoidalis* and *cornu trabeculae* may be cartilaginous (Ramaswami 1940) and in *Rana hexadactyla* it is the earliest cartilaginous connection of the palatoquadrate with the ethmoidal region. The ligament between the *processus quadrato-ethmoidalis* and *cornu trabeculae* is absent in *Breviceps* (Swanepoel 1970).

There is much confusion in the use of some of these terms. Whereas most authors used the term "*processus pterygoideus*" in agreement with Gaupp (1893), others (e.g., N. G. Stephenson 1951) used it for the connection of the palatoquadrate to the *trabecula*, i.e., as a synonym of the *commissura quadratocranialis anterior*. De Jongh (1968) used it as a synonym of the *processus quadrato-ethmoidalis* in the later developmental stages of *Rana*.

In *Xenopus*, there is a slender bar extending between the palatoquadrate and the outer angle of the ethmoidal region, at the base of the tentacle. This bar was termed the quadrato-ethmoidal cartilage by Paterson (1939, her plate 13, figure 23). This cartilage and the tentacular cartilage are both resorbed later, and neither of them is apparent at the end of metamorphosis. It is not clear whether the quadrato-ethmoidal cartilage is homologous with the *ligamentum cornu-quadratum posterior* or with some other ligamentous connection between the palatoquadrate and the ethmoidal region in other anurans.

Another ligament, besides the *ligamentum cornu-quadratum posterior*, appears during metamorphosis in *Rana*. It also inserts on the *processus quadrato-ethmoidalis* and runs to the dorsal side of the *pars quadrata palatoquadrati* (de Jongh 1968).

In contrast to the *ligamentum cornu-quadratum posterior*, the *ligamentum cornu-quadratum anterior* ("*ligamentum cornu-quadratum*" of de Jongh [1968, his figure 7]; probably the "prenarial ligament" of Parker [1876, his plate 55, figure 3] which may be cartilaginous in *Xenopus*) stretches anteriorly between the *pars quadrata palatoquadrati* and the *cornu trabeculae* lateral to the latter's articulation with the suprarostral. In *Heleophryne*, there is a ligament called the *ligamentum cornu-quadratum laterale* that connects the *pars quadrata* with the anterior lateral wing of the internasal plate (van der Westhuizen 1961). In *Xenopus*, there is a process called the *processus cornu-quadratum lateralis* in this location (see Sedra and Michael [1957, their figure 3]; Trueb and Hanken [1992]). The *ligamentum cornu-quadratum anterior* is independent of the *suprarostrale* in *Rana* (Pusey 1938) but in *Ascaphus* it is attached to the lateral wing of the *suprarostrale* (Pusey 1943; van Eeden 1951); a similar condition is also found in *Caudiverbera* (Reinbach 1939a). Because it is stretched between the anterior part of the palatoquadrate *(pars quadrata)* and the anterior part of the trabecular horn, close to the opening of the larval mouth, the *ligamentum cornu-quadratum anterior* was called the *ligamentum circumoralis* by Sokol (1981, his figure 2) and "lateral circumoral ligament" by Cannatella (1999, his figure 4.4), whereas Reinbach (1939a) termed it the *ligamentum quadratosuprarostrale*, because of its attachment to the lateral process of the upper labial cartilage.

In *Rana*, on the posterior surface of the *commissura quadratocranialis anterior*, close to the *trabecula*, there can be another outgrowth that Gaupp (1893) called the *processus pseudopterygoideus* (Fig. 6). This is a temporary structure that disappears before, or at the beginning of, metamorphosis. Several structures described in various other taxa have been designated by this term. However, it is not clear whether they are all homologous with the original structure reported by Gaupp. Haas (1995, 1996a, his figures 4, 11, 1996b, his figures 2–4), Hall and Larsen (1998), and some others reported on an obviously homologous structure in species not closely related to *Rana*. By contrast, Reinbach (1939a, his table 13, figure 1) used this term for a process running from the posterior part of an outgrowth arising from the medial margin of the palatoquadrate at the level of the *processus muscularis*; this structure disappears completely later in development. The pseudopterygoid process is absent altogether in some other anuran species (e.g., *Bufo regularis*, Sedra [1950]; *Breviceps*, Swanepoel [1970]).

Located on the ventral surface of the *commissura quadratocranialis anterior* of *Heleophryne* and of some other anurans, is still another process that Ramaswami (1944) called the *processus neutralis*. It is not homologous with the *processus hyoquadratus*. It contributes to the articulation between the palatoquadrate and the *ceratohyale*.

During the development of *Ascaphus*, the midsection of the palatoquadrate becomes detached from the braincase by enchondral destruction, starting from the canal for the ophthalmic nerve. As a consequence, the subocular vacuity ("*fenestra subocularis*" of Stöhr 1882) develops. In *Rana*, a membrane called the *membrana subocularis* (Gaupp 1893) stretches over the subocular vacuity and serves as a surface for the insertion of muscles. The destruction of the palatoquadrate does not reach all the way forward. At its anterior end the palatoquadrate remains fused with the *trabecula* by means of the *commissura quadratocranialis anterior*.

Later, the larval palatoquadrate is subject to two processes. The proximal part of the *commissura* becomes destroyed, so that its connection with the wall of the braincase is interrupted (van der Westhuizen 1961; de Jongh 1968; Hall and Larsen 1998; Reiss 1998). This proceeds simultaneously with the appearance of the *lamina orbitonasalis*. Also, in *Rana* (de Beer 1937; Plasota 1974a) and *Discoglossus*, the *commissura* loses its contact with the wall of the braincase and becomes attached to the developing postnasal wall (also see Wiens 1989). At the point where the *commissura* bends anteromedially, there arises a strip of mesenchyme that is directed anteriorly to the most lateral corner of the nasal capsule. Although later chondrified, this structure is distinguishable from the nasal capsule and from the *commissura* (Gaupp 1893; van Eeden 1951, his figure 16; Swanepoel 1970). It is the *processus maxillaris posterior* ("quadrato-ethmoidal connexion" of Ramaswami [1940]). Sewertzow (1891) observed two parallel connections of the palatoquadrate in late larval stages of *Pelobates*; he termed these connections the nasal and pterygoid parts.

Only in the course of subsequent development does the *processus maxillaris posterior* fuse with the nasal capsule anteriorly, and with the anterior portion of the *commissura* posteriorly (Fig. 31) (but see van der Westhuizen [1961] who maintained the *processus maxillaris posterior* to be an outgrowth of the *lamina orbitonasalis*). This new synchondrotic connection was interpreted by Hall and Larsen (1998) in *Scaphiopus* as a connection of the "distal portion of the quadratoethmoid process (now identified as the adult pterygoid process) and the ventrolateral and posteriorly oriented extension of the antorbital plane, the posterior maxillary process". Where these structures come into contact there arises a foramen (de Jongh 1968, his plate 13; Swanepoel 1970; Kraemer 1974) called the lateral orbitonasal foramen by Hall and Larsen (1998, their figure 7). Through this foramen the *ramus communicans* ("*ramus postchoanalis*" of Swanepoel [1970]) passes between the *ramus maxillaris* V and the *ramus palatinus* VII. Later, when the *lamina orbitonasalis* and the *processus maxillaris posterior* coalesce this nerve is either enclosed in a foramen or lies in a groove. In post-metamorphic anurans, or in those in advanced stages of metamorphosis, the nerve either runs free with only its course indicating the former line of coalescence of skull elements (e.g., *Ascaphus*; van Eeden 1951) or passes through a foramen (e.g., *Caudiverbera* [Reinbach 1939a] and *Xenopus* [Sedra and Michael 1957]). Reinbach (1939a) distinguished two nerves in this area, namely (1) the "*ramus communicans cum nervo palatino des nervus maxillaris*", passing through a slot between the *commissura quadratocranialis anterior* and the *processus maxillaris posterior*, and (2) what he termed the "*ramus praechoanalis nervi maxillaris*" or "*ramus palatonasalis des nervus maxillaris*". Whereas the first nerve runs over the medial surface of the former *processus maxillaris posterior* in the adult (because the *commissura*

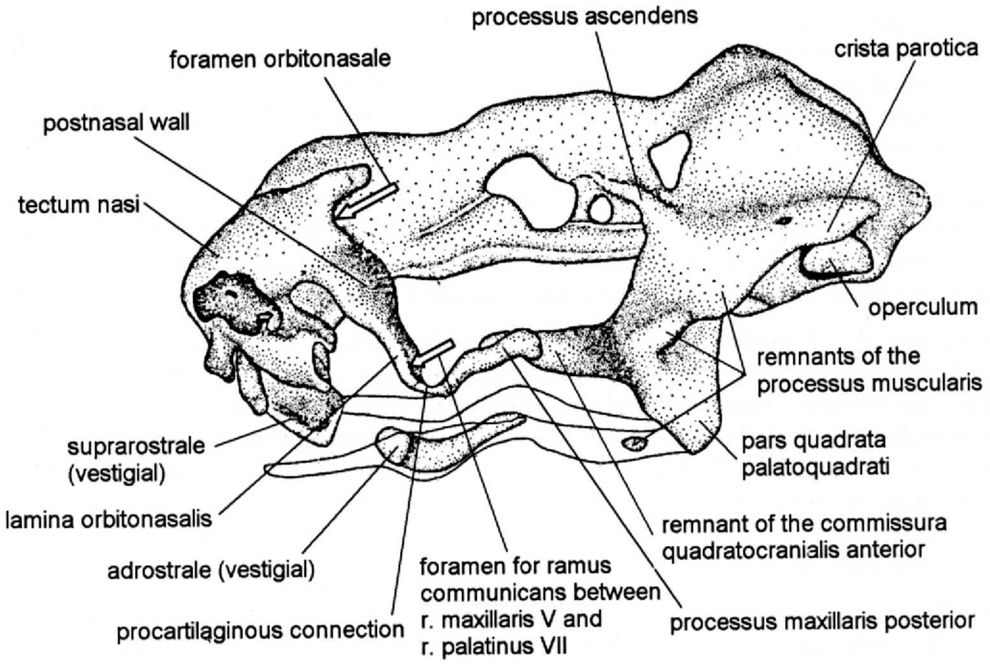


Fig. 31. Left lateral view of the chondrocranium of an advanced metamorphic stage of *Ascaphus*, showing the composition of the subocular bar and the topographic relations of the palatoquadrate. From van Eeden (1951).

quadratocranialis has disintegrated), the second runs through a canal. The condition seems to be highly variable (the second nerve may be lacking on one side of an individual; see Reinbach [1939a]) and it is difficult to determine which branch is homologous with the branch usually designated as the "*ramus communicans*" in other anurans.

Later, the contact of the *commissura* with the nasal capsule is also interrupted (de Beer 1937; de Jongh 1968; Swanepoel 1970; Kraemer 1974). The detachment of the wall of the braincase and the anterior part of the palatoquadrate is a common feature of anuran development (Jurgens 1971; Plasota 1974a). However, de Beer (1937) expressed the view that the pterygoid process of the palatoquadrate in anurans may fuse with the ethmoid capsule, and Reinbach (1950b) maintained that the adult postnasal wall included the *commissura quadratocranialis anterior*. After the destruction of the proximal portion of the *commissura*, the subocular bar connecting the *pars quadrata palatoquadrati* with the nasal capsule consists of the residual *commissura* posteriorly ("pterygoid" and "palato-pterygoid process" of Winslow [1898]; "*processus pterygoideus*" of Gaupp [1893]; "*cartilago pterygoidea*" of Reinbach [1939a]) and the *processus maxillaris posterior* anteriorly. The contact is clearly discernible histologically (de Jongh 1968). Sokol (1962) correctly noted that the *commissura quadratocranialis anterior* "gives rise to the *processus pterygoideus palatoquadrati* in adults" thereby indirectly confirming that the two structures are synonymous. Similarly, Swanepoel (1970) confirmed that the ventral part of the *commissura* remains intact and forms the pterygoid process that connects the *pars quadrata* and the *lamina orbitonasalis*. His "subocular bar" involves the *commissura quadratocranialis anterior* and the *processus maxillaris posterior*. In contrast, some authors, such as de Beer (1937) and Ramaswami (1940) followed Gaupp (1893) in designating the subocular bar in adults as the pterygoid process, thereby incorrectly considering the *commissura quadrato-cranialis* to be completely lost; Okutomi (1937) explicitly mentioned the "connection of the *processus pterygoideus* and the *processus maxillaris posterior*".

Hence, the original, simple, medial connection of the anterior section of the palatoquadrate, by means of the *commissura quadratocranialis anterior*, was functionally substituted by the lateral one present in adult anurans. Besides the vestigial *commissura*, the latter also includes the *processus maxillaris posterior* and is therefore a composite structure (Fig. 23). Only in *Hymenochirus* (Paterson 1945, her figures 1, 2) is the adult subocular bar incomplete, probably because the *processus maxillaris posterior* failed to fuse with the residual *commissura*.

The second process relates to the position of the palatoquadrate. The originally horizontal subocular part is shortened by means of resorption from its posterior side (Gaupp 1893) and then rotates posteroventrally, passing through the vertical plane to ultimately attain an oblique posteroventral position (Fig. 32). As a consequence, the jaw joint (articulation between the *pars quadrata palatoquadrati* and the articular portion of Meckel's cartilage) is shifted below the level of the *foramen ovale*. This shift of the *pars quadrata* beneath the otic capsule is accompanied by an increase in the length of the originally anterior connection of the palatoquadrate to the walls of the braincase (Roček 1981, his figures 22, 24; Wassersug and Hoff 1982, and references therein). Consequently, the horizontal subocular bar of adult anurans may be considered homologous with the vestigial *commissura quadratocranialis anterior*. This also is true in *Xenopus* (see Trueb and Hanken 1992). Generally, this bar is called the *processus pterygoideus palatoquadrati* or the *pars pterygoidea palatoquadrati*.

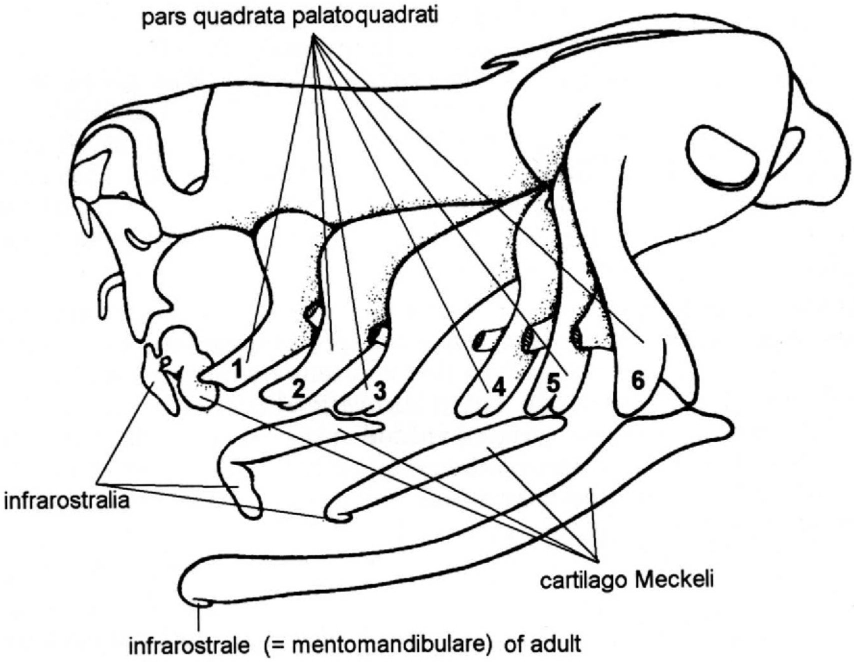


Fig. 32. Composite semi-diagrammatic representation of the six developmental stages (indicated by numbers) in the backward rotation of the palatoquadrate during metamorphosis in *Bufo regularis*. The position of the palatoquadrate in the earlier stages is shown as if overlapped by later ones. The *commissura quadratocranialis anterior* is cut away and only its basal part is illustrated. The lower jaw is illustrated in only four stages. The outline of the neural endocranium is that of the last developmental stage. After Sedra (1950).

The early developmental stages of the palatoquadrate are suppressed in those anurans with abbreviated larval development (e.g., *Eleutherodactylus nubicola*; Lynn 1942, his figures 25–30) and the palatoquadrate develops as a free element consisting of horizontal and vertical components (Fig. 25). The horizontal component (vestigial *commissura quadratocranialis anterior*) later fuses with the posteriorly-directed *processus maxillaris posterior*, thereby establishing the subocular bar, i.e., a connection between the lateral part of the postnasal wall and the quadrate portion of the palatoquadrate, as in other anurans. The vertical component (the palatoquadrate itself) fuses to the anterior portion of the *crista parotica* by means of the adult *processus oticus* (Lynn 1942, his figure 31). Thus, the development of the anterior connection of the palatoquadrate is the same as in other anurans, except for early stages when the *commissura quadratocranialis anterior* is attached to the wall of the braincase and to the *lamina orbitonasalis*.

C. Posterior Connections of the Palatoquadrate

As mentioned above, the posteromedial end of the early larval palatoquadrate becomes connected medially to the *pila antotica*; this part of the palatoquadrate is termed the *processus ascendens* (*sensu* Stöhr 1882; "*pediculus*" or "pedicle" of Parker [1876, his plate 55, figure 3]; "*cartilage craniofacial*" of Dugès [1834]; "*oberste Abteilung des zweiten Visceralbogens*" of Reichert [1838]; "*Schläfenflügelknorpel*" of Goette [1875] "*apophyse ascendente*" of van Seters [1922]). The ascending process has specific topographic relations to the branches of the *nervus trigeminus*; the *nervus profundus V* passes forward ventromedially to it and the *ramus maxillaris V* and *ramus mandibularis V* dorsolaterally to it (van der Westhuizen 1961). In *Leiopelma*, the ascending process is pierced by the *ramus mandibularis V* (N. G. Stephenson 1951). Between the *processus ascendens* and the anterior wall of the otic capsule is a passage carrying the *vena jugularis interna*. The ascending process also serves as an insertion area for attachment of the eye muscles (van Seters 1922). It never forms in some anurans in which the free-living larval stages are suppressed (e.g., *Eleutherodactylus coqui*; Hanken *et al.* 1992).

Later, another connection to the otic capsule is established posteriorly. The connection is to the anterior part of the *crista parotica* by means of the larval *processus oticus* (*sensu* Parker [1876]; "*primäre processus oticus*" of Gaupp [1893]; "primitive otic process" of Sokol [1981]). According to Sokol (1981) the larval otic process is the chondrified otic ligament. This ligament (termed the quadrato-otic ligament by Sedra [1950, his plate 1, figures 2,3 and plate 2, figure 4] and the "otic ligament" by Sokol [1981], runs backward along the ventrolateral surface of the capsule and above the *fenestra ovalis* (see also Ramaswami 1944; van der Westhuizen 1961, his figure 11). It should be noted that this ligament is not homologous with the "quadrato-otic ligament" of Ramaswami (1944) that runs in adults between the bottom of the otic capsule and the posterior part of the palatoquadrate shifted as far as the level of the posterior wall of the capsule.

In the larvae of some anurans (e.g., *Caudiverbera*; Reinbach 1939a), the *crista parotica* projects anterolaterally as the *processus anterolateralis capsulae auditivae*. This projection resembles the chondrified otic ligament in that it is only temporary and disappears during the course of later development. In larval *Ascaphus* also (Reiss 1997), the connection between the otic capsule and the palatoquadrate involves chondrification of connective tissue. In *Breviceps*, the anterior part of the *crista parotica* is interpreted as the upper part of the otic process fused on to the lateral wall of the otic capsule (Swanepoel 1970).

The ascending process no doubt occurs in the majority of larval Anura. However, Haas (1995) followed earlier authors (e.g., Ramaswami 1944) in maintaining it to be absent in *Heleophryne*, *Otophryne*, and *Philautus*. Swanepoel (1970) did not find it in *Breviceps*, nor did Lynn (1942) in *Eleutherodactylus*. Ramaswami (1938, 1944) did not exclude its absence in larval *Philautus* (but cf. van der Westhuizen 1961). In *Ascaphus*, the *processus ascendens* is almost completely ossified (van Eeden 1951).

The occurrence of the otic process is variable in anuran larvae. In some, e.g., *Heleophryne* (Ramaswami 1944), the quadrato-otic ligament and the otic process are both present, each of which separately assists in connecting the palatoquadrate to the otic capsule. The otic process is absent in *Bufo* (Ramaswami 1940; Sedra 1950; Barry 1956), *Rana curtipes* (Ramaswami 1940), *Alytes* (Peeters 1910; van Seters 1922), *Discoglossus* (Pusey 1938), *Philautus* (Ramaswami 1938), *Polypedates* (Okutomi 1937), *Pseudophryne*, *Crinia* (Jacobson 1968), and *Flectonotus* (Haas 1996b), and closely approaching but not articulating with the otic capsule in *Scaphiopus* (Hall and Larsen 1998). Provided that the otic process is actually the chondrified quadrato-otic ligament, its absence or underdevelopment may be dependent on the larval stage being examined. By contrast, in adults the otic process is invariably present (see below) which means that it can arise at different stages of development.

The ascending and descending processes are separated from each other by a distinct slot called the *incisura posterior palatoquadrati* (Roček 1981). Another configuration, known in *Ascaphus* (Reiss 1997) consists of these two processes broadly fused. Sokol (1962) found probable homologues of the ascending and larval otic processes in *Hymenochirus*, but which were not directly connected to the palatoquadrate.

In the Pipidae, the posterior connections of the palatoquadrate arise in a different way. In the early stages of *Xenopus* (Kotthaus 1933, his figure 1), the palatoquadrate is represented by a thin, posteriorly-free bar on its anterior quadrate portion. A moderately later stage was recorded by Trueb and Hanken (1992, their figure 2); this bar (called the "subocular bar") points toward a new, isolated cartilaginous element located lateral to the *trabeculae*, and at the level where the *trabeculae* bend laterally. This element was called the "ventrolateral process" by Trueb and Hanken (1992, their figure 2) in conformity to the term *processus ventro-lateralis quadrati* used by Sedra and Michael (1957, their figures 1, 3, 5). This process later fuses with the braincase medially and with the subocular bar anteriorly. The latter fusion is by means of an anteriorly-directed process arising on the anterior margin of the medial connection (Trueb and Hanken 1992, their figure 3). A process arises from the posterior margin of this medial connection and later becomes attached to the anterior wall of the otic capsule (Kotthaus 1933, his figure 4). These are the reasons why the medial connection was homologized with the ascending process, and the posterior one with the larval otic process (also see Ramaswami 1940). The so-called ventrolateral process is restricted to the expanded ventrolateral portion which becomes more pronounced in the later stages of development. This description of the early stages indicates that the ascending process becomes attached to the *trabecula* before the *pila antotica* arises (Trueb and Hanken 1992) but long after the *commissura quadratocranialis anterior* appears; both these sequences are reversed in non-pipids.

The posterior end of the ventrolateral process of *Xenopus* later produces a thin commissure with the anterior part of the *crista parotica* (Sedra and Michael 1957, their figure 5); this process is lateral to the larval otic process. Thus, a second, parallel connection with the *crista parotica* is established. It should be noted that Pusey (1943) also found in *Ascaphus* two connections of the palatoquadrate with the otic capsule, instead of one.

During metamorphosis in *Rana*, but in much earlier larval stages in *Heleophryne* (van der Westhuizen 1961) the *processus ascendens* breaks down and disappears at approximately the same time as the anterior part of the *commissura quadratocranialis anterior* disintegrates and detaches from the postnasal wall. A presumed exception to this process is found in *Ascaphus* (Pusey 1938; van Eeden 1951; but cf. Reiss 1997). In *Leiopelma*, the lower part of the ascending process detaches from the palatoquadrate and secondarily fuses to the capsular wall (N. G. Stephenson 1951, her figure 9). A similar situation is found in *Spea*, in which the *processus ascendens* was described as though it changed its attachment from the braincase to the anterolateral surface of the otic capsule (Wiens 1989).

The larval otic process may persist only until the end of metamorphosis when its connection with the *crista parotica* is eroded, so that the outer edge of the *crista* is devoid of perichondrium for some time. In a few cases (e.g., *Leiopelma*) the larval otic process remains unbroken and the otic process retains its continuity throughout development (N. G. Stephenson 1951). Swanepoel (1970) reported that in *Breviceps* the otic process was only partly resorbed during remodelling of the palatoquadrate.

The adult *processus oticus* ("*processus oticus definitivus*" of Reinbach [1939a]) develops in front of the former larval process (also see Reiss 1997) and appears as an outgrowth from the lateral semicircular canal (Ramaswami 1935). According to Gaupp (1893), in *Rana* it arises during metamorphosis as a derivative of the otic capsule. Its lower part seems to re-chondrify in the mass of cartilage cells liberated by the erosion and disintegration of the larval otic process and the posterior portion of the palatoquadrate (van der Westhuizen 1961). Although its juvenile cartilage is histologically distinguishable from the older cartilage of the larval otic process, no perichondrium intervenes between them (van der Westhuizen 1961). In *Caudiverbera*, the *processus oticus* appears at the site where the *processus anterolateralis* of the *crista parotica* had developed in an earlier larval stage (Reinbach 1939a). In *Leiopelma* the continuity of the larval and adult otic processes shows that during metamorphosis the otic process turns backward and begins to form the *crista parotica*. In other words, the *crista parotica* represents a backward extension of the otic process (N. G. Stephenson 1951), a condition that also may be common in other anurans (Fig. 26).

The secondary connection of the palatoquadrate with the otic capsule is established as a result of backward displacement and rotation of the palatoquadrate and its *processus muscularis*. These come into contact with the *crista parotica* to form the definitive otic process. The otic process maintains the same relations to nerves and other structures as did its predecessor (de Beer 1937). The *pars quadrata*, however, acquires a new attachment to the otic capsule. Hence, in adults the cartilage of the *crista parotica* is a derivative of the palatoquadrate. The *crista parotica* is intimately associated with the otic capsule in most anurans. *Ascaphus* and *Leiopelma* (de Villiers 1936) may be exceptions although de Beer (1937) maintained that even in *Ascaphus* the otic process is fused with the *crista parotica*.

In those anurans in which the larval otic process is absent, e.g., *Alytes* (de Beer 1937), the section of the palatoquadrate posterior to the *processus muscularis* shortens and ultimately is resorbed, so that its vestigial remnant is located next to the lateral wall of the otic capsule; the *pars quadrata* is located below the lateral part of the otic capsule. Only at this stage is the palatoquadrate-otic connection established.

During metamorphosis in *Xenopus* the ventrolateral process, subocular bar, *processus ascendens*, and *processus oticus* become eroded and later the entire posterior part of the palatoquadrate disappears. The anterior part migrates posteriorly beneath the eye and then posterodorsally to become associated with the anterolateral corner of the otic capsule. The elongated vestigial *commissura quadratocranialis anterior* forms the subocular bar as in other anurans. A spur of cartilage develops from the dorsolateral aspect of its posterior part where it is underlain by the pterygoid process of the palatoquadrate. This spur was called the "zygomatic spur of the pterygoid process" by Trueb and Hanken (1992) because it serves as a point of articulation with the *ramus paroticus* ("zygomatic ramus") of the squamosal. However, it is obvious that this is a re-established connection between the palatoquadrate and the anterior part of the *crista parotica* and, consequently, of the otic process of adults (also see Sedra and Michael 1957).

There is still another connection between the palatoquadrate and the otic capsule. According to de Beer (1937) in reference to observations by Gaupp (1893), this connection arises only during metamorphosis in most anurans. Exceptionally, it is present in larvae as a block of cartilage beneath the anterior end of the otic capsule, e.g., in *Heleophryne* (van der Westhuizen 1961), *Ascaphus* (van Eeden 1951; Reiss 1997), *Rana curtipes* (Ramaswami 1940), and *Rana afghana* (Ramaswami 1943); also see Swanepoel (1970). It fuses both with the *pars quadrata* of the palatoquadrate and with the floor of the otic capsule. Gaupp (1893) called it the *processus basalis* (also see Ramaswami 1935; Reinbach 1939a); it is the "palatobasal connection" of Reiss (1997) but probably not the "hyobasal process" of Swanepoel 1970).

The *ramus palatinus VII* passes downwards in front of this process, whereas the *ramus hyomandibularis VII* runs backwards and downwards over it and then descends (Gaupp 1893; van der Westhuizen 1961). Because of these topographic relations, de Beer (1926) claimed that the *processus basalis* cannot be held as a true basal connection and he proposed the term "pseudobasal connection" instead. However, Shishkin (1973) pointed out the instability of ganglion VII (see also de Villiers 1934) and rejected reasons given by de Beer for distinguishing piscine and anuran basal processes. Reiss (1997) pointed out that the *processus basalis* (his "palatobasal connection") forms in early larval *Ascaphus* from a mesenchymal strand connecting the anterior end of the basiotic lamina with the palatoquadrate below the facial ganglion; at this stage, the *ramus palatinus VII* passes down from the ganglion in front of this connection, whereas in older larvae it passes through a foramen in the base of this connection. This developmental pattern confirms the view that this connection is indeed the true *processus basalis*.

The *processus basalis* is originally part of a connection between the palatoquadrate and the *trabecula*, called the basal or palatobasal connection. This structure is of double origin; its proximal part arises from the base of the neurocranium (floor of the otic capsule in adults), whereas its distal part (the basal process) re-chondrifies from cells liberated by the destruction of the posterior part of the palatoquadrate. These two parts soon fuse with each other (also see E. M. Stephenson 1951), but a discontinuity and a joint is formed between the basal process and the otic capsule in some anurans, e.g., in *Rana* (Gaupp 1893; de Beer 1937).

In *Alytes* and *Megophrys*, the basal process arises as an independent chondrification; however, it is attached by mesenchyme to the plectrum or to a process that projects from the ventral edge of the *fenestra ovalis* (de Beer 1937). The basal articulation gives off a dorsal process that stretches up and adjoins the *crista parotica* immediately medial to the otic process. This dorsal process was termed the laterohyal by Kruijtzer (1931) and homologized with isolated nodules of cartilage found in the same position in *Pipa*.

In *Heleophryne*, the larval basal process stretches between the hind border of the *fissura prootica* and the anterior edge of the *fenestra ovalis* (van der Westhuizen 1961). The larval process undergoes enchondral erosion but its perichondrium remains intact; gradually cells occupying the same position replace those of the larval basal process to reconstitute another process called the adult basal process by van der Westhuizen (1961, his figure 27). At no stage of its development does the adult basal process fuse with the floor of the capsule (van der Westhuizen 1961) as it does in *Rana* (Pusey 1938) and *Bufo* (Ramaswami 1937).

With a few exceptions, e.g., *Rhinophrynus* (Trueb and Cannatella 1982), it seems that the basal process arises fundamentally in the same way in all anurans that possess this structure. However, there are differences in the timing of its appearance. In some genera it develops in larvae; in the majority, however, it arises during metamorphosis as the last connection of the palatoquadrate.

The basal process has been described in *Bombina* (Slabbert 1945) and *Xenopus* (Trueb and Hanken 1992) although it is not clear if it arises as an independent chondrification in the latter. Note, however, that Paterson (1939) maintained the basal process to be absent in *Xenopus*. This structure has also been reported as absent in *Breviceps* (Swanepoel 1970) and *Litoria* (Haas and Richards 1998).

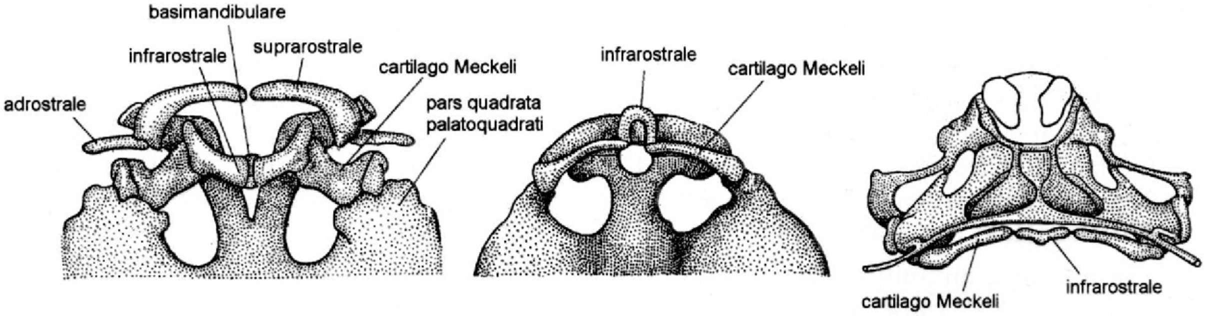
In *Breviceps*, an anuran with suppressed larval development, the backward rotation of the palatoquadrate causes it to come into contact with the otic capsule (as in other anurans) and it is secondarily applied to the capsule's anteroventral wall. This part of the capsule's wall is usually called the "otic ledge" (van der Westhuizen [1961, his figure 27]; also called the "auditory ledge" by van Eeden [1951], the "otical shelf" by Jarvik [1954], and the "otohyoid ledge" by Swanepoel [1970]). Between the palatoquadrate and the otic ledge is a mesenchymatous mass, the ventral part of which subsequently chondrifies and fuses with the palatoquadrate, whereas the dorsal part remains unchondrified during larval development, and chondrifies only during metamorphosis (Swanepoel 1970). This dorsal part originates from the same tissue as the otic ledge and *pars interna plectri* and is therefore derived from the upper end of the hyoid arch. Swanepoel (1970) considered this connection not to be homologous with the basal articulation of other anurans and he proposed the name "hyobasal articulation" to designate it. The otic ledge and otic process are separate in larvae but fuse at metamorphosis.

Finally, Reinbach (1939a, his figures 11, 12) described a connection of the *pars quadrata palatoquadrati* with the otic capsule in adult *Caudiverbera* that he called the *processus endopterygoideus* (or *cartilago endopterygoidea*). It is a robust, medial outgrowth from the *processus basalis*, extending from beneath the anterior part of the otic capsule to the lower margin of the *fissura prootica*. It is enclosed by the medial branch of the pterygoid.

D. *Cartilago Meckeli* and Associated Cartilages

The *cartilago Meckeli* ("*androstrale inférieure*" of Dugès [1834]; "articulo-Meckelian rod" of Parker [1876]; "posterior jaw cartilage" of Pusey [1838]; "*mandibulare*" of Reinbach [1939a]) and the lower labial cartilage are among the earliest parts of the skull observable in *Rana*; they appear even before the *trabeculae cranii* (Stöhr 1882; Spemann 1898, his plate 28, figure 2). In early larval development, Meckel's cartilage and the infrarostral cartilage are confluent and the latter is only distinguishable later (although still not separated). The early larval connection between these two elements may be preserved in some taxa as the cartilaginous confluence of the dorsomedial process of Meckel's cartilage with the lower labial cartilage; this confluence was called the *commissura intramandibularis* by Haas (1996b, his figure 4).

Meckel's cartilage and the infrarostral cartilage, as well as the palatoquadrate, arise from a single mesenchymatous primordium. However, Okutomi (1937) could distinguish Meckel's cartilage, the palatoquadrate, and the lower labial cartilage as distinct condensations of mesenchyme in early development. Trueb and Hanken (1992) observed that although the infrarostral is distinct from Meckel's cartilage in *Xenopus*, these cartilages later fuse. According to Swanepoel (1970) and Nikitin (1986) Meckel's cartilage arises from two chondrification centres. Chondrification proceeds from the symphysial region posteriorly and from the articular region anteriorly. Also, Jacobson (1968) mentioned that in *Pseudophryne* Meckel's cartilage (his "posterior jaw cartilage") consists of two separate elements, the inner and the outer, and that the inner fuses with the infrarostral (his "anterior jaw cartilage"). However, in the context of his other statements he may have been dealing with elements of the hyobranchial apparatus. The larval *cartilago Meckeli* is a transverse, robust cartilage articulating with the *pars quadrata palatoquadrati* posteriorly, and with the *infrarostrale* anteriorly (Fig. 33). The articular portion may ossify as the *os articulare* in *Leiopelma* (E. M. Stephenson 1951), *Petropedetes* (du Toit 1943), *Xenopus* (Stadtmüller 1936), and *Pipa* (Parker 1876), and in hyperossified anurans such as *Caudiverbera* (Reinbach 1939a).



Pelobates fuscus **Microhyla inornata** **Xenopus laevis**

Fig. 33. Larval lower jaw in ventral view (*Pelobates* and *Microhyla*) and anterior view (*Xenopus*), showing Meckel's cartilage and the infrarostral cartilages. From Nikitin (1986).

The *infrarostrale* ("*rostrale inférieure*" of Dugès 1834]; "inferior labial" of Parker [1876]; "*cartilago labialis inferior*" of Gaupp [1893]; "anterior jaw cartilage" of Pusey [1938]) develops as an independent centre of chondrification (van Seters 1922; Okutomi 1937). The lower labial cartilages, like the upper ones, are absent as functional larval jaws in anurans with suppressed larval development, for instance *Eleutherodactylus nubicola* (Lynn 1942) and *Pipa pipa* (Trueb *et al.* 2000). Infrarostral cartilages are also absent in *Leiopelma* (N. G. Stephenson 1951). The infrarostrals remain separate from one another as in *Pelobates* (Sewertzow 1891) or may be fused with little evidence of being paired, as in *Xenopus* (de Beer 1937; Trueb and Hanken 1992); obviously, this reflects the condition of the suprarostrals in non-pipids. Finally, the infrarostrals ossify as the *mentomandibulare* ("*mentum*" or "mento-Meckelian bone" of Parker [1876]; "*dentale*" of Dugès [1834]; "*pars mentalis*" of Gaupp [1893]; "*os mentomandibulare*" of Reinbach [1939a]) and coalesce with the *dentale*.

The lower labial cartilages become interconnected by a small unpaired cartilage (Fig. 33) (Reinbach 1939a, his figure 14), termed the *basimandibulare* (*sensu* Ridewood [1898]; "mandibular copula" of Gaupp [1893], de Beer [1937], Jacobson [1968], and Nikitin [1986, his figure 1A]; "*copulare*" of Reinbach [1939a, his figures 14, 17, 18]; also see Sedra [1950, his plate 3, figure 1A]); this connection arises simultaneously with the fusion of the upper labial cartilages with each other. The unpaired basimandibular cartilage may become a fibrous tissue after metamorphosis (Gaupp 1893) and remains movable even in adults, thus forming the symphysial articulation between the two halves of the lower jaw (Reinbach 1939a). The ligament connecting the *cartilago Meckeli* with the *infrarostrale* is called the *commissura intramandibularis* (Sedra 1950).

The *pars quadrata* projects anteriorly, parallel to the trabecular horns, in the larval cranium. It articulates with Meckel's cartilage so that the latter acquires a somewhat transverse position. However, in pipids and in anurans with suppressed early larval stages and metamorphosis, Meckel's cartilage is already an elongated element that despite its articulation with the *pars quadrata palatoquadrati*, is approximately in the same location as in adult anurans, i.e., directed anteriorly and not transversely (Lynn 1942, his figures 25, 27).

There is an additional, distinct cartilage found adjacent to the lower part of Meckel's cartilage in pre-metamorphic *Pelobates*, *Heleophryne*, *Alytes*, and *Bombina*. This is called the *admandibulare* (*sensu* van Seters 1922; "*paramandibulare*" of Peeters [1910] ex van Seters [1922]; "sub-meckelian cartilage" of Ramaswami [1944]; "*ceratopraemandibulare*" of Roček [1981, his figures 15, 18]). It is later reduced and ultimately disappears before the end of metamorphosis (also see van Seters 1922; van der Westhuizen 1961; Maglia and Púgener 1998). Approximately the same position is held by the "tentacular cartilage" in *Xenopus* (de Beer 1937) but this structure is attached to the palatoquadrate at the anterior edge of the *processus muscularis*.

During metamorphosis, the subocular bar, consisting of the *processus maxillaris posterior* and the *commissura quadratocranialis anterior* forms and lengthens. Simultaneously with this event, Meckel's cartilage also becomes long and slender (Fig. 34). On its anterior end,

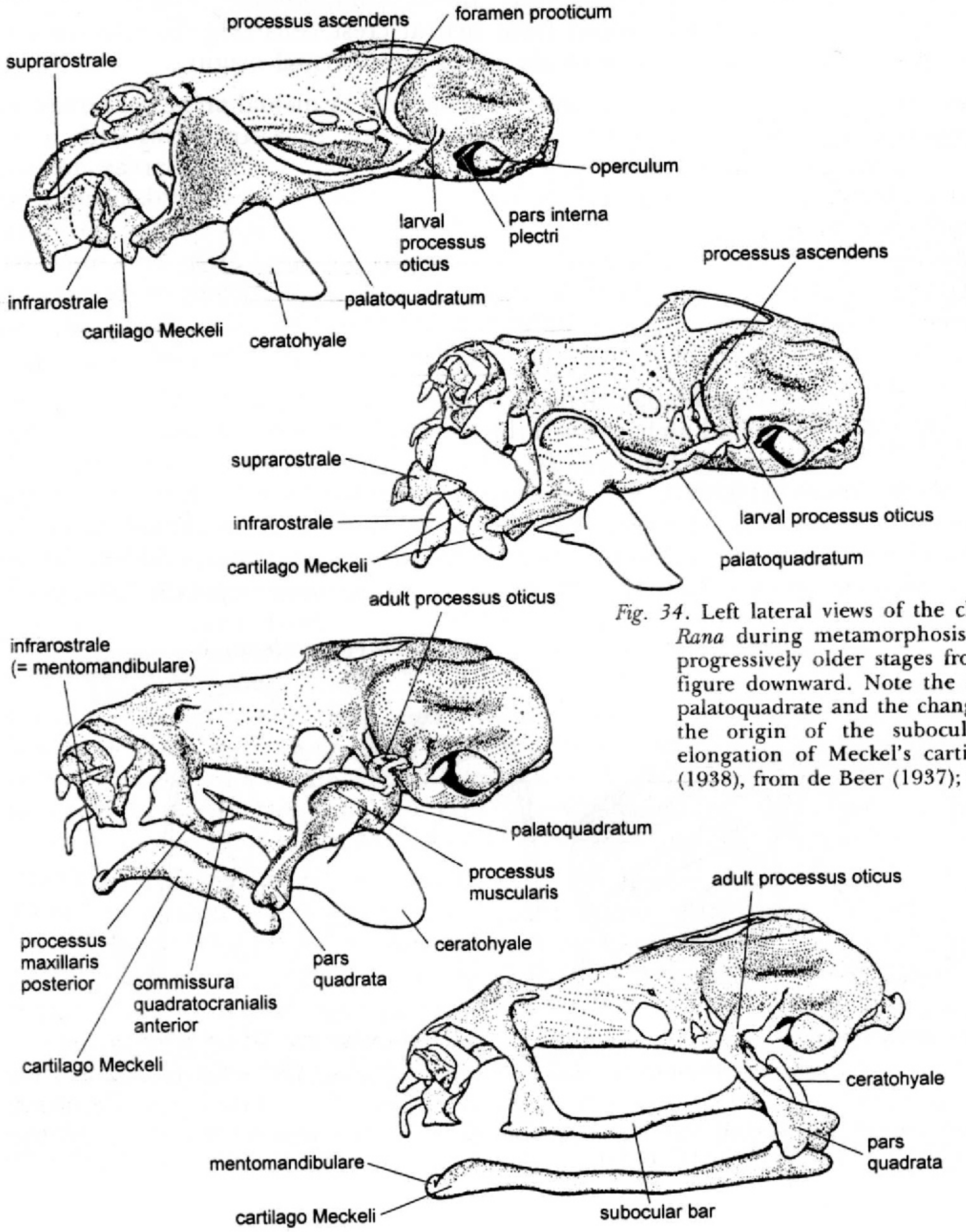


Fig. 34. Left lateral views of the chondrocranium of *Rana* during metamorphosis. Drawings are of progressively older stages from the top of the figure downward. Note the shortening of the palatoquadrate and the changes in its position, the origin of the subocular bar, and the elongation of Meckel's cartilage. After Pusey (1938), from de Beer (1937); also see Figure 1.

the infrarostral becomes fused as a direct anterior prolongation of Meckel's cartilage (e.g., Gaupp 1893) and the basimandibular becomes a movable, fibrous intramandibular articulation. Finally, the infrarostral cartilage ossifies as the mentomeckelian bone (also see Hall and Larsen 1998) and acquires synostotic contact with the anterior end of the dentary. By contrast, Meckel's cartilage usually remains cartilaginous, with only its articular part ossifying. Even the articular part remains cartilaginous in adult *Bombina* (Slabbert 1945).

VI. HYOBRANCHIAL SKELETON AND DEVELOPMENTAL ORIGIN OF THE HYOID

The hyobranchial skeleton basically consists of the paired set of postmandibular branchial arches. To properly understand their structure and terminology in larval Anura, it should be mentioned that in primitive water-dwelling gnathostomes each arch was segmented into a series of branchials, termed (in dorsal to ventral order): suprapharyngobranchial, and infrapharyngobranchial, epibranchial, ceratobranchial, and hypobranchial. The suprapharyngobranchials and infrapharyngobranchials attach the arch to the neurocranium (braincase and otic capsules). The hypobranchials of either side join an unpaired, longitudinal median element called the basibranchial, which connects neighbouring branchial arches ventrally. All these components, except for the basibranchials, take their embryonic origin from neural crest cells (Fig. 5) (Olsson and Hanken 1996, their figure 5). The basibranchials are of mesodermal origin.

As a consequence of the transition from water to land, the branchial arches of terrestrial vertebrates generally became transformed from gill-supports into structures with other functions, e.g., the hyoid supports the tongue muscles. Although anuran larvae are still water-dwelling organisms, their postmandibular branchial arches have also taken on other functions. Rather than supporting gills they serve as filter-feeding devices. All the posthyoid branchial arches (i.e., those that are posterior to the hyoid branchial arch) are connected proximally and distally to form a branchial basket in which the original identity of the majority of the branchial segments (branchials) is lost (Fig. 35). Transformation into the hyoid takes place only during metamorphosis of the aquatic larva into the terrestrial adult (Fig. 36).

In anurans, the first postmandibular element to appear is a procartilaginous rudiment of the ceratobranchial of the hyoid arch, termed the *ceratohyale* ("*Zungenbeinknorpel*" of Stöhr [1882]; "hyoid" of Spemann [1898]; "*Hyale*" of Stadmüller [1936, his figure 511]; "*Keratohyale*" of Reinbach [1939a]). It arises simultaneously with rudiments of the *suprarostrale* and palatoquadrate (Fig. 9). In this early stage, it is separated from the palatoquadrate; later these two elements come into contact (Spemann 1898) or are temporarily interconnected by a ligament, or, when chondrification begins to take place,

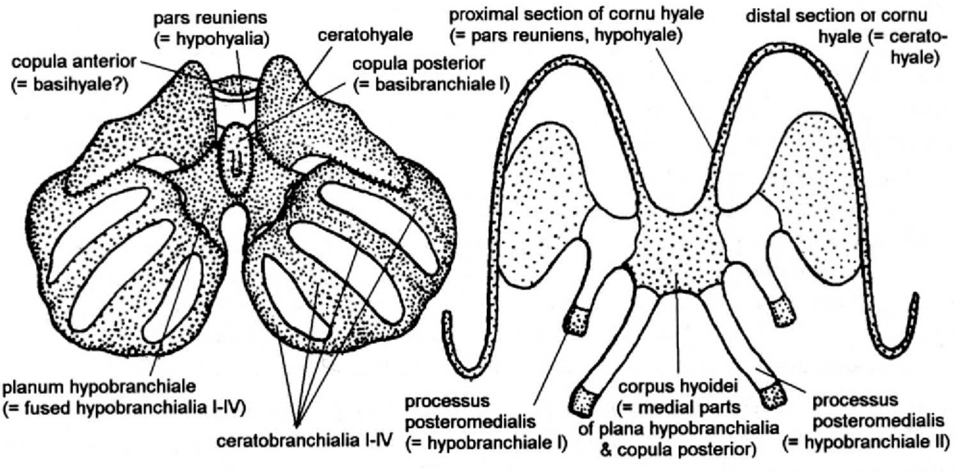


Fig. 35. Ventral view of the hyobranchial apparatus in larval (left) and adult (right) *Bombina bombina*. Terms in parentheses refer to the homologous components (branchials) of the gill arches in osteolepiform ancestors. Modified from Severtzov (1980b).

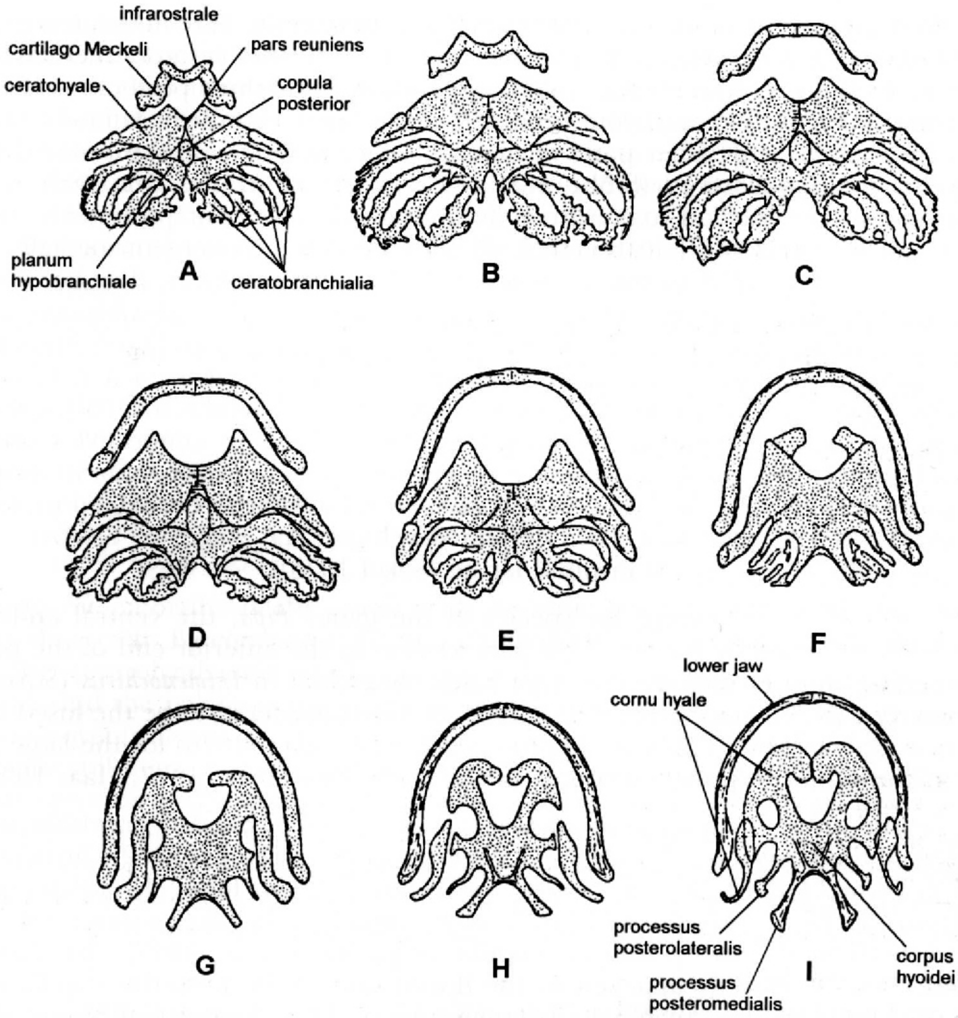


Fig. 36. Development of the hyobranchial skeleton and the lower jaw in *Pelodytes punctatus*, showing the origin of the hyoid. Drawings are of progressively older stages from A to I. A–G in dorsal view; H, I in ventral view. From Ridewood (1897).

by a strip of cartilage (de Beer 1937). Still later, the cartilaginous continuity of the palatoquadrate with the ceratohyal is replaced by a joint (Stöhr 1882). According to Stöhr, soon after the ceratohyals can be distinguished, and approximately at the same time as the *trabeculae* appear, the ceratohyals fuse with one another in the midline to form the *pars reuniens*; each ceratohyal gives off a *processus anterior* and a *processus posterior*, the latter fitting into a short, but deep, groove on the dorsal surface of the anterior part of the hypobranchial plate (Roček 1981). The anterior processes of both ceratohyals are connected by a ligament called the *ligamentum interhyale* by Reinbach (1939a) and *ligamentum interhyoideum* by de Jongh (1968). The lateral part of the ceratohyal extends dorsally as the *processus lateralis dorsalis*. The *processus lateralis dorsalis* fits into a concavity on the ventral surface of the palatoquadrate, thereby taking part in the formation of the *articulatio quadratohyalis*. In *Rhinophrynus*, a small, biconcave cartilage inserts into this articulation; this cartilage was called the symplectic cartilage by Swart and de Sá (1999). The lower lateral process, called the *processus lateralis ventralis* ("*processus lateralis*" of Kothe 1910), is directed ventrolaterally and is a site of muscle attachment (Stadtmüller 1936).

The anterior copula (the "copula I", "*basihyale*" and "*copulare*" of Stöhr [1882], but not the "*basihyale*" of Ridewood [1897]) appears in the midline as an independent chondrification within the *ligamentum interhyale*, close in front of the *pars reuniens*. The anterior copula is large in some Discoglossidae (e.g., *Alytes*) but is lacking in the Pipidae and in some other taxa (Haas 1995, 1996b, 1997).

The four posthyoid branchial arches arise independently, and in sequence, as free procartilaginous (later cartilaginous) rods representing the ceratobranchials ("*pièces thyroïdiennes*" of Dugès [1834]). Stöhr (1882) suggested that the three posterior arches might be derivatives of a single posthyoid arch. All arches first chondrify laterally and then medially; however, as with other parts of the skull (e.g., in *Hyla*), they are united as early as the precartilaginous stage (Stöhr 1882). The position of the first arch is nearly perpendicular to the median axis, with only the lateral ends bent posteriorly. With the appearance of the third and fourth arches, all arches become convergent medially, so that the fourth is nearly parallel to the median axis. Like the ceratohyals, they become fused in the midline to their counterparts of the opposite side, and they also become attached to a median cartilage (histologically different from surrounding cartilages) known as the posterior copula (*copula II*). This structure appears to represent *basibranchiale I*. It was called the "*Urobranchiale*" by Stöhr (1882), and the "*Copulastiel*" by Reinbach (1939a), the latter maintaining that it was connected to the anterior copula only by connective tissue. Haas (1997, his figure 1) described a bifurcating process on the posterior copula in *Ascaphus* as the *processus urobranchialis*. The *processus urobranchialis* is indistinctly developed in *Alytes* and *Discoglossus* (Haas 1997), as well as in certain developmental stages of *Leiopelma* (N. G. Stephenson 1951), and is absent in pipid larvae (Sokol 1975).

In all anuran larvae, except for species of the genus *Pipa*, the ventral ends of the ceratohyals are attached by means of the *pars reuniens* to the anterior end of the posterior copula. Judging from etymology, the large basihyobranchial in *Hymenochirus* (Sokol 1962) and in *Leiopelma* (N. G. Stephenson 1951) is apparently considered to be the fused *basihyale* and the first *basibranchiale*. This was suggested earlier by Parker (1876) for the large median element in *Xenopus*. The posterior copula is missing in *Pipa* (Sokol 1977; Haas 1996a).

The ventral ends of the ceratobranchials are large and expanded on either side into a plate termed the *planum hypobranchiale* ("*Kiemenbogenplatte*" of Stöhr [1882]; "hypobranchial plate" of Ridewood [1898]; "hypohyal plate" of Wiens [1989, his figure 4]) which represents fused hypobranchials. There is considerable variation in the connection of the ceratobranchials with the posterior copula (e.g., see Haas 1997). In *Rana*, the ceratobranchials are directly attached to the dorsal side of the posterior copula whereas in *Alytes* they are not in cartilaginous continuity with the hypobranchial plates (de Beer 1937). With few exceptions, the *planum hypobranchiale* on either side is flexibly connected by small-celled cartilage to the posterior copula; however, in suspension-feeding tadpoles of the family Microhylidae the contributing cartilages are fully fused (de Sá and Trueb 1991; Haas 1996a).

In most anurans, the ventral ends of the second through fourth ceratobranchials are attached to the base of the first ceratobranchial, whilst the dorsal ends of all the ceratobranchials of each side are interconnected by the *commissurae terminales*. Similar proximal fusions (the *commissurae proximales*) can be found in the Discoglossidae and Pipidae (Sokol 1977; Haas 1996a), but some or all of them may be missing in other anuran taxa, e.g., ceratobranchials II and III may have free proximal ends (Haas 1995). In many species, *ceratobranchialia II* and *III* each bear on their proximal parts a process serving as an attachment for the long hyobranchial muscles. These processes are termed the *processus branchialis II* and *processus branchialis III* respectively (*sensu* Schulze 1892; Haas 1997, his figure 8; "*processus interbranchialis*" of Gaupp [1906]). It is called the *synapticulum* and may connect the second and third ceratobranchials near their proximal (i.e., ventral) ends, thus restricting the aperture of the third branchial slit. A short dorsally-directed *spiculum* arises from the ventral end of each ceratobranchial. These *spicula* are particularly long in suspension-feeding larvae (Haas 1996a) whereas in others they may be absent, e.g., *spicula II* and *III* in *Ascaphus* and *Bombina* (Haas 1997). All the ceratobranchials and their dorsal commissures bear short, irregular cartilaginous rays.

In *Leiopelma* (N. G. Stephenson 1951, his figure 12A), the ceratobranchials are not interconnected distally by the *commissurae terminales*, the *spicula* are absent and, contrary to other anurans in which there are only four ceratobranchials, there is a trace of a fifth one (quite distinct in the late intracapsular embryo). The terminal commissures are also absent in some other anurans with suppressed larval development (e.g., *Breviceps*) and the basibranchials of the hyoid arch and of the first branchial arch form a continuous structure in which the *copulae* cannot be recognized (Swanepoel 1970). Only the first two ceratobranchials are preserved in larval *Hymenochirus* (Sokol 1962) and *Pseudohymenochirus* (Sokol 1975) because there is no branchial filter; according to Buckey (1970, ex Sokol 1975), however, the preserved ceratobranchials are the first and the fourth.

The cartilages of the branchial arches and the ceratohyal fuse by means of various contacts to form the branchial basket. This configuration, in turn, articulates with the rest of the skull by means of the joint between the palatoquadrate and the ceratohyals.

Usually, the anterior copula disappears as early as at metamorphosis, e.g., in *Caudiverbera* (Reinbach 1939a) but in some anurans it may appear later and, consequently, its disappearance is delayed as well, e.g., in *Scaphiopus* (Hall and Larsen 1998). In the majority of anurans the anterior copula does not contribute to the structure of the adult hyoid. As an exception, it persists as the ossified hyoid copula in adult *Hymenochirus* (Ridewood 1899; Sokol 1975).

During metamorphosis the ceratohyals become more slender and their posterior processes disappear. By contrast, their anterior processes become accentuated. The lateral part of the ceratohyals shift backward, as do the palatoquadrates. At this stage the ceratohyals and the palatoquadrates are no longer articulated, but the ceratohyals extend freely posteroventrally. As the ceratohyals lose their connection with the palatoquadrates, they become still thinner and longer, so that they run backwards as cylindrical rods beneath and then upwards and behind the tympanic cavities, finally becoming attached to the ventral surface of the otic capsule, beneath the anterior margin of the *fenestra ovalis*. This was observed long ago by Cuvier (1824). The *processus anterior* of the ceratohyal becomes the anteromedial (anterior) process of the hyoid plate. It should be noted that in *Pipa carvalhoi* the ceratohyals are resorbed during metamorphosis, and consequently they are lacking in the adult (Paterson 1955).

The posterior copula (*copula II*), including its urobranchial process, is involved in the formation of the *corpus hyoidei*, much as it is in the development of the *pars reuniens* and *planum hypobranchiale*, although these last two structures are substantially resorbed (Reinbach 1939a, his figure 21). The posterior copula represents the basibranchials and urobranchials of caudate larvae (Sokol 1975).

During metamorphosis, all four ceratobranchials (including the *commissurae terminales*) are resorbed, leaving only the hypobranchial plate. This plate is continuous anteriorly with the ceratohyals and projects posteriorly into the paired thyroid processes. These processes are vestiges of the posterior part of the hypobranchial plate and are preserved, probably because of the hyoglossal muscles attached to them. The hypobranchial plates on either side fuse with each other and with the posterior copula, thus forming the *corpus hyoidei*. The *pars reuniens* becomes U-shaped, with its branches constituting the proximal parts of the *cornua anteriores*. Later, in the Pelobatidae and Pelodytidae (Ridewood 1897), the thinned posterolateral portions of the ceratohyals ("posterior hyoid horns" of Hall and Larsen [1998, their figure 9C,D]) may become separated from their proximal parts (called the *processus anteriores*) that enclose a median *sinus hyoglossus*. This separation does not take place in *Discoglossus* (van Zyl 1950, his figure 13), *Chiromantis* (Swanepoel 1966, his figure 15), and many other species. In those in which separation occurs, both the anterior process and the detached part are considered collectively as the *cornu hyale* (Trewawas 1933; "*cornu principale*" of Swanepoel [1970]). Reinbach (1939a, his figure 22) called the proximal section the *manubrium*, and the distal one the *cornu hyale*. The tip of the *cornu hyale* fuses synchondrotically with the anteroventral part of the otic capsule in mature animals. The *processus anterolateralis* ("*processus alaris*" of Gaupp [1896]; "*processus lateralis anterior*" of Fuchs [1929, his figure 19]) and the posterolateral processes of the adult hyoid are formed as a result of new cartilaginous growth at the sides of the original posterior copula and hypobranchial plate, while the thyroid processes ("*cornu thyroidea*" of Dugès [1834]; "*processus posteromediales*" of Trewawas [1933]) of the hypobranchial plates become the posteromedial processes ("*cornua posteriores*" of Severtzov 1980a) of the hyoid plate. These ultimately ossify as the *ossa thyroidea* ("*os postero-mediale*" of Reinbach [1939a]; "hyoids" of Wiens [1989]; "hypohyoid bones" of Hall and Larsen [1998]) and invest the larynx laterally. In *Pelodytes punctatus*, the posterolateral process is the persistent stump of the first ceratobranchial (Ridewood 1897, his plate 35).

The hyobranchial skeleton is the last structure to undergo transformation; it takes place even after the animal has fully changed into a small froglet externally (Fig. 37). This may be illustrated by changes in adult *Pelobates* (Roček 1981). Whereas in younger individuals the hypoglossus nerve passes between the anterolateral process and the proximal part of the *cornu hyale (sinus nervi hypoglossi)*, in larger ones it is completely enclosed in a foramen ("*foramen nervi hypoglossi*" and "*foramen laterale*" of Stadtmüller (1936]) by a stripe of cartilage called the *processus confluens* (Kothe 1910; "processus alaris" of van Zyl [1950, his figure 13]). Such postmetamorphic variation has also been confirmed in *Scaphiopus* (Hall and Larsen 1998).

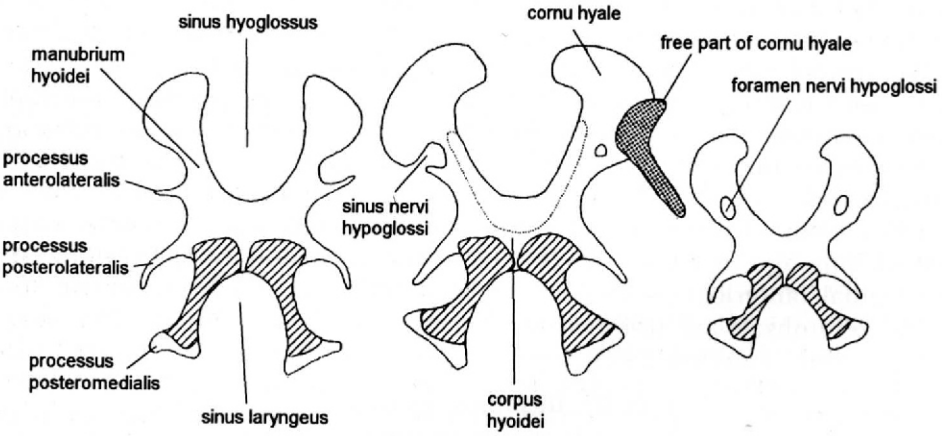


Fig. 37. The three last post-metamorphic developmental stages of the hyoid of *Pelobates fuscus*, showing the progression from the presence of a *processus anterolateralis* (left), through the development of the *sinus nervi hypoglossi* (centre), and finally to enclosure to form the *foramen nervi hypoglossi* (right). Hatching indicates the ossified part of the posteromedial processes (*ossa thyreoidea, thyrohyalia*). The free segment of the *cornu hyale* of one side, and the part of the hyoid adjoined by the *os parahyoideum* are illustrated in the middle specimen. Note also the asymmetrical occurrence of the *foramen nervi hypoglossi* in the middle specimen. From Roček (1981).

It should be emphasized that the only skeletal elements connecting the hyoid of adults to the other parts of the skull are the tips of the *cornua anteriores*; these permit considerable dorso-ventral respiratory movement (Severtzov 1971).

In anurans with suppressed free-living larval development, the earliest cartilaginous stages of the hyobranchial skeleton (Fig. 38) consist of a rather broad central plate (*corpus hyoidei*) with four pairs of lateral outgrowths. The most anterior of these lateral extensions are homologues of the ceratohyals; as in other anurans, later they establish contact with the otic capsule (van Zyl [1950, his figure 2]; Swanepoel [1966, his figure 14]). According to Lynn (1942), the second and third pairs extend dorsally around the pharynx as ill-defined ligaments representing the vestigial posthyoid arches. Later, these ligaments are reduced to mere processes extending from the body of the hyoid. In summary, the hyobranchial apparatus in anurans with direct development lacks the early stages that are present in other anurans with water-dwelling tadpoles that use gills in the exchange of respiratory gases.

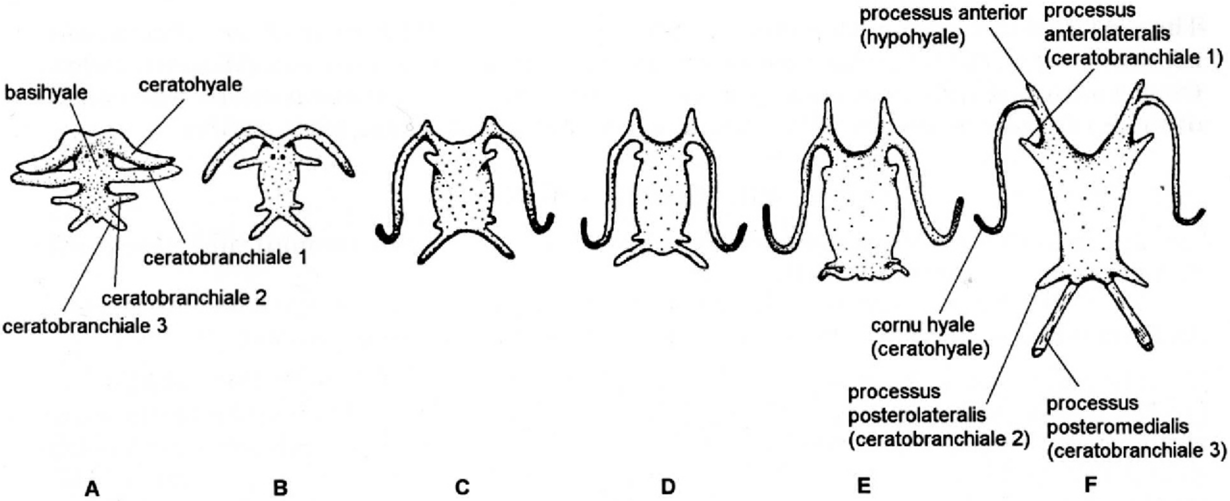


Fig. 38. Development of the hyoid in an anuran with suppressed early larval stages (*Eleutherodactylus nubicola*). A–E are progressively older developmental states; F is the adult. From Lynn (1942).

The laryngeal skeleton (Fig. 39) arises in comparatively early developmental stages. In *Caudiverbera* (Reinbach 1939a, his figures 23–25), the first structure to chondrify is a *cartilago arytaenoidea*, one on each side of the body. These are elongated antero-posteriorly, with their anterior and posterior ends respectively called the *prominentia apicalis dorsalis* and *prominentia apicalis ventralis* (*sensu* Reinbach 1939a; "*prominentia apicalis posterior*" and "*prominentia apicalis anterior*" respectively of Gaupp [1906]). Another pair of cartilages, termed the *cartilago cricoidea* or *cartilago cricotrachealis*, develops later. These cartilages are situated transversely, with their lateral sides moderately bent dorsally. Later, at the beginning of metamorphosis, they expand to form a complete cartilaginous ring, whose ventral part is sharply bent posteriorly in the form of a "V"; at the tip to this "V" *Caudiverbera* has a small cartilaginous element (Reinbach 1939a). The ring extends posteriorly on either side into the tracheobranchial processes (*processus tracheobranchiales*) that form the wall of the larynx and may chondrify to various extents; later, in the course of metamorphosis, these processes may disappear. In metamorphosed individuals, the *cartilagines arytaenoidae* are enclosed between, and run nearly parallel with, the cricotracheal cartilages. On the posterior end of the cricotracheal cartilages is a common median spine called the *spina oesophagea* (*sensu* Reinbach 1939a, his figure 25). In adults, an independent additional cartilage may occur in various anurans, dorsal or anterior to the *prominentiae apicales dorsales* of the arytenoid cartilages; this cartilage was called the *cartilago wrisbergi* by Blume (ex Reinbach 1939a) and others ("*cartilago apicalis seu cartilago santoriniana*" of Henle [ex Reinbach 1939a]; "*cartilago apicalis intermedia*" of Blume [ex Reinbach 1939a]).

Only limited information is available about the cartilaginous larynx and how it develops in anurans (Blume 1930, 1932; van Zyl 1950, his figure 14; Maglia and Púgener 1998; Hall and Larsen 1998). In *Bombina*, the *cartilagines arytaenoidae* are comparatively small, whereas the *cartilago cricotrachealis* is well developed and syndesmotically connected with the arytenoid cartilage (Slabbert 1945, his figures 10, 11). No information about how they relate developmentally to the hyobranchial skeleton is available.

Among the last bones to ossify are those originating on the hyobranchial apparatus (Fig. 37) (also see Kothe 1910; Roček 1981).

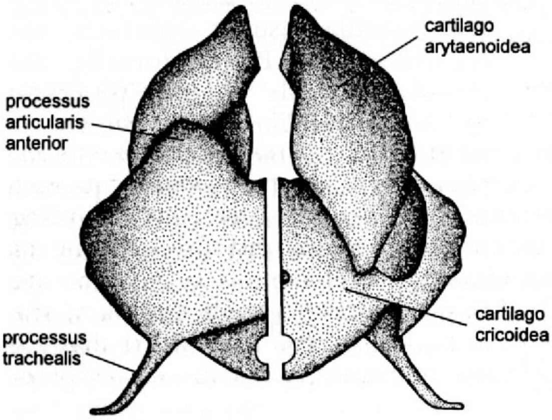


Fig. 39. Larynx of an adult *Discoglossus pictus* in ventral (left half) and dorsal (right half) views. From van Zyl (1950).

The proximal part of the posterolateral process, as well as the portion of the *corpus hyoidei* adjoining it, ossify both perichondrally and enchondrally in *Bombina* (Slabbert 1945). Ossifications within the posterior processes of the hyoid are called *ossa thyroidea*. The extent of these cartilage bones vary with the age of the individual (Fuchs 1929, 1937).

VII. DERMAL BONES

Approximate relations between the endocranium (chondrocranium) and exocranial dermal elements are shown in Figure 40.

A. Premaxilla

The *praemaxilla* ("*intermaxillaire*" of Cuvier [1824]; "premaxillary" of Parker and Baettany [1877]; "premaxilla" by common English usage) is paired, each member of the pair consisting of a basal, tooth-bearing part (*pars dentalis*) and a dorsal outgrowth (*pars facialis*) directed toward the nasal. The tooth-row is roofed by a narrow *lamina horizontalis*. The medial part of the bone extends posteriorly along the median symphysis as the *pars palatina*. The latter may be a continuation of the *lamina horizontalis*. In *Pelobates*, *Rana*, and *Hyla regilla* (Gaudin 1973), the earliest ossification is within the dorsal part of the *pars facialis praemaxillae*, in the vicinity of the *cartilago alaris*. The *pars facialis* later expands towards the *cartilago praenasalis inferior* and the anterior part of the *cornu trabeculae* (Born 1876). The elastic tissue of the symphysis allows some dorso-ventral movement, in which both prenasal cartilages serve as a leading pulley. The distal section of the *pars facialis* is adjoined by the septomaxilla.

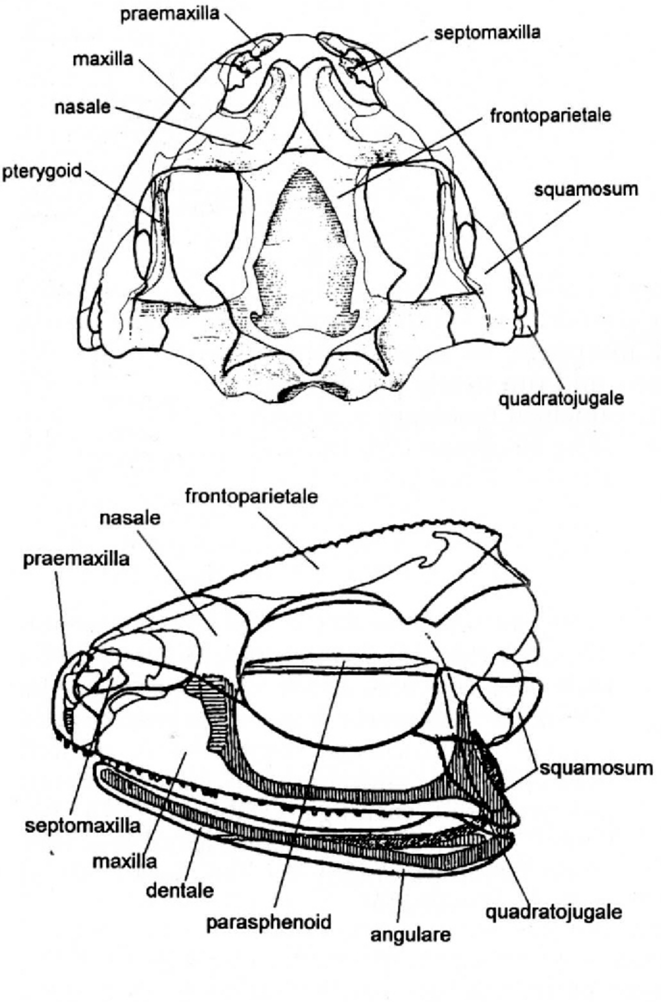


Fig. 40. Topographic relationships of the dermal exocranial bones to the endocranium in adult *Pelobates fuscus* in dorsal (upper) and left lateral (lower) views. Stippling indicates viscerocranial elements. From Roček (1981).

B. Maxilla

The maxilla ("*os maxillaire*" of Cuvier [1824]; "*os maxillo-jugaux*" of Dugès [1834]; "*os maxillare superior*" of Gaupp [1896]) is similar to the premaxilla; the lower part of the bone, called the *crista dentalis* is dentigerous and roofed by the *lamina horizontalis*. The lamina may be terminated posteriorly by a distinct *processus pterygoideus* that is in contact with the *ramus anterior pterygoidei*. The posterior toothless part of the bone is called the *processus posterior*, by which the maxilla usually contacts the quadratojugal. Posterodorsally, the maxilla extends as the processus *zygomatico-maxillaris* by which it establishes contact with the *lamella alaris squamosi*. The anterior portion of the maxilla may project as the *processus frontalis* that may contact the *nasale*, and take part in the formation of a groove for the *ductus nasolacrimalis*. The most anterior part of the maxilla is the *lamina anterior*, which is in contact with the premaxilla. The dorsal margin of the maxilla between the frontal and zygomatico-maxillary processes is the *margo orbitalis*. The prominent oblique outgrowth running anterodorsally from the horizontal lamina towards the lower surface of the postnasal wall in some anurans is the *processus palatinus*, originally an independent bone called the palatine (see section VII G, page 1946).

The maxilla covers most of the residual *commissura quadratocranialis anterior* of adults (= *processus pterygoideus palatoquadrati*) laterally, the *processus palatinus* encloses the *processus maxillaris posterior*, the *lamina anterior* covers the *processus maxillaris anterior*, and the lateral part of the endocranial postnasal wall intervenes between the frontal and palatine processes. The anterior maxillary process fits into the *recessus vaginiformis* of the maxilla.

The first part of the maxilla to develop is its anterior part, which later expands posteriorly as a thin dental process. Only afterwards, does the *lamina horizontalis* appear (Gaudin 1973). In *Bombina* and *Xenopus*, the maxilla lacks the *processus frontalis* and consequently there is no contact with the nasal (Slabbert 1945). However, a small *processus frontalis* (= *processus praeorbitalis* of the *pars facialis*) may develop in extremely old (12 years of age) individuals of *Xenopus* (Smirnov 1994a).

C. Quadratojugal

The quadratojugal ("*jugau*" of Cuvier [1824]; "*os jugale*" and "*Quadratjochbeine*" of Ecker [ex Gaupp 1896]; "*tympano maléaux*" of Dugès [1834]; "quadrato-jugals" of Parker and Bettany [1877]; "*quadrato-maxillare*" of Gaupp [1896]; "*quadratojugale*" of Reinbach [1939a]) is a short rod-like dermal bone connecting the *processus posterior maxillae* to the *pars quadrata palatoquadrati*. The quadratojugals are among the last bones to appear, at the end of metamorphosis, or just after. In *Rana* (Gaupp 1892), the quadratojugal is supposed to have originated as an ossification of the ligament lying lateral to the muscles of mastication, and it stretches between the maxilla and the *pars quadrata palatoquadrati*. According to Sedra (1950), the quadratojugal begins to develop from osteoblasts invading the posteriormost portion of the *ligamentum cornu-quadratum laterale* close to its attachment to the palatoquadrate. The quadratojugal no doubt arises by endesmal ossification and it fuses with the cartilage of the *quadratum*, which later also ossifies (de Villiers 1936; E. M. Stephenson 1951). Curiously, in some anurans the quadratojugal may develop a marrow cavity similar to that in enchondral bone. This cavity communicates with the marrow cavity of the quadrate (de Villiers 1936). The quadratojugal does not develop in some taxa, e.g., *Ascaphus* and *Leiopelma* (Wagner 1934a; Slabbert 1945), *Pipa pipa* (Trueb 1989), *Xenopus* (Paterson 1939), *Scaphiopus* and *Spea* (Roček 1981). De Villiers (1933) surmised that the quadratojugal disappeared in forms in which the parasphenoid and pterygoid fused. Also, it is lacking in *Ascaphus* in which these bones do not fuse (Ramaswami 1935). According to van der Westhuizen (1961), in the majority of the Anura the quadratojugal does not coalesce with the ossified quadrate. Rather, the quadratojugal of adults arises by invasion of the quadrate cartilage by the quadratojugal, and the combination is known as the quadratojugal. In *Bombina*, the quadrate and quadratojugal retain their individuality (Slabbert 1945), probably as a paedomorphic trait.

D. Septomaxilla

The septomaxilla ("*lacrimale*" of Born [1876]; "*turbinale*" and "*le cornet*" of Dugès [1834]; "septomaxillary" of Parker and Bettany [1877]; "*os intranasale*" of Gaupp [1896]; "*os nariale*" of Reinbach [1939a]; "*nasale*" of Bernasconi [1951]; "*internasale*" of de Jongh [1968]) is a dermal bone of complicated structure bordering the *fenestra exonarina posterior* and pierced by the *ductus nasolacrimalis*. Its descriptional terminology is as yet considerably unstable. The following description is principally based on wax models, constructed from serial sections, of the septomaxilla of *Pelobates* (Roček 1981, his figure 30). Viewed laterally, the septomaxilla extends anteriorly as a large, rounded outgrowth, termed the *extremitas anterior*, directed into the space between the *cartilago alaris* and the *lamina inferior cristae intermediae*.

The basal part of the septomaxilla is called the *pars horizontalis* or *corpus septomaxillae* (also see Stadtmüller 1936). The posterior part of the *pars horizontalis* gives off the *processus infrafenestralis*. In its anterior part, the *pars horizontalis* may be rounded dorsally (*margo libera*). Medially, this part of the *pars horizontalis* is bordered by a thin horizontal ledge (*crista contacta*) adjoining the *lamina superior cristae intermediae*. Posteriorly, this ledge is terminated by a sharp apex that is directed into the nasal cavity. The ventral surface of the *pars horizontalis* is flat, passing laterally on to the *facies externa*. Dorsally, the *pars horizontalis* gives off the *processus infrafenestralis*, part of whose posterior surface adjoins the *cartilago obliqua* and supports the posterior margin of the external nostril. The basal part of the *pars horizontalis* has a medial, rather sharp edge (*crista interna*) separating the *diverticulum principale* from the *diverticulum medium*. In its posterior part, the *lamina horizontalis* is pierced by the *canalis nasolacrimalis* and it is terminated posteriorly by the dorsal and ventral processes adjoining the *planum terminale*.

The septomaxilla develops on the *lamina superior cristae intermediae* (Wagner 1934a), independently of the cartilaginous nasal skeleton (Hasurkar 1957, ex de Jongh 1968), and in close association with the anterior part of the *ductus nasolacrimalis*. According to Parker (1882), the septomaxilla is absent in *Bombina bombina* and many other forms, including *Pelobates*. By contrast, Slabbert (1945), Ramaswami (1935) and Roček (1981) found the septomaxilla to be well developed in *B. variegata* and in *Pelobates*.

E. Nasal

The nasal, or *nasale,* has also been known as the "*frontaux antérieurs*" by Cuvier (1824), the "*fronto-nasale*" and "*Nasenstirnbein*" by Ecker (ex Gaupp 1896), "*fronto-nasaux*" by Dugès (1834), and "supraethmoid" by Bernasconi (1951), but is not the same as the "supraethmoid" of Paterson (1939, her plate 9, figure 3). This element covers the dorsolateral part of the nasal capsule (roofing the *cavum principale*, if this is not already covered by the *tectum nasi*) and extends laterally to the *planum terminale.* In *Bombina*, it may reach the anterior tip of the pterygoid (Slabbert 1945, his figure 1). In *Megophrys*, a considerable gap exists between the nasals, so that the dorsal surface of the sphenethmoid is exposed (Ramaswami 1935); the same holds for young *Pelobates syriacus* (Basoğlu and Zaloğlu 1964; Roček 1981, his figure 12) and young *Scaphiopus* (Ramaswami 1935) in which the exposed part of the sphenethmoid is sculptured similarly to the surrounding nasals and frontoparietal. The paired nasals fuse into an unpaired element in *Xenopus* (Trueb and Hanken 1992).

F. Frontoparietal Complex

The frontoparietal complex was called the "*pariétaux*" by Cuvier (1824), "*fronto-pariétaux*" by Dugès (1934), "parietofrontal" by Parker and Bettany (1877), and "*os fronto-parietale*" by Gaupp (1896). It is one of the most characteristic features of the anuran skeleton. In most anurans, the complex arises from anterior and posterior ossification centres supposedly representing the frontal and parietal respectively, (Fig. 41) (also see Parker [1871, his plate 7, figure 3]; Gaupp 1896; Erdmann 1933; Reinbach 1939a; Griffiths [1954b his plate 1, figure 1]; Lebedkina [1968, her figure 9, 1979, her figures 84, 85]), of which the frontal develops first (Fig. 42). However, in some anurans (e.g., Pipidae) it is not possible to trace a separate origin for the frontals and parietals (Sedra 1949; Trueb 1966, 1970; Gaudin 1973) even in early, pre-calcified stages (Královec 2000), and some authors have even denied such a possibility (Eaton 1939a, 1942). Lebedkina (1979) noted that the rate of dermal bone development in amphibians is so high that examination of only a limited number of developmental stages is inadequate for detection of separate frontal and parietal ossifications. However, she did find separate centres in bufonids, ranids, hylids, and discoglossids. Also, Griffiths (1954b) found discrete frontal and parietal centres in some species previously claimed to have but a single centre, and in some cases (e.g., *Bufo marinus*) he found at least one centre clearly divided into anterior and posterior parts. According to the latter author, within the Anura there seems to be a trend for the frontal and parietal ossification centres to gradually approach each other, with this process having been completed in the early developmental stages of some taxa.

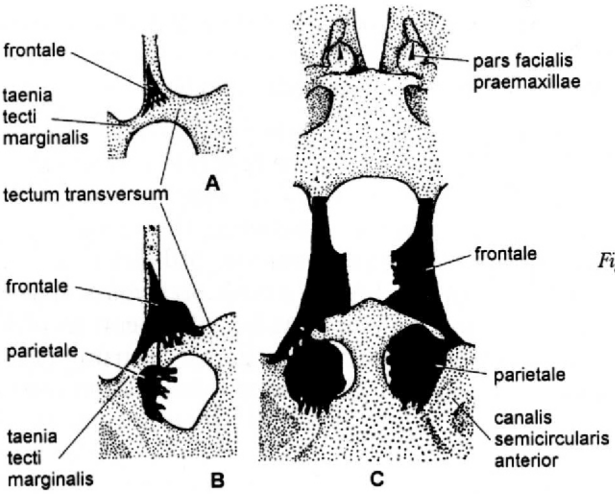


Fig. 41. Development of the frontoparietal in *Rana ridibunda* over three successive stages: 56 mm total length (A), 57 mm total length (B), and 58 mm total length (C). Only the left part of the skull is illustrated in A and B. From Lebedkina (1979).

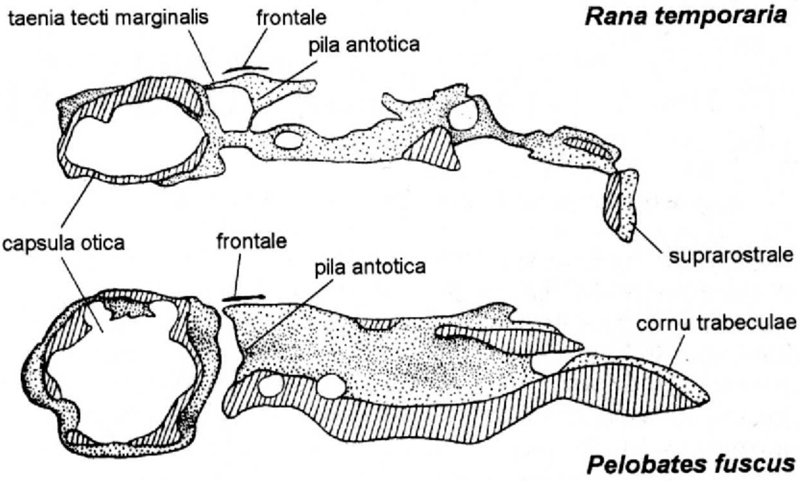


Fig. 42. Sagittal section of the larval endocranium of *Rana* (15 mm total length) and *Pelobates* (19 mm total length) showing the position of the early rudiments of the frontal in relation to endocranial structures. Also compare Figure 60. From Lebedkina (1979).

In the early stages of development of the frontoparietal in *Bombina variegata*, there are three pairs of clearly discernible clusters of osteoblasts within the region of the future frontals. These are similar to those found in later, calcified, developmental stages of some teleosts and primitive caudates (Lebedkina 1979, her figures 81–83). These clusters fuse with each other to form the frontal at the time the bone matrix begins to become calcified. This composite frontal ultimately fuses with the parietal to form the frontoparietal (Královec 2000). Note, however, that Hanken and Hall (1988), in agreement with Trueb (1973) claimed that in *Bombina*, and other discoglossid frogs, the frontoparietal forms from a single ossification centre on each side. In *Bombina* and other anurans showing paedomorphic characters, the frontoparietals remain separated anteriorly by a wide expanse of connective tissue (frontoparietal fontanelle). In *Bombina orientalis*, each member of an additional paired ossification may partially fuse posteriorly with the parietal portion of the ipsilateral frontoparietal (Smirnov 1997, his figure 4). In some individuals, there is also fusion of the frontoparietal with an unpaired ossification adjoining the *tectum synoticum*.

In *Pelobates*, as in all other anurans, the frontoparietal begins to develop as a paired ossification above the posterior section of the lateral walls of the orbitotemporal region of the braincase (Fig. 43) (Sewertzow 1891, his figure 7; Luther 1914; Roček 1981; Smirnov 1992). Slightly later, an unpaired element (termed the interparietal by Smirnov 1992, his figure 1) is added above the *tectum synoticum*. Finally, a further paired element arises above the medial part of the otic capsules (also see Sewertzov 1891; Smirnov 1999, his figure 3d) and encloses the *arteria occipitalis* and *arteria orbitonasalis* in a canal (Fig. 44). The paired ossifications in the orbitotemporal region expand anteriorly and medially until they reach the postnasal wall and meet each other at the midline. Between the anterior ends of the future frontoparietal complex there is a deep triangular fontanelle that only later becomes covered by a separate ossification. This ossification may protrude between the two nasals and may leave a considerable part of the sphenethmoid uncovered in young individuals; the space is closed only in fully-grown animals (Basoğlu and Zaloğlu 1964).

In extinct *Eopelobates* (Fig. 45) the condition is essentially the same as in *Pelobates*. Consequently, the single frontoparietal in adults arises from five independent ossifications that only later fuse with each other. Positional similarities with *Rana* suggest that the first elements to form are a pair of frontoparietals proper, located between the orbits. Later, these are joined by an unpaired element adjacent to the *tectum synoticum*. Still later, another pair of ossifications, separated from the former elements by the *arteria occipitalis*, appears on the dorsal roof of the otic capsules. This second pair of elements has also been recorded in tadpoles of *Pelobates* (see above; also Reinbach [1939b, his figure 2a,b]; Smirnov [1999, his figure 3d]). Reinbach (1939a) erroneously considered these as dorsal ossification centres of the squamosal (see below) but Griffiths (1954a) correctly interpreted them. Camp (1917) found an independent bone occupying the same position in the presumably Tertiary toad, *Bufo nestor*, as did Wild (1997, his figure 14) in contemporary *Ceratophrys cornuta* (Fig. 46). So far as is known, the condition found in larval *Eopelobates* and *Pelobates* is unique among anurans, except for a pelobatid anuran from the Green River Formation (Eocene, North America) which, remarkably, is an adult (Roček and Rage 2000b, their figure 22).

In *Scaphiopus*, the frontoparietals are paired and contact each other in a median suture; no unpaired median element on the *tectum synoticum* is involved (Hall and Larsen 1998, their figures 11A, 12A; Roček 1981, his figure 58).

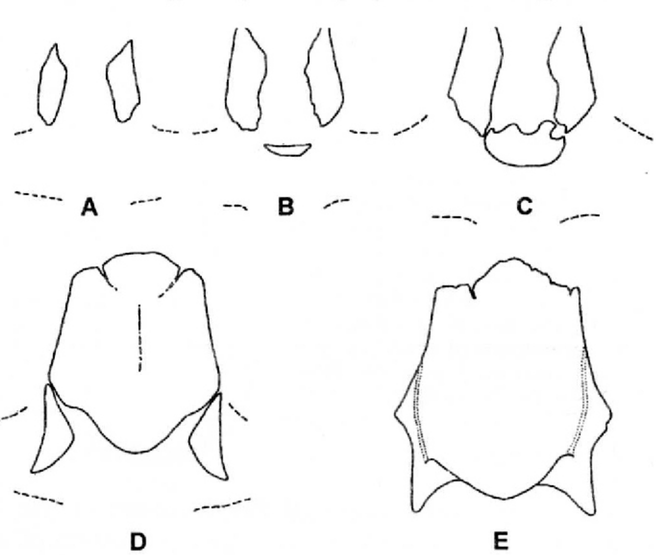


Fig. 43. Progressive development (A through D) of the frontoparietal in *Pelobates fuscus*. Outlines of the otic capsules are indicated by broken lines, and the canals of the *arteria occipitalis* and *arteria orbitonasalis* by dotted lines. From Roček (1981).

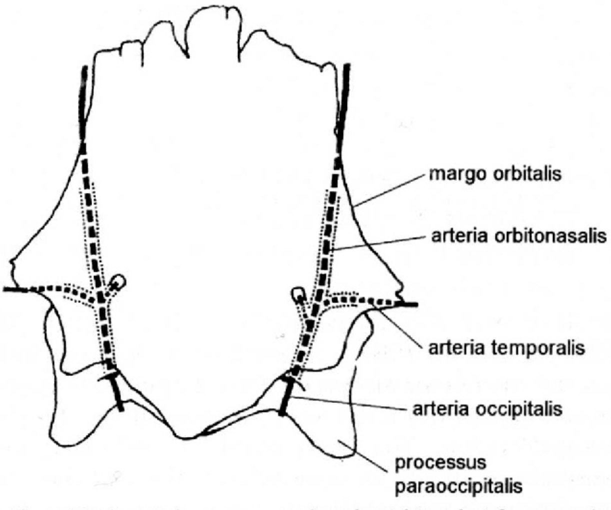


Fig. 44. Arterial system enclosed within the frontoparietal complex of *Pelobates fuscus*. From Roček (1981).

In the Pipidae (*Pipa* and *Xenopus*), ossification begins in paired longitudinal centres adjoining the dorsal edge of the orbitotemporal region of the wall of the braincase, at the level of the eye (Fig. 47) (Trueb and Hanken 1992; Trueb *et al*. 2000; Královec 2000). This indicates that the frontals are involved. Ossification then proceeds posteriorly until the strip of ossified tissue makes contact with the anteromedial surface of the otic capsule. Later stages are rather different in the two genera. In *Xenopus*, ossification then spreads towards the midline throughout the length of the ossification (Sedra and Michael 1957; Královec 2000). In *Pipa*, it continues both anteriorly and posteriorly along the well-delimited margins of the frontoparietal primordium. Then, ossification proceeds quite rapidly from the margins toward the centre of the primordium; no median suture can be observed (also

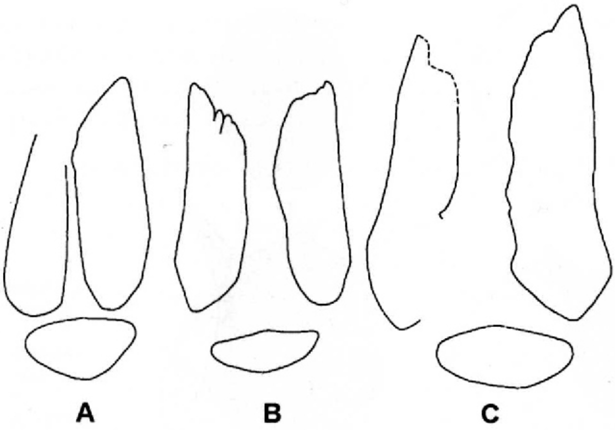


Fig. 45. Early larval stage of the tripartite frontoparietal complex (corresponding to Fig. 43C) in three tadpoles of the extinct *Eopelobates bayeri* from the Early Oligocene deposits of Bechlejovice, Czech Republic. From Roček (1981).

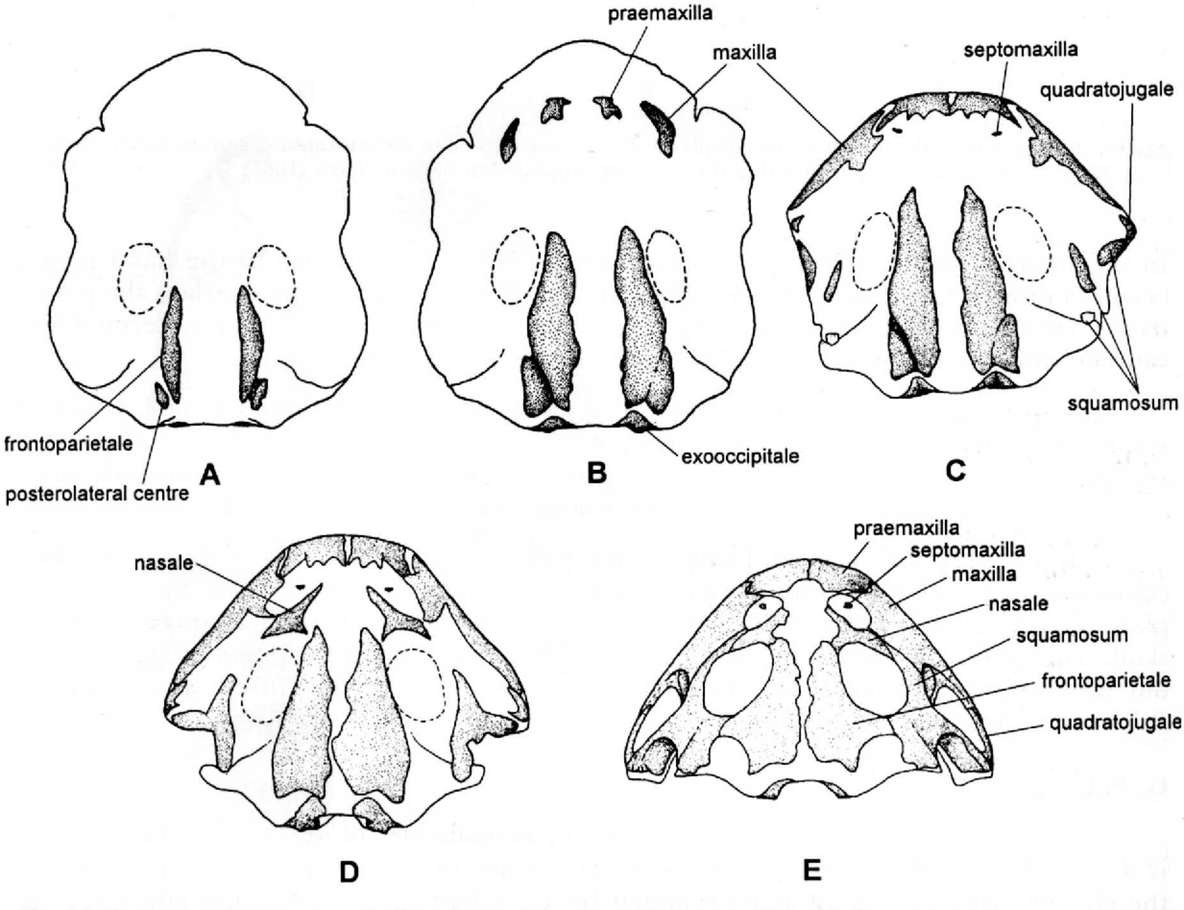


Fig. 46. Progressive development (A through E) of the exocranial bones of the skull roof (plus the *exooccipitale*) of *Ceratophrys cornuta*. Note the posterolateral ossification centre of the frontoparietal complex lateral to the *arteria occipitalis*, and the composite origin of the squamosal. Dashed lines indicate the position of the eyeball. Based on cleared and stained specimens in which bone tissue was calcified. Not to scale. From Wild (1997).

see Ramaswami 1956). Parker's (1876, his plate 56, figure 2) statement that the frontoparietal in *Pipa* is formed from four centres is no doubt based on structures as seen through transparent bone. This stage corresponds to the final stage in *Xenopus* and is completed during further development by the formation of vertical ridges adjoining the postnasal walls (Trueb and Hanken 1992) that subsequently form anterolateral flange-like processes called the frontoparietal *alae* and the suprarostral flange (Trueb *et al*. 2000). The pineal foramen develops between the anterior parts of the frontoparietals in *Xenopus* (Winterhalter 1931, his figures 55–60) and *Pipa* (Trueb and Hanken 1992, their figure 4).

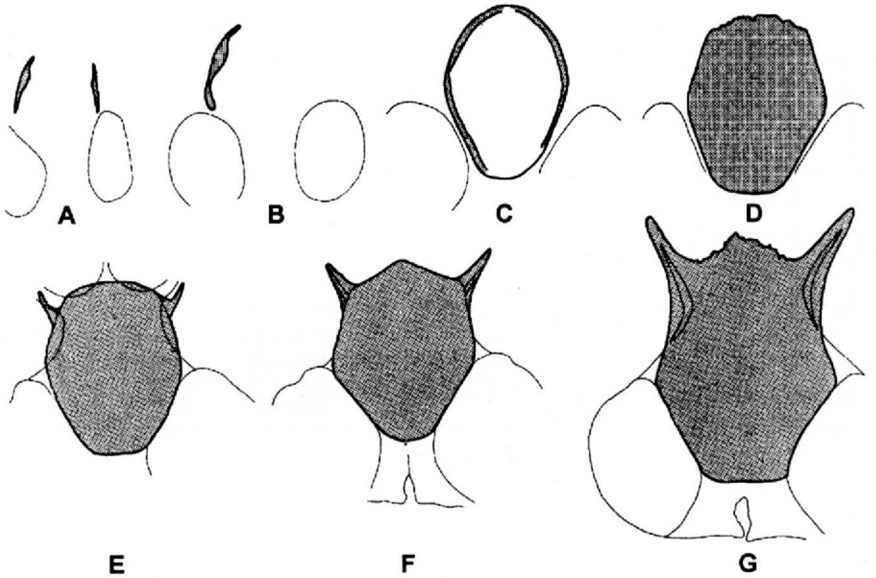


Fig. 47. Development of the frontoparietal complex in *Pipa pipa* in relation to the otic capsules and the *tectum synoticum*. Only the left frontal was developed in the specimen illustrated in B. From Roček (1987).

In metamorphosing *Xenopus*, the frontoparietal extends forward and in the nasal region becomes directly continuous with a slightly arched membrane bone that overlaps the paired nasals (Paterson 1939, her plate 9, figure 3); this membrane bone was termed the supraethmoid by Gilchrist and von Bonde (1919 ex Paterson 1939).

The frontoparietal of *Hymenochirus*, including the pineal foramen (Sokol 1962), is similar to that of pipids. Also, the frontoparietal of the Palaeobatrachidae develops in a similar way as in pipids, as far as can be judged from a fossilized developmental series (Špinar 1972, his figure 60). A characteristic feature shared with pipids is the pineal foramen.

It is obvious that paired frontals and paired parietals always arise as the first components of the future frontoparietal complex, and then soon fuse into a thin elongated plate dorsally rimming the walls of the braincase within the orbitotemporal region of the skull. This holds true not only for those anurans having paired frontoparietals as adults, but also for those whose definitive frontoparietal is completely fused (e.g., Pipidae, Pelobatidae, some Leptodactylidae).

G. Palatine

The palatine, or *palatinum* of Cuvier (1824) ("neopalatine" of de Sá and Trueb [1991]), is a dermal bone that develops on the lower surface of the postnasal wall, posterior to the choana (Figs 48, 49). It is represented by an independent ossification adjoining the lower surface of the postnasal wall in larvae; it may also occur in some adults, e.g., the microhylid genus *Hamptophryne* (de Sá and Trueb 1991). Later, in the adult, its fate varies among taxa. In *Caudiverbera*, it comes into contact with the maxilla (Reinbach 1939a). In *Hyla*, *Pelobates*, and *Chiromantis*, it coalesces with the maxilla (Sewertzow 1891; Boulenger 1899; Ramaswami 1935; Swanepoel 1966; Gaudin 1973) to form a compound bone (called the maxillopalatine, similar to that of adult caecilians [Reiss 1996]) or with the vomer. In *Phrynomerus* (de Villiers 1930), *Leiopelma* (Wagner 1934a, his figure 5), *Alytes* (Maree 1945, his figure 6; but see below), *Scaphiopus* and *Spea* (Roček 1981, his figure 59; Hall and Larsen 1998, their figures 11B, 12B; Wiens 1989), it fuses with the vomer. It may also fuse with the vomer in extremely old (12 years of age) individuals of *Xenopus* (Smirnov 1994a, his figures 2, 4); however, it does not develop in normal adults of *Hymenochirus* (Paterson 1945), *Xenopus laevis* (Parker 1876; Paterson 1939), *Pipa carvalhoi* (Paterson 1955) or *Pipa pipa*

(Trueb 1989). It was reported as absent in adults of *Alytes* (Ramaswami 1942), *Bombina* (Slabbert 1945), *Ascaphus* (de Beer 1937; de Villiers 1934). Ramaswami (1935) also reported it as absent in *Megophrys*, although he was obviously looking for an independent bone, which does not occur in adults.

The *palatinum* may bear some tooth-like structures, e.g., in *Bufo* (Héron-Royer 1886).

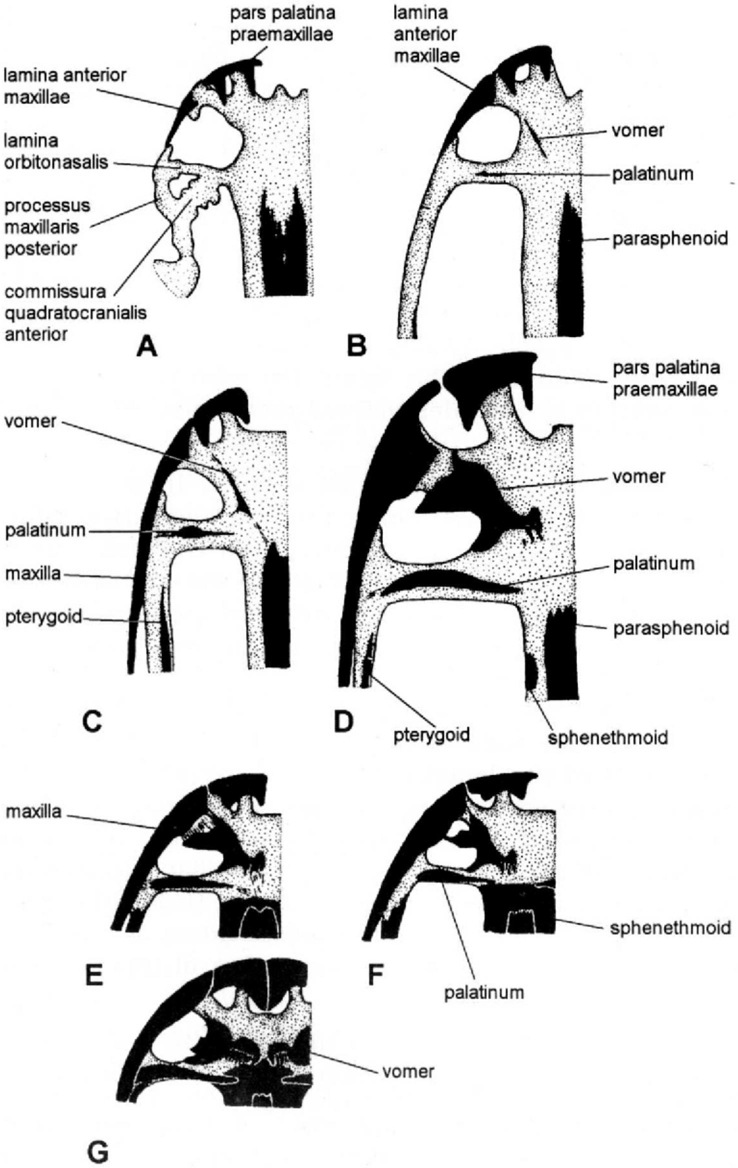


Fig. *48*. Ventral view of the development of the dermal bones in the right anterior part of the anuran palate.

A. *Rana temporaria* at the beginning of metamorphosis.

B. *Rana esculenta* in mid-metamorphosis.

C. *Rana esculenta* at the end of metamorphosis.

D. *Rana esculenta* eight months after metamorphosis.

E. *Rana esculenta* 28 months after metamorphosis.

F. *Rana esculenta* three years after metamorphosis.

G. Adult *Rana esculenta* of unknown age.

From Lebedkina (1979).

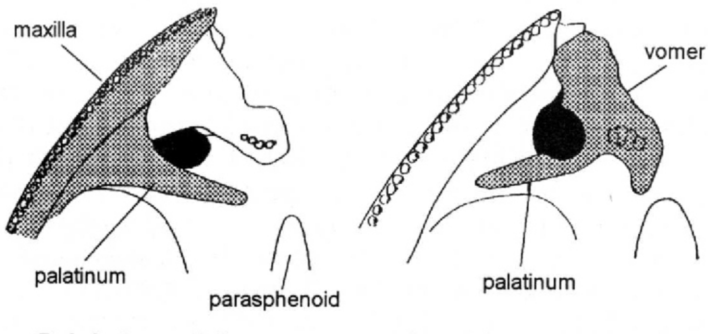


Fig. *49*. Ventral view of the right preorbital part of the palate in *Pelobates* and *Scaphiopus*, showing the final position of the *palatinum* in adults. From Roček (1981).

H. Squamosal

The squamosal, or *squamosum,* was called the "*tympanique*" by Cuvier (1824). Other names that have been used for it include "*temporo-mastoïdien*" (Dugès 1834), "squamosal" (Parker and Bettany 1877), "*os tympanicum*" (Sewertzow 1891), "*paraquadratum*" (Gaupp 1892), and "*os squamosum*" (Gaupp 1906). Reinbach (1939a) called it the "*supratemporo-squamosum*" and "*supratemporale*" as well as the *squamosum.*

The *squamosum* is a dermal bone consisting of an upper lamellar plate and a slender lower part. The dorsal plate, called the *lamella alaris* (Bolkay 1919, his figure 17) may be covered with sculpture on its outer surface. Its anterior margin (*margo orbitalis*) takes part in the formation of the orbit. Its posterior margin is either free or the lower part may support the *annulus tympanicus,* when that structure is present (Fig. 27). Anteriorly, the lamella may be in contact with the zygomatico-maxillar process of the maxilla. The inner surface of the lamella produces the *ramus paroticus* that contacts (and morphologically reflects) the *crista parotica.* The *ramus* forms a dorsal prong that usually invests the *crista parotica,* but is absent in *Bombina* (Slabbert 1945). Similarly, the *lamella* may be in contact with the parietal portion of the frontoparietal, thus forming a bridge over (but not in direct contact with) the dorsal surface of the otic capsule. Examples are *Pelobates cultripes* (Boas 1915, his figures 16, 18) and *Ceratophrys* (Wild 1997, his figure 16) (also see Fig. 46E). The *ramus paroticus* continues posteroventrally as a slender *processus posterolateralis,* adjoining the *pars quadrata palatoquadrati* laterally.

The two morphologically distinct parts of the *squamosum* develop from separate ossification centres (Fig. 50) (Reinbach 1939a; Griffiths 1954a; van der Westhuizen 1961, his figure 27; Lebedkina 1979, her figure 99; Wild 1997, his figure 15A; Hall and Larsen 1998). The lower part originates as a vertical blade of bone lateral to the anterior edge of the *processus muscularis palatoquadrati* with which it is carried backward, passing laterally to the lower part of the orbit until it lies in its definitive position (also see Sewertzow 1891; Gaupp 1893). Shortly before the lower part reaches the posterior border of the eye, the dorsal lamellar part develops as a crescent-shaped centre over the *crista parotica* (see above) and is closely associated with the *processus oticus palatoquadrati.* Later, the lamella becomes separated from the otic capsule; the part of the lamella previously in contact with the *processus oticus* (*crista parotica*) becomes preserved as a groove with raised margins. Both ossifications fuse to give rise to a compound bone. Subsequent to fusion, the *squamosum* completes its backward migration and growth; in the adult skull, its lamellar part may be in contact with other bones, such as the frontoparietal and/or maxilla (Fig. 46E). This developmental pattern has been observed in some Leptodactylidae, Bufonidae, Atelopodidae, and Ranidae (the various taxa differing only in the timing of these events) and it may be a common feature among anurans.

It should be noted that the element described as the "*os supratemporale*" in *Pelobates* (Reinbach 1939b) is not homologous with the dorsal ossification centre of the squamosal because it develops on the dorsal part of the otic capsule, just next to the *arteria occipitalis.* It is therefore part of the frontoparietal (page 1944).

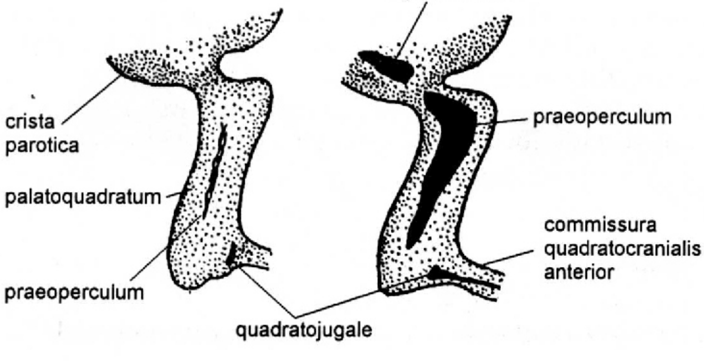


Fig. 50. Right view of the development of the squamosal complex in *Rana esculenta* larvae in mid-metamorphosis (left) and at the end of metamorphosis (right). From Lebedkina (1979).

Sedra (1949) found an independent ossification centre in *Bufo regularis* that he identified as the postfrontal and which later becomes fused to the squamosal, thus forming the "postfrontosquamosal". In *Caudiverbera*, a similar bone was interpreted by Reinbach (1939a) as the *supratemporale*. Also, Wild (1997) found an additional ossification centre that he identified as the otic element or supratemporal of Griffiths (1954a). It is difficult to decide if Sedra's centre corresponds to the dorsal ossification centre of the squamosal that arises in the normal pattern of anuran development, or whether it is an additional centre.

In some hyperossified anurans, e.g., *Pipa pipa*, the *squamosum* is synostotically united with the *annulus tympanicus* ("tympanosquamosal bone" of Trueb *et al*. 2000).

I. Pterygoid

The pterygoid ("*os ptérygoïdien*" of Cuvier [1824]) is a dermal bone consisting of three basic parts: (1) the *ramus maxillaris* directed anteriorly where it contacts the posterior part of the *lamina horizontalis maxillae*, (2) the *ramus posterior* directed posterolaterally and enclosing the *pars quadrata palatoquadrati*, and (3) the *ramus interior* directed dorsomedially to reach the lower surface of the otic capsule. The pterygoid develops on the lower surface of the palatoquadrate (Gaupp 1893). In *Hyla regilla*, it arises from three independent ossification centres, one in the anterior process (*ramus maxillaris*), the second appearing slightly later in the lateral part (*ramus posterior*), and finally the third in the medial arm (*ramus interior*) (Gaudin 1973). Sedra (1950) suggested that in *Bufo regularis* the osteoblasts invading the *ligamentum quadrato-ethmoidale* take part in the formation of the pterygoid.

J. Vomer

The vomer (*sensu* Cuvier [1824]; "praevomer" of Broom [1903] ex Paterson [1939]; "prevomer" of Ramaswami [1935]) develops on the *solum nasi* medial to the *fenestra endochoanalis* (choana) and consists of an antero-posteriorly compressed part that bears teeth on its edge (*torus dentigerus*), and a thin, horizontal part that may give out processes bordering the endochoanal fenestra anteriorly and posteriorly. The vomer arises from two ossification centres in *Hyla regilla*. The first occurs at the posteromedial corner of the choana and the second appears later as a transverse bar, anterior to the first centre (Gaudin 1973). Since Gaudin provided no information about their position relative to endocranial structures, homologization of these two elements of the vomer would be mere speculation. However, it is obvious that the palatine is fused with the posterior part of the vomer in *Scaphiopus* and *Spea* (Boulenger 1899; Ramaswami 1935; Roček 1981, his figure 59; Wiens 1989). In *Hamptophryne* (Microhylidae), the vomer is divided into anterior and posterior components (de Sá and Trueb 1991). In *Megophrys* (Ramaswami 1935) the vomer was also observed to consist of two parts: a small, inner one, and a larger one disposed towards the maxillary. In *Xenopus*, the vomer arises from a pair of small ossification centres flanking the anterior part of the parasphenoid. Both centres later fuse with each other beneath the parasphenoid, so that in adults the vomer is an unpaired median bone (Parker 1876; Trueb and Hanken 1992, their figures 6B–D). Paterson (1939) also described the vomer as a median bone in *Xenopus* but noted no indication of a paired origin; she even considered that the vomer might merely be an anterior part of the sphenethmoid. Smirnov (1994a, his figure 2) observed that in very old individuals of *Xenopus* (9 years of age and older), the vomer may be paired, thereby resembling other anurans, and may fuse with a vestigial palatine. In *Rana* and *Ascaphus* the vomer is penetrated by the *ramus palatinus VII* (de Villiers 1934), probably because of the composite origin of this bone. The vomer is absent in *Pipa pipa* (Trueb 1989; Trueb *et al*. 2000) and *Hymenochirus* (Paterson 1945).

K. Parasphenoid

The parasphenoid (Huxley 1864) has also been called the "*os sphenoideum*", "*Keilbein*" (Ecker and Wiedersheim 1886), "*parabasale*" (Gaupp 1896), and "*os parasphenoidale*" (Reinbach 1939a). It is an unpaired, mostly T-shaped bone, except in the Palaeobatrachidae and Pipidae in which the lateral processes are absent (Špinar 1972, his figure 61; Sokol 1977; Trueb and Hanken 1992, their figure 4; Smirnov 1994a, his figure 1), except for rudimentary ones in very old *Xenopus* (9–12 years of age) (Smirnov 1994a, his figures 1, 4). The median part of the parasphenoid is known as the *pars medialis* ("rostrum" of Sokol 1977). It adjoins the braincase ventrally and extends from the sphenethmoid anteriorly to the orbitotemporal region. Its two lateral processes, the *processus lateralis dexter* and the *processus lateralis sinister* ("subotic *alae*" of Sokol 1977), when present, support the otic capsules ventrally. The median part of the parasphenoid may project posteriorly, as the *processus posterior*, over the posterior margins of the lateral processes. Because the parasphenoid extends over the cartilaginous part of the braincase between the sphenethmoid and prootic, it is of great importance in the architecture of the skull.

The parasphenoid appears as the first bone in *Rana* (de Beer 1937). It develops very rapidly and gives the impression of arising from a single ossification centre. This has been confirmed for *Xenopus* (Trueb and Hanken 1992), but in caudates, which are otherwise quite similar, three centres of ossification are involved (Marcus *et al.* 1935; Lebedkina 1979, her figures 20, 21), one in the orbitotemporal region and a pair of centres below the otic region.

L. Parahyoid

The parahyoid appears late in development and is usually a V-shaped bone (Fig. 51). It is known to appear on the ventral surface of the *corpus hyoidei* in *Alytes*, *Pelodytes*, *Ascaphus*, *Leiopelma*, *Discoglossus*, *Bombina*, *Pelobates*, and *Rhinophrynus* (Fuchs 1929; Stadtmüller 1936; Ramaswami 1942; van Zyl 1950, his figure 18; E. M. Stephenson 1951; N. G. Stephenson 1951; Trueb and Cannatella 1982, their figure 36; Smirnov 1990, his figure 1), but according to Slabbert (1945) is absent in *Bombina*. However, this structure appears late in development and Slabbert may merely have missed it. According to Smirnov (1990), the youngest animal of *Bombina orientalis* to exhibit this bone was a two-year-old, but some older ones still lacked it. The frequency of its occurrence increased with age. The parahyoid is still paired in *Discoglossus* (e.g., van Zyl 1950).

M. Dentary

The dentary, or *dentale* ("*os dentale*" of Ecker and Wiedersheim [1886]; "*sur-angulaire*" of Dugès [1834]), develops as an elongate ossification on the anterolateral surface of Meckel's cartilage. In later developmental stages, the anterior part of the *dentale* fuses with the mentomeckelian.

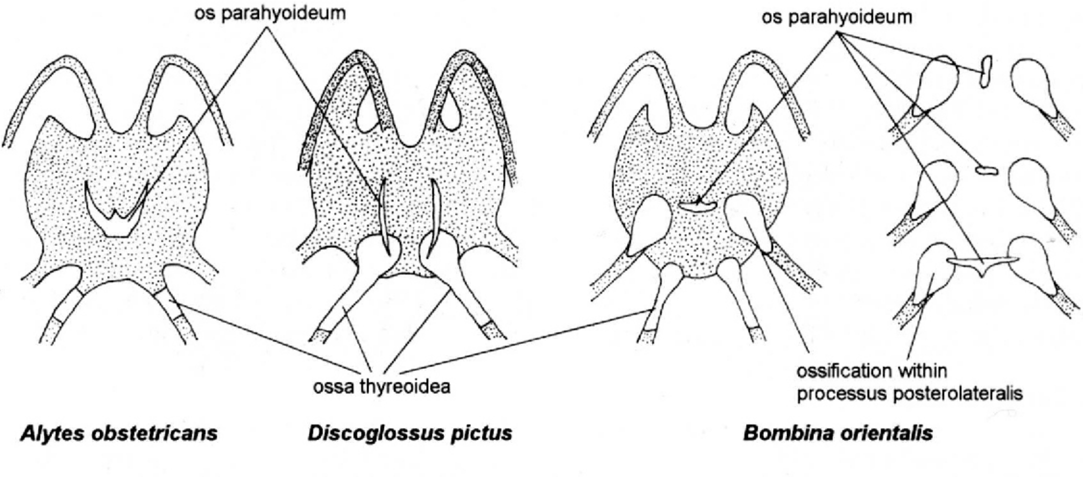


Fig. 51. Ventral view of the hyoid in various discoglossids showing variation in shape of the parahyoid among taxa. Stippling indicates cartilage. From Smirnov (1990).

N. Angular

The angular, or *angulare* (*sensu* Gaupp [1896]; "*angulaire*" of Cuvier [1824]; "*operculo-angulaire*" of Dugès [1834]; "articular" of Parker and Bettany [1877]; "*postoperculare*" of Gaupp [1905]; "*praearticulare*" of Bolkay [1919]; "*dermarticulare*" and "*goniale*" of de Villiers [1930; "*angulospleniale*" of de Sá and Trueb [1991]), develops on the posteromedial surface of Meckel's cartilage. Unlike its counterpart in other anurans, including *Rhinophrynus* (Swart and de Sá 1999), it arises from two centres of ossification in *Xenopus laevis* (Bernasconi 1951; Trueb and Hanken 1992, their figure 7). The primary centre appears along the medial surface of Meckel's cartilage where it grows until it covers about three-quarters of the length of that bone. Then, a secondary centre appears lateral to the posterior third of Meckel's cartilage. Both centres later fuse both dorsally and ventrally so that the posterior third of Meckel's cartilage is encased within the resulting cylindrical bone, with only a knob of cartilaginous *articulare* protruding posteriorly.

O. Additional Dermal Ossifications

Supplementary bones, besides those described above in association with the frontoparietal complex, may develop in the dermal skull of some anurans. These elements can be divided into two categories. The first represents bones that vary in number, shape, and location (especially in relation to the underlying endocranium). For instance, supplementary ossifications occasionally develop in the dermal roof of the skull between the two frontoparietals. Tschugunova (1981), Hanken and Hall (1984), and Smirnov (1989, his figure 1B) termed such bones between the frontal portions of the frontoparietals as "interfrontals" (Fig. 52). They number between 1 and 4, and they vary in position. In old individuals, these ossifications fuse with adjacent frontoparietals, thereby enclosing the frontoparietal fontanelle to varying degrees (Smirnov [1997, his figure 3]). Because of the variation and instability of such bones, and because of the fact that in fossil amphibians they are located only between the anterior parts of the frontals or between posterior parts of the parietals, they can hardly be taken as homologues of the usual bones of early amphibians or their piscine ancestors.

The second category of supplemental dermal bones are those developing in aged individuals, thus giving evidence of latent capacities to develop bones normally lost in the course of phylogeny. For instance, *Pelobates* does not normally have supratemporal, postfrontal, postorbital or tabular bones, as their dissorophid ancestors did. However, in *Pelobates cultripes*, occasionally presumed homologues of these bones can be clearly distinguished within the *arcus postorbitalis*, in precisely the locations they occupied in dissorophids (Smirnov [1993], [1995, his figures 3, 4], [1999, his figures 3, 4]).

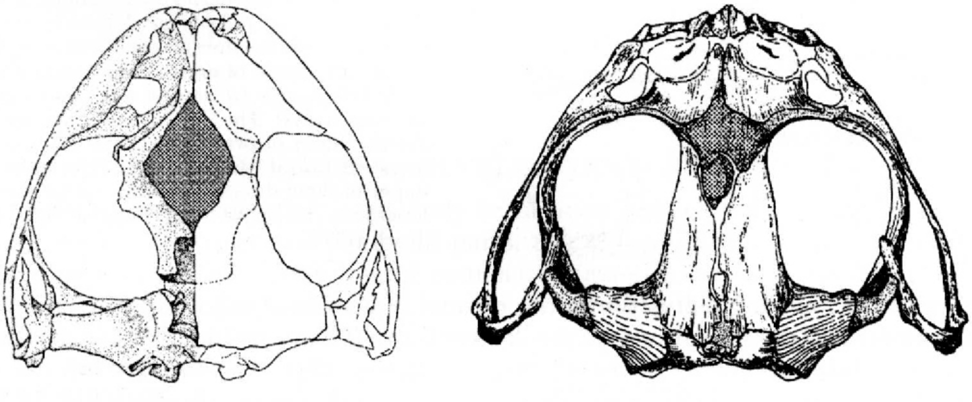


Fig. 52. Dorsal views of an additional dermal ossification (stippled) developing on the dorsal surface of the sphenethmoid. Broken lines indicate the outline of the sphenethmoid. The frontoparietal and nasal bones were removed from the left side of the skull in *Hyla*. *Hyla* from Trueb (1966); *Bombina* from Smirnov (1997).

Also perhaps included among the bones of the second category are the so-called "*(derm-) internasofrontale*" (Reinbach 1939a, his figure 27), "co-ossified ethmoid", and "dermal sphenethmoid" (Trueb 1966, her figures 3, 4, 1970; Duellman and Trueb 1985) of some casque-headed hylids. The dermal sphenethmoid is a dermal ossification adjoining the dorsal surface of the sphenethmoid; it might be homologous with the "internasofrontal" described by Tschugunova (1981) and Smirnov (1997) in *Bombina*. This ossification is remarkably stable both in topography and occurrence. For example, Smirnov found it in 100% of investigated individuals of *Bombina*. Because of their stability, such bones may be taken as homologues of bones regularly occurring in the early Amphibia and their piscine ancestors.

It is sometimes difficult to distinguish whether additional ossifications represent homologues of ancestral bones, or whether they merely result from hyperossification. Nevertheless, some bones cannot be taken as ancestral ones. So-called "rostrals" (Fig. 53) arise in the thickened outer layer of the dermis anterior to the *praemaxillae* in *Peltophryne* (Pregill 1981, his figure 7) and the unpaired "prenasal" and "internasal" (Trueb 1970, her figures 32, 93–95) and later articulate with the anterior tip of the *maxillae*, thereby completing the maxillary arch anteriorly and excluding the premaxillaries from the tip of the snout. These "rostrals" cannot be taken as homologues of ancestral rostral bones because they do not occupy an appropriate area of the endocranium (but see Smirnov 1997). Rather, these elements are associated with hyperossifications in the dermis that also occur in other parts of the skull, and which may later co-ossify with the surface of dermal bones. Hyperossification usually begins after all cranial bones are present; this has been found to be true of *Ceratophrys* (Boas 1915), some Hylidae (Trueb 1966, 1970), and the Discoglossidae (Roček 1993b, his figure 11). A paired (but later fused), weak ossification adjoining the premaxillary symphysis, and another one in the region of the anterior part of the nasals was recorded in a 12-year-old *Xenopus* (Smirnov 1994a); these ossifications remained separate both from the premaxillaries and the nasals.

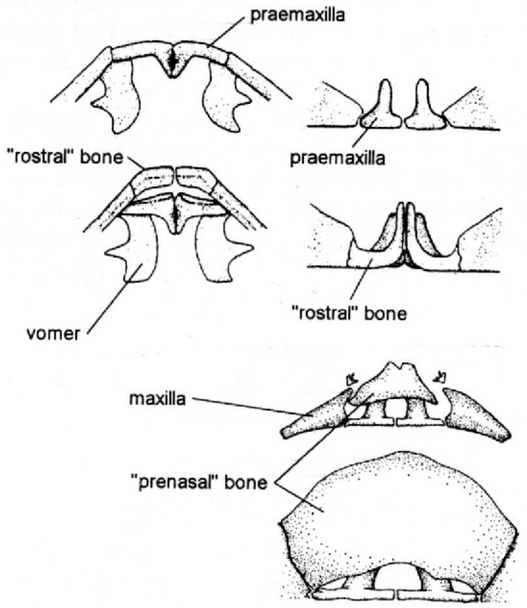


Fig. 53. Additional paired dermal ossifications developing on the rostrum of *Peltophryne longinasa* (middle row) compared with the normal condition in *P. fluviatica* in which only a band of mineralized dermis occurs (upper row). Left figures are ventral views and right ones are anterior views. The lower two drawings represent anterior views of two stages in the development of an unpaired rostral ossification in *Triprion petasatus*. The upper of these drawings is at an earlier stage than the lower one. *Peltophryne* from Pregill (1981); *Triprion* from Trueb (1970).

One needs to distinguish between the dermal ossifications adjoining the sphenethmoid and the uncovered dorsal surface of the sphenethmoid as found in *Pelobates* (Bolkay 1919; Basoğlu and Zaloğlu 1964; Roček [1981, his figure 12]). The surface of the latter is sculptured similarly to neighbouring dermal bones, and is sometimes confused with them (Jarvik 1968; Smirnov 1997). However, the cartilaginous nature of the sphenethmoid is also evidenced by the fact that the open area is progressively covered by the adjacent dermal bones in old individuals. The same phenomenon has been observed in the Eocene leptodactylid *Thaumastosaurus* (Roček and Lamaud 1995, their figure 1A).

VIII. THE SEQUENCE OF OSSIFICATION

There exists a substantial body of literature dealing with the sequence of ossification of the cranial dermal bones in anurans. Besides papers especially targeting this subject, some valuable data may also be gleaned from the normal tables of development for various taxa. Such information is obtained mainly from cleared whole-mounts that were stained *in toto*. However, data obtained by this method differ in some cases from earlier information based on histological analysis of sectioned material. The latter technique sometimes revealed ossifications that were not evident from cleared and stained whole-mounts. For example, the parasphenoid generally is the first bone to appear in whole-mounts. However, in *Pelobates* and *Rana*, histological preparations indicate that well before the gross appearance of the parasphenoid, ossification has already begun in the dorsal part of the *pars facialis praemaxillae*, in the vicinity of the *cartilago alaris*. Also, Hanken and Hall (1988) found that bones were fully differentiated in sectioned specimens long before they were detectable in cleared and stained whole-mounts. Nevertheless, for overall comparative purposes and for establishing the relative time of formation of ossification centres, both within and among species, staining *in toto* provides convenient landmarks (also see Trueb and Hanken 1992).

The order of appearance of the bony elements is probably correlated with functional demands (de Jongh 1968). According to a summary by Trueb (1985, her table 2) and data provided by Erdmann (1933), Trueb (1966, her table 1), Kemp and Hoyt (1969), Davies (1989), Wiens (1989, his table 1), de Sá and Trueb (1991, their table 1), Smirnov (1992, his tables 3, 4), Trueb and Hanken (1992, their table 2), Maglia and Púgener (1998), Hall and Larsen (1998, their table 1), Trueb *et al.* (2000), and many others, generally the first exocranial bone to show ossification in whole-mounts is the parasphenoid, followed by the frontoparietals; sometimes this order is reversed (see Hanken and Hall 1988). Next (during the shift from larval to adult modes of feeding), the ossification of the septomaxilla, premaxilla, maxilla, dentary and angular takes place, followed by that of the squamosal and quadratojugal, and finally that of the pterygoid, palatine and vomer. There is a great deal of taxonomic variation in the time of appearance of the dermal bones in advanced developmental stages; there is also extensive intraspecific variation in the sequence of ossification and its correlation with the development of external morphology, e.g., in *Bombina orientalis* (Hanken and Hall 1984). Trueb and Hanken (1992) indicated that this variation may be dependent on environmental variables, such as temperature, density of larvae, and photoperiod, all of which may influence rate of development (also see Smirnov 1992). Nevertheless, it can be concluded that in normal development most of the skull ossifies during metamorphosis or shortly thereafter. In some species in which premetamorphic development is suppressed, dermal ossification may be delayed; for example, the nasals may not appear until after metamorphosis (Davies 1989). It is of some interest that in such species, unlike other anurans, the earliest bones to ossify are the angular, squamosal and (to a lesser degree) the parasphenoid (Lynn 1942; Hanken *et al.* [1992, their table 2]).

IX. ANURAN DENTITION: DEVELOPMENT AND EVOLUTION

Tadpoles do not possess true teeth, only keratinous denticles. The true anuran tooth of the adult form consists of two principal parts, the crown and pedicel, with a relatively narrow strip of non-calcified dentine and connective tissue between them. Such a tooth is generally called "pedicellate", and is characteristic of all adult caecilians and caudates, except for those that do not complete metamorphosis (Greven 1989), and of those anurans in which the dentition has been retained. However, in some dentate anurans this general structure of the tooth is modified in that there is no dividing non-calcified zone. Such "non-pedicellate" teeth have been reported within the families Pipidae (*Xenopus laevis*, *X. tropicalis*, *Pipa carvalhoi*), Ranidae (*Pyxicephalus adspersus*, but see below), Dendrobatidae (*Phyllobates bocagei*, *P. granuliventris*, *Dendrobates tricolor*, *D. anthonyi*), Leptodactylidae (*Ceratophrys*), and Hylidae (*Hemiphractus proboscideus* and *Gastrotheca riobambae*) (Parsons and

Williams 1962; Lehman 1968; Schultze 1970, his figure 4; Katow 1979; Greven 1984, his figure 2b,d; Shaw 1985; Trueb and Cannatella 1986; Greven and Laumeier 1987; Shaw and Ellis 1989; Tesche and Greven 1989; Smirnov and Vasil'eva 1995; Smirnov 1999). An indistinct zone of division was observed in adults of *Discoglossus* and *Bombina* (Oltmanns 1952; Clemen and Greven 1980).

The first tooth generation may be non-pedicellate in *Discoglossus*, *Bombina*, and *Rana* that otherwise have normal pedicellate teeth in the juvenile and adult stages. Thus, the pedicellate condition seems to develop during metamorphosis in these anurans (Tesche and Greven 1989). In contrast, Smirnov and Vasil'eva (1995) observed some pedicellate teeth in the early developmental stages of *Pyxicephalus adspersus*, as well as in adults, although earlier authors (see above) reported such teeth to be absent in this species.

Some adult anurans have no dentition at all, e.g., *Cacosternum namaquense* (de Villiers 1931b), *Notaden*, *Myobatrachus*, *Pseudophryne*, and some *Uperoleia* (Davies 1989). There is considerable variation, even among congeners, in the presence or absence of teeth. For instance, teeth are present in the upper jaw of *Pipa carvalhoi* but absent in *P. parva* (Trueb and Cannatella 1986); similarly, teeth are present in *Uperoleia laevigata* but absent in *U. rugosa* (Davies 1989).

In contrast to the Caudata and the Gymnophiona, teeth in the Anura appear comparatively late in development. They arise in the dental lamina and after a certain period of growth and calcification, become ankylosed to the jaw bones. In *Pyxicephalus adspersus*, the first indications of teeth in the upper jaw appear in tadpoles of about 55 mm in total length as several cone-shaped tooth-primordia within the dental lamina covering the premaxilla and maxilla (Fig. 54). Calcification of these primordia begins distally and spreads over about 2/3 of the length of the tooth. Another calcification centre then appears on the labial surface of the proximal portion and spreads towards the distal centre. Temporarily there is a narrow strip of non-calcified tissue between the two centres but ultimately even this may disappear. The teeth at this stage of development are already ankylosed to the jaw bone. Their replacement teeth appear as early as the stage of pronounced distal calcification. Resorption begins at the base of the lingual side in the most highly developed teeth of the first generation soon after they become completely calcified. The resulting cavity is partly filled by a small dental germ of a replacing tooth of the next generation. Loss of the first teeth occurs just after completing metamorphosis. The teeth form in units of several tooth-primordia each, and development progresses from the anterior end of the tooth row to the posterior end.

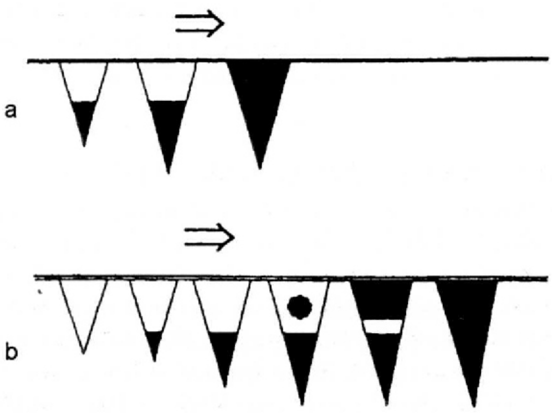


Fig. 54. Tooth development in *Pyxicephalus adspersus* in the first tooth-generation (a) and in second and later generations (b). The extent of calcification is indicated in black. From Smirnov and Vasil'eva (1995).

In the lower jaw of *Pyxicephalus*, the dentary bone bears on its anterior end a prominent dorsal process, called the dentary tusk or odontoid (Sheil 1999) and serves as a "tooth".

The development of anuran teeth of the second and later generations can be summarized as six stages: (1) small non-calcified tooth-primordium, (2) small primordium with calcified tip, (3) tooth with calcified distal part, (4) tooth calcified for 2/3 of its length and with additional calcification centre in its proximal portion, (5) ankylosed teeth with calcified distal and proximal portions separated by a non-calcified zone (the pedicellate condition), and (6) completely calcified and ankylosed teeth. The terminal state is suppressed in most anurans due to morphosis. The development of the teeth of the first generation differs in that calcification spreads from a single centre over the whole tooth, thereby producing the non-pedicellate condition (Smirnov and Vasil'eva 1995).

X. HETEROCHRONY AND ABBREVIATED DEVELOPMENT

Heterochrony and developmental constraints are important in the evolutionary morphology of amphibians (Trueb and Alberch 1985; Davies 1989; Smirnov 1991). It is not possible to treat all examples of heterochrony in the anuran skull, but a few examples can be provided. For instance, *Pelobates varaldii*, *P. syriacus* and *P. cultripes* have the original condition of a complete bony bridge, the *arcus postorbitalis*, connecting the frontoparietal complex to the squamosal. Abbreviated development of the exocranium in *Pelobates fuscus* results in the replacement of this bridge by an unossified ligament (Roček 1981). However, a nearly complete bony *arcus postorbitalis* may develop in extraordinarily old individuals of *P. fuscus* (Smirnov 1995), suggesting that this species is a paedomorphic derivative of an ancestor that had a well-developed *arcus*. This interpretation is consistent with palaeontological data. The first record of *Pelobates* in Europe was of *Pelobates decheni* from the late Oligocene; this species had a broad *arcus postorbitalis* (Böhme *et al.* 1982; Roček and Rage [2000b, their figure 7]). *Pelobates fuscus* appeared only in the Pliocene (possibly in the late Miocene) (Venczel 1997).

A second example of heterochrony is variation in shape of the frontoparietal complex due to restricted development. The bones of this complex may be fused and hyperossified in the European Neogene discoglossid *Latonia*, but not fused in *Discoglossus* (bones separated by a median suture) and *Bombina* (bones separated by a wide fontanelle).

Heterochrony affecting establishment of the posterior connections of the palatoquadrate (e.g., otic process) was mentioned above. Among numerous other examples of heterochrony or abbreviated development in endocranial structures is the variation of the middle ear (Smirnov 1991). Presence or absence (underdevelopment) of the middle ear ossicle in closely related species such as *Bombina orientalis* and *B. bombina* would seem to result from developmental heterochrony. For the same reason, the entire middle ear may either be fully present or reduced in some Microhylidae. Usually, the underdevelopment of one particular structure is correlated with that of other skeletal elements, especially those that are among the last to appear in the sequence of cranial ossification.

XI. ORIGIN OF THE ANURAN SKULL

It is now widely accepted that anurans evolved from temnospondyl ancestors by means of paedogenesis, i.e., the retention of ancestral larval or juvenile morphology in adult descendants (see Roček and Rage [2000a] for review). Following is a summary, partly historical and including rejected opinions, of views on the origin of various structures of the anuran skull.

A. Nasal Region

Morphological and experimental studies have indicated that in adult vertebrates the *trabeculae cranii* (and therefore the nasal septum as well) represent a cartilage of the premandibular visceral arch (Toerien and Rossouw 1977). The *suprarostralia* and the *trabeculae* (including their *cornua*) have long been believed to be part of the premandibular branchial arch (Allis 1923, 1931; Parker ex Born 1876; de Beer 1937; Okutomi 1937); even as early as 1858 Huxley considered the *trabeculae* to be of visceral origin. Bertmar (1959) expressed the view that there are two types of *trabeculae*, one type formed entirely from ectomesenchyme (Teleostomi, Dipnoi, Amphibia) and one formed from both endomesenchyme and ectomesenchyme (Agnatha, Elasmobranchii). Bjerring (1977) believed the trabecular portion of the early gnathostome skull to be of mesodermal origin, and regarded the median nasal septum as the *suprapharyngealia* of the terminal arch united into one structure. It is now generally agreed that the *trabeculae* and their *cornua*, as well as the posterior part of the septum derived to some extent from them, are modified branchial arches and, therefore, originally part of the viscerocranium derived from the neural crest cells (Kuratani *et al.* 1997). The anterior part of the anuran *septum nasi* took its origin from a fusion of the medial walls of the nasal capsules.

Comparison of living anurans with primitive amphibians (as exemplified by *Benthosuchus*, *Dvinosaurus*, and *Palaeoherpteton*) and with osteolepiform fishes (*Eusthenopteron*) can be used as a basis for summarizing evolutionary trends leading towards the formation of the anuran nasal capsule (Figs 55–57). When this is done, one of the principal features is the progressive retention of an ossification process that began as early as in the osteolepiforms. In *Eusthenopteron* the posterolateral part of the nasal capsule was probably cartilaginous (Jarvik 1942). In labyrinthodont amphibians the ethmoidal endocranium was cartilaginous except for the posterior part of the *septum nasi* and the medial sections of the postnasal wall, i.e., approximately as in most living anurans. However, this ossified part of the ethmoidal endocranium, i.e., the sphenethmoid, was still confluent with the ossified braincase. The transition from the temnospondyls to the anurans was accompanied by reduction (fenestration) of the capsular walls. It is remarkable that this reduction included the posterolateral part of the capsule (an area claimed by Jarvik [1942] to be cartilaginous in *Eusthenopteron*]) and affected the *tectum nasi* to a considerable extent (*fenestra nasolateralis*) as well as the lateral wall (the *fenestra endochoanalis* opens laterally).

In most temnospondyls, the ethmoidal endocranium is preserved only as the ossified sphenethmoid. In only a very few of them can the complete structure of the ethmoidal endocranium be reconstructed by means of latex casts or natural casts. In representatives of the Melosauridae, Capitosauridae, and Benthosuchidae, the ethmoidal endocranium consists of a single horizontal plate, the anterior margin of which is arch-like, thus corresponding to the outlines of the snout (Roček 1991a). No horns or structures resembling the prenasal cartilages of anurans are present (cf. Bystrow and Efremov [1940]; Säve-Söderbergh [1936, his figure 8]). The plate is pierced by two fenestrae: the *fenestra endonarina* on the dorsolateral surface and the *fenestra endochoanalis* on the ventral surface. The position of the *fenestra endonarina* is anterior to the level of the anterior margin of the *fenestra endochoanalis*. The distance between these two fenestrae is greater in those individuals in which a septomaxilla is present. If presence of this bone is taken as indicative of greater age (it is not fully developed in some, supposedly younger, specimens), one can conclude that the fenestrae are more widely separated in older individuals. Both fenestrae are connected by a short, broad canal that houses the olfactory organ. A similar condition occurs in pipids (e.g., *Pipa carvalhoi*, pers. obs.) in which both the *fenestra endonarina* and the *fenestra endochoanalis* are located in a vertical plane in young animals, whereas in older ones the latter fenestra has shifted posteriorly. In a natural cast of *Benthosuchus sushkini* there is a broad *septum nasi*, but the *solum nasi* and *tectum nasi* are thin (Roček 1990, his figure 6). The bottom of the anterior fenestra is horizontal and extends on to the lateral margin of the skull. In contrast, the posterior fenestra is rimmed laterally by the vertical wall of the maxilla, on the inner surface of which is a distinct horizontal groove. This suggests that these fenestrae were bounded laterally both by endocranial (cartilaginous) and exocranial (maxillary) walls (cf. Bystrow and Efremov 1940, their figures 32, 33; Säve-Söderbergh 1936, his figure 8).

On the basis of currently available data it seems that the structure of the ethmoidal endocranium of temnospondyl amphibians was essentially uniform. It was compressed dorsoventrally and plate-like. No free elements like those observed in larval anurans were present. Although traces of comparatively subtle connections of the palatoquadrate with the ethmoidal endocranium are preserved in some cases (see below, page 1963), none were found that could be identified unqualifiedly as the *cartilago alaris* and *cartilago obliqua*. There were ambiguous structures in *Buettneria* that could equally well be interpreted as insertions of muscles (cf. Wilson 1941). The alar and oblique cartilages seem to be remnants of the lateral wall of the ethmoidal capsule. Likewise, no structures comparable to the *cornua trabecularum* were identified. Generally, the ethmoidal endocranium of adult labyrinthodonts

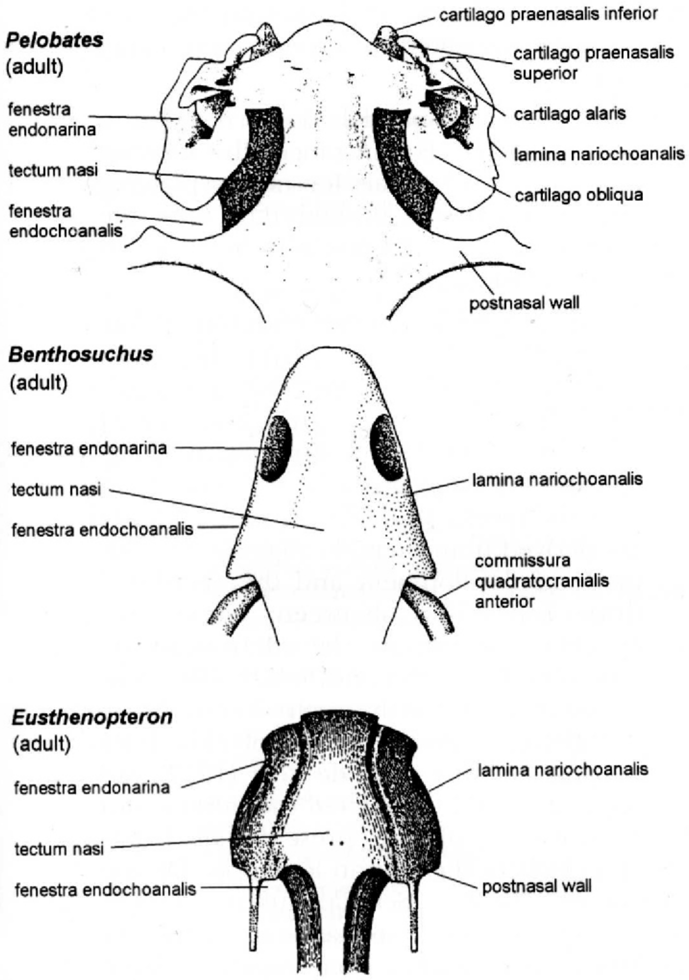


Fig. 55. Dorsal view of the nasal endocrania of anurans (*Pelobates*) compared with those of primitive amphibians (*Benthosuchus*) and osteolepiform fishes (*Eusthenopteron*). Compiled from Jarvik (1980a) and Roček (1981, 1991a).

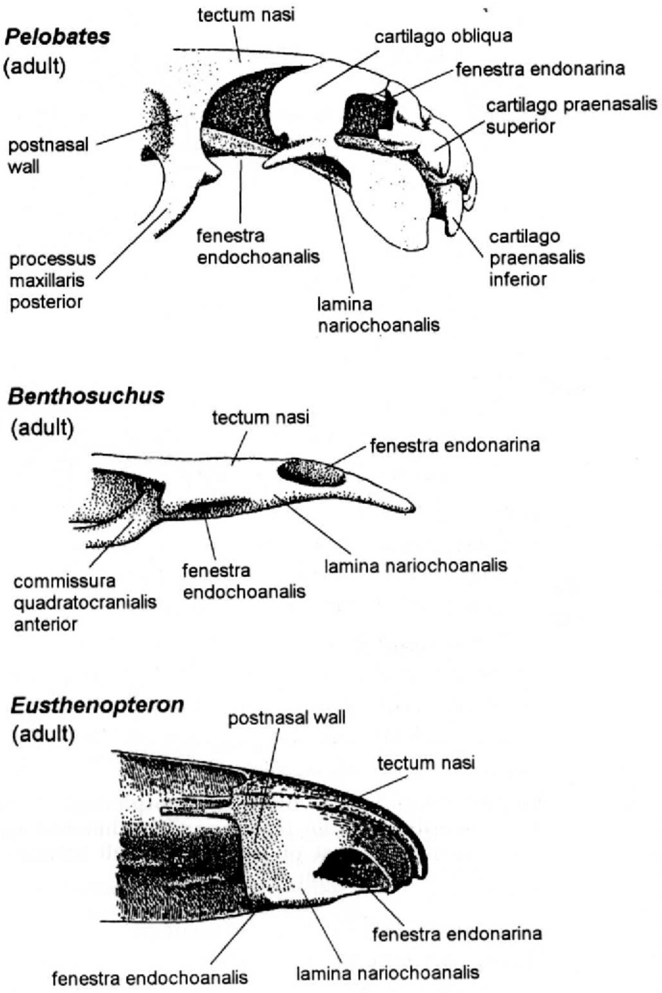


Fig. 56. Lateral view of the nasal endocrania of anurans (*Pelobates*) compared with those of primitive amphibians (*Benthosuchus*) and osteolepiform fishes (*Eusthenopteron*). Compiled from Jarvik (1980a) and Roček (1981, 1991a).

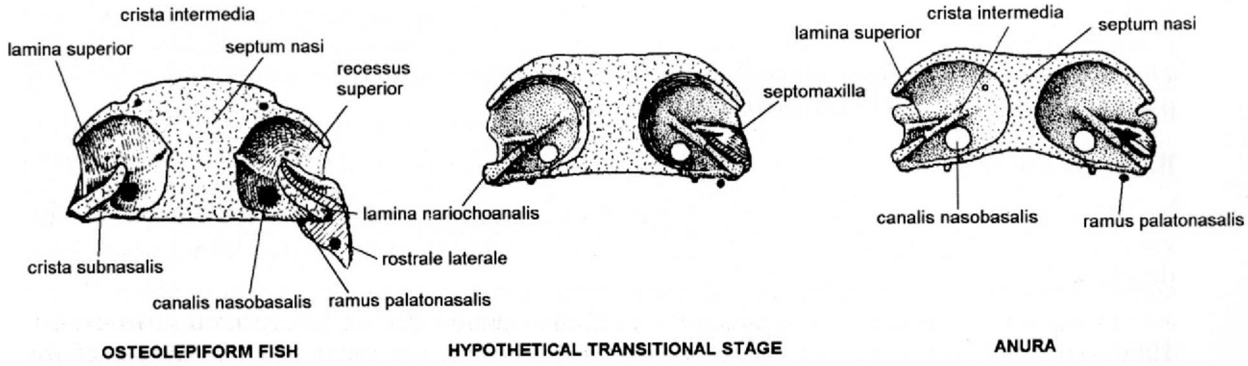


Fig. 57. Posterior view into the nasal cavities, showing the possible transformation of the inner structures during the transition from osteolepiform fishes to anurans. From Jarvik (1981b).

is reminiscent of the condition in larval pipids, but not of that in adult anurans (Fig. 58). It is possible that the *cornua trabecularum* of non-pipids originated by a medial separation of the internasal plate of temnospondyl amphibians.

By contrast, there are other features in which some temnospondyls do correspond to adult anurans. For instance, the number and location of canals for nerves piercing the postnasal wall undoubtedly have the same developmental origin in both groups of amphibians.

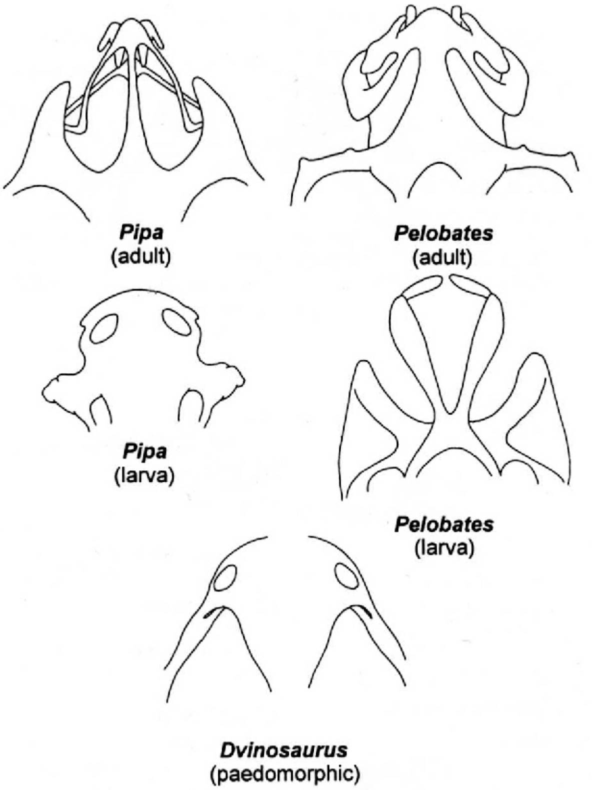


Fig. 58. Hypothetical trends in morphological transformation of the temnospondyl ethmoidal endocranium to that of larval and adult anurans (in dorsal view). From Roček (1990).

In the premandibular region of the anuran larval viscerocranium, the most peculiar feature is the jaw apparatus consisting of the upper and lower labial cartilages covered by a dentigerous horny sheath. The suprarostrals are articulated with the *cornua trabecularum* and probably are derived from them, as suggested by the mode of development and the occasional firm connection between these two elements. By contrast, the infrarostrals are undoubtedly hypomandibulars (Fig. 59), interconnected with each other by a vestigial basimandibular (Nikolyukin 1924 ex Nikitin 1986). Also, de Beer (1937) and Bjerring (1977) considered the infrarostrals as evidence of the presence of hypobranchials in the anuran lower jaw. On the other hand, Schmalhausen (1968) considered them as separate parts of Meckel's cartilages that ossified later. Nikitin (1986) maintained that the lower labial cartilage is derived from the anterior part of Meckel's cartilage, i.e., from the *ceratomandibulare*. An homologue of the *infrarostrale* occurs in *Propterus* and *Lepidosiren* (Peeters 1910 ex van Seters 1922). The kind of jaw apparatus found in tadpoles did not occur in the larvae of temnospondyls, nor is it maintained in adult frogs. Therefore, it must be considered a specialization of anuran larvae. The palatoquadrate (the piscine *epimandibulare* and *epipraemandibulare*) and Meckel's cartilage (*ceratomandibulare)* become functional jaws only after metamorphosis.

The origin of the independent cartilages in the larval ethmoidal region is difficult to explain. The *admandibulare* may be homologized (although with some doubts) with the *paramandibulare* of *Propterus* and *Lepidosiren* (Peeters 1910 ex van Seters 1922). Both the *admandibulare* and *adrostrale* (as well as the *lamina orbitonasalis*) may be considered as vestigial premandibulars or as chondrified ligaments.

B. Postnasal Wall

As evidenced by Reiss (1998), the anuran postnasal wall is actually part of the viscerocranium incorporated into the neural endocranium, as it does not belong developmentally to the nasal capsule.

In adult osteolepiforms, exemplified by *Eusthenopteron* (Jarvik 1942, his figures 49–51, 1980a), the postnasal wall is large. It is pierced by several foramina, the most conspicuous being the *fenestra endonarina posterior* (*sensu* Jarvik 1942, 1980a) which is the canal for the lateral branch of the profundus nerve (*sensu* Bjerring 1989, his figure 2B); this fenestra is

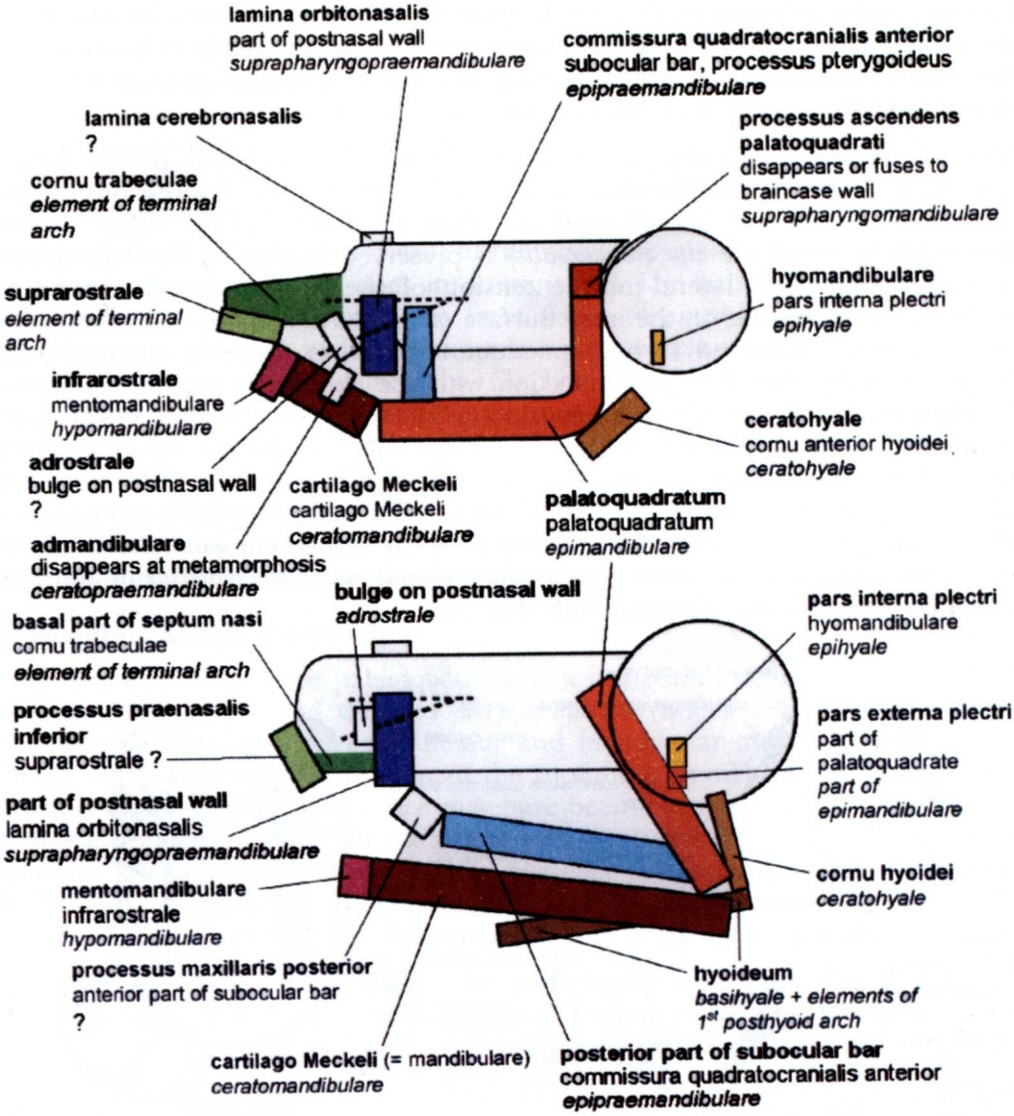


Fig. 59. Scheme showing homologous viscerocranial elements of anuran larvae (above) and adult frogs (below). Part of the larval viscerocranium becomes incorporated into the neurocranium of the adult. Medial and lateral branches of the ophthalmicus nerve are marked by broken lines. The posterior part of the hyobranchial skeleton is omitted. Terms in boldface are the names of structures pertaining to the same developmental stage (names of larval structures in the upper diagram and the names of adult structures in the lower one). Terms in ordinary type indicate the name of the structure in the alternative stage (i.e., in the upper diagram they indicate the name of the homologous structure in the adult; in the lower diagram they indicate the name of the homologous structure in the tadpole). Terms referring to the branchial arches are in italics. To facilitate comparisons, homologous structures, or their derivatives, appear in the same colour.

located in the lower part of the postnasal wall. Two other foramina are important for comparison with anurans. The first is the orifice of the orbitonasal canal (*seu* profundus canal, *seu* the canal for the *ramus ophthalmicus profundus*). This canal enters the nasal cavity dorsolateral to the orifice of the olfactory canal. The second is the canal for the *ramus lateralis narium proprius* (*seu ramus ophthalmicus lateralis*) located almost in the same vertical plane as the orbitonasal canal.

There is limited evidence as to how the postnasal wall developed in labyrinthodonts. The most valuable data are those of Panchen (1964). In a specimen of *Palaeoherpeton* (Anthracosauria) he found signs of growth of the lateral walls of the olfactory canals downward from the roof of the braincase, at the level of the postnasal wall. These downward extensions do not coalesce with the ventral part of the sphenethmoid, thereby recalling the anuran condition, pages 1900–1901. Despite the fact that in some labyrinthodonts there are two additional canals for the vomeronasal nerves (Panchen 1964, 1970) medial to those for the olfactory nerves, it would seem that labyrinthodonts and anurans have a similar origin of the median portion of the postnasal wall.

The lateral portion of the postnasal wall of labyrinthodonts is poorly documented because it did not ossify. In *Palaeoherpeton* it can be restored from impressions on the inner surface of the roof of the dermal skull and from the course of the *ramus medialis nervi ophthalmici* whose canal (*canalis orbitonasalis*) is preserved in part of the lateral surface of the sphenethmoid. The lateral-most extension of the postnasal wall can be restored exclusively from its imprint on the inner surface of the dermal bones. In *Dvinosaurus primus* (Brachyopoidea), considered to be a paedomorphic form, there is an impression of a semilunar convexity that has no connection with the *commissura quadratocranialis anterior* via the *processus maxillaris posterior*, as does occur in *D. egregius*. Shishkin (1973, his figures 47–48, 73A) presumed that the *processus maxillaris posterior* was not developed (Fig. 60). He called the semilunar lateral extension the "*pars postchoanalis*". In *Benthosuchus* there is an horizontal, thin extension of the roof of the postchoanal part of the postnasal wall that in older individuals even comes into contact with the *commissura quadratocranialis anterior*. This extension occurs in the same area as the *processus maxillaris posterior* in anurans but is always continuous with the postnasal wall (Fig. 55).

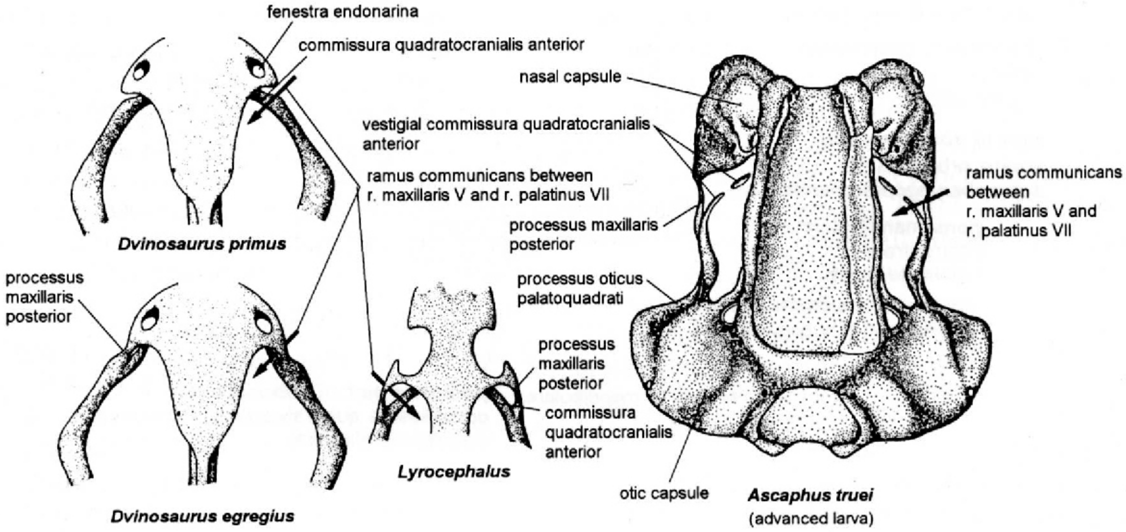


Fig. 60. Ethmoidal endocrania and the anterior part of the palatoquadrate in the primitive amphibians *Dvinosaurus* and *Lyrocephalus*, compared with larval anurans (*Ascaphus*). *Dvinosaurus primus* is a paedomorphic form in which larval characters are retained in adults. From Säve-Söderbergh (1936), van Eeden (1951), and Shishkin (1973).

The *processus maxillaris anterior*, when present in labyrinthodonts (Säve-Söderbergh 1936, his figure 8), seems to be a vestige of the *lamina nariochoanalis*.

Homology of the dorsal portion of the postnasal wall that roofs the olfactory canal in anurans and labyrinthodonts seems to be beyond doubt. A similar supposition may be made in the case of the lateral portion of the postnasal wall, although the development of the area adjacent to the canal for the *ramus lateralis* is not evidenced in fossils. On the other hand, comparison between anurans and osteolepiforms is difficult (Bjerring 1989, his figure 2B; Jarvik 1942).

Comparison of *Eusthenopteron* with larval anurans reveals that the part of the postnasal wall between the orbitonasal canal and the canal for the lateral ophthalmicus branch (*ramus lateralis*) should be considered homologous with the *lamina orbitonasalis*. In modern amphibians, this lamina is often considered to be a process emanating from the *trabecula* (hence its name of "antorbital process") but in fact it develops from a separate blastema that fuses on to the *trabecula* and the anterior end of the orbital cartilage in primitive gnathostomes (Fig. 6) (Holmgren 1943). Noteworthy is the position of the canal for the *ramus lateralis*. In *Eusthenopteron* this canal is located close to the dorsolateral border of the postnasal wall and is roofed only by a small, but distinct, *processus supraorbitalis*, whereas in anurans it is roofed by a rather massive bulge of cartilage (the adrostal) that is fused dorsally to the orbitonasal lamina.

To summarize: (1) The posterior wall of the nasal capsule of *Eusthenopteron* comprises more structural elements than it does in anurans. (2) The proportional changes in the skull that occurred during the transition from fishes to amphibians caused the ventral portion of the postnasal wall, including the *fenestra endonarina posterior*, to become part of the floor of the nasal capsule in anurans. (3) The position of the canals carrying the branches of the *nervus ophthalmicus* suggests that a substantial part of the postnasal wall in fishes and amphibians could have arisen from the same elements. However, the structure of the wall in *Eusthenopteron* can be regarded as specialized to such a degree that the wall in amphibians could more easily be derived from structures in larval osteolepiforms than from those of adults (cf. Jarvik 1942, his figures 65, 67). This is, however, impossible to confirm at present as no larval osteolepiforms have yet been found.

C. Palatoquadrate and its Connections

In osteolepiform fishes, the palatoquadrate is a compound structure consisting of two parts, the *pars autopalatina* and the *pars pterygoquadrata* (Roček 1991b). These structures represent epibranchials of the premandibular and mandibular arches respectively (Jaekel 1897; Jarvik 1980a,b). Also, the location of the profundus branch of the trigeminal nerve supplying the snout suggests that it once may have been a separate nerve that supplied the premandibular segment, whereas the main trunk of the trigeminal supplied the mandibular segment (Gans 1993). Evidence for the putative existence of the premandibular branchiomeric segment can also be derived from the development of the neural crest (Kuratani *et al.* 1997) and from the serial segmentation of the nervous system of the head (Bjerring 1977).

An interesting question is whether the palatoquadrate of anurans (and primitive amphibians) is homologous with the bipartite palatoquadrate of osteolepiforms. It should be noted that the anuran palatoquadrate was recognized as early as 1838 by Reichert (ex Stöhr 1882) as a derivative of two branchial arches, the anterior part consisting of the *epipraemandibulare* and the posterior part consisting of the *epimandibulare*. If the anuran palatoquadrate corresponds to the *pars pterygoquadrata* of osteolepiforms, then it would be reasonable to expect that in anurans there should only be articulations corresponding to the supratemporal and infratemporal (*processus ascendens* and *processus basalis* respectively). However, the two anterior commissures suggest that the *pars autopalatina* is also involved, and that the anuran palatoquadrate is a compound structure incorporating elements of the premandibular and mandibular arches (van der Westhuizen 1961).

The palatoquadrate in osteolepiforms is connected to the neurocranium by seven synchondrotic articulations. These are: (1) the anteromedial ethmoidal articulation with the nasal capsule (rostropalatine articulation in actinopterygians), (2) the posterolateral ethmoidal articulation with the nasal capsule (ethmopalatine articulation in actinopterygians), (3) the interarcual orbital articulation with the *crista suspendens* of the interorbital wall, (4) the suprapterygoid articulation between the *processus ascendens* of the palatoquadrate and the suprapterygoid process of the neurocranium, (5) the basal articulation between the basal process of the *pars pterygoquadrata* and the basipterygoid process of the neurocranium, (6) the paratemporal articulation between the paratemporal area of the *pars pterygoquadrata* and the medial paratemporal area of the otic shelf, and (7) the articulation between the otic shelf and the inner side of the paratemporal process.

The connection of the palatoquadrate with the nasal endocranium in adults cannot easily be traced over the transition between the osteolepiforms and the labyrinthodonts.

In the former, both structures were bony and the connections between them were either synchondrotic or immovable joints. In labyrinthodonts, both connections were represented by continuous cartilages. Since the *commissura quadratocranialis anterior* is connected to the lateral wall of the braincase in the early stages of anuran development, either the anteromedial ethmoidal articulation or the connection between the commissural lamina and the *crista suspendens* (or both) may be homologous with the commissure. Thorough topoanatomical analysis of the region adjacent to the anterior connections of the palatoquadrate in osteolepiforms is needed to decide whether these connections are homologous with those of labyrinthodonts and anurans. It is obvious from comparison of the two groups (Fig. 61) that the condition in labyrinthodonts is more like the earlier developmental stages of anurans than they are to adult frogs. Clearly, adult frogs are more advanced than adult labyrinthodonts, and the two are not equivalent in the connections of their palatoquadrates.

In primitive amphibians, only four connections of the palatoquadrate are preserved (Shishkin 1973). As mentioned above, two of them are homologous with the anterior ethmoidal commissures of fishes (and are thus connections of the premandibular portion of the palatoquadrate); two others, the basipterygoid and suprapterygoid commissures (*processus ascendens* and *processus basalis* respectively) are connections of the mandibular portion.

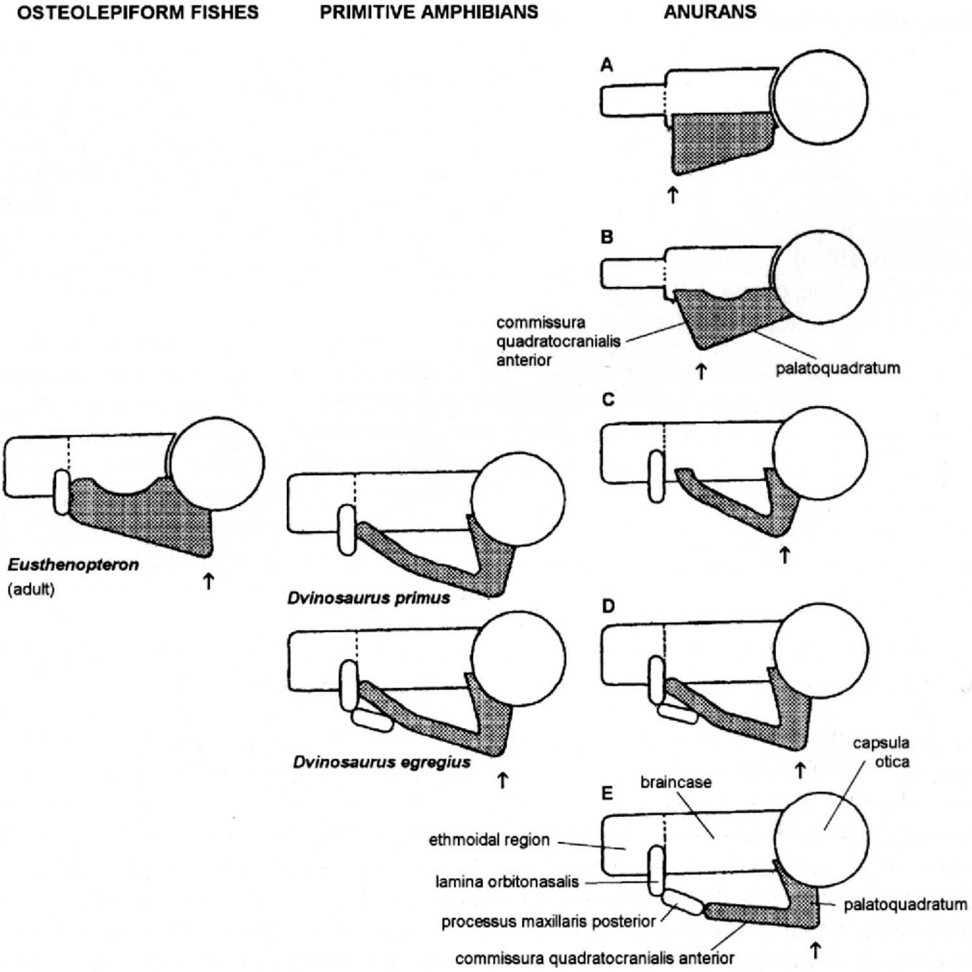


Fig. 61. Diagrams portraying the progressive development of the palatoquadrate and its anterior connections in anurans (*Ascaphus*) from early larva (A) to adult (E), compared with labyrinthodont amphibians (early developmental stage deduced from the paedomorphic brachyopoid *Dvinosaurus primus*), and with osteolepiform fishes (*Eusthenopteron*). *Eusthenopteron* and both species of *Dvinosaurus* are placed at the corresponding levels in the diagram as the corresponding stage of anuran development. Arrows indicate the position of the jaw joint. Stippling indicates the palatoquadrate and its *commissura quadratocranialis anterior*. From Roček (1993a).

In labyrinthodonts (whose sphenethmoid makes up only the mid-section of the postnasal wall and a small part of the orbitonasal partition) the only way to reconstruct the anterior connections of the palatoquadrate is to deduce them from impressions on the inner surface of the covering dermal bones. Accordingly, data on the endocranial structures in such fossil amphibians are scarce. Despite this limitation, Säve-Söderbergh (1936, his figures 8, 14) found imprints of two connections of the palatoquadrate with the nasal capsule in *Lyrocephalus* (Trematosauridae) (Fig. 60). He considered the medial one of these connections to be homologous with the *commissura quadratocranialis anterior* and the lateral one to be an homologue of the *processus maxillaris posterior*. Watson (1940, his figure 23) interpreted similar imprints in *Branchiosaurus*, and followed Säve-Söderbergh's interpretation. A similar condition was found by Shishkin (1973, his figures 49, 73) in three species of *Dvinosaurus* (Dvinosauridae), and he called the equivalent connections the *commissura quadrato-ethmoidalis medialis* and *commissura quadrato-ethmoidalis lateralis* respectively.

There does not seem to be any contradiction to Säve-Söderbergh's interpretation. Moreover, his view is supported by the fact that in paedomorphic forms (such as *Dvinosaurus primus*) the lateral commissure is not closed, thereby resembling the condition in larval anurans before the appearance of the *processus maxillaris posterior* (Shishkin 1973, his figure 73). In *Benthosuchus* there is only a medial commissure; however, in larger (and presumably older) individuals the lateral, postchoanal part almost contacts the palatoquadrate, the two structures being separated only by a narrow slot that most probably was filled by a dorsal outgrowth of the palate. Thus, the condition in younger and older individuals of *Benthosuchus* rather resembles those in *Dvinosaurus primus* and *D. egregius* respectively (Fig. 60). That the medial commissure precedes the lateral one in ontogeny is, aside from topographic relations, the most important fact favouring homology of the medial commissure between anurans and labyrinthodonts. Only Pusey (1943) denied such an homology. He did so on the basis of his assumption that the *commissura quadratocranialis anterior* develops from the posterior basal process. However, Pusey's interpretation of the posterior maxillary process as the anterior maxillary process, seems untenable in the light of Shishkin's findings (also see van Eeden 1951).

The lateral ethmoidal commissure is problematic. In old individuals of *Benthosuchus korobkovi* the *lamina postchoanalis* comes into contact with the anterior section of the palatoquadrate. Consequently, the *processus dorsalis palatini* is reduced to a thin lamina, and only its medial part remains as a column pierced by a canal for the *arteria maxillaris* and its accompanying nerve. Theoretically, further development should result in complete fusion of the *lamina postchoanalis* and palatoquadrate, and consequently in the disappearance of the partition between them. The lateral connection that could arise in this way might be considered the lateral ethmoid commissure or in a broader context, the *processus maxillaris posterior*.

If tracing the anterior connections of the palatoquadrate is extended to those remote anuran ancestors, the osteolepiform fishes, the information is far more complete because of the higher degree of endocranial ossification. The palatoquadrate in *Eusthenopteron* is a single element (Jarvik 1942, 1954, his figure 23B, 1980a, his figure 109; Bjerring 1977, his figure 26), thickened in its anterior (*pars autopalatina*) and posterior (*pars pterygoquadrata*) portions. These two parts are connected by a thin layer of bone called the commissural lamina (*sensu* Jarvik), or the *vinculum* (*sensu* Bjerring). The *vinculum* varies considerably in the extent of its ossification, suggesting that in younger specimens (Jarvik 1954, his figure 23B; Bjerring 1977, his figure 26) it was partly cartilage, whereas in adults (Jarvik 1972, his figure 26A, 1980a, his figure 109) it was completely ossified. The *pars autopalatina* is connected to the ethmoidal endocranium by two commissures (Jarvik 1954, 1980a), the anteromedial ethmoidal articulation (rostropalatine articulation in actinopterygians) and the posterolateral ethmoidal articulation (ethmopalatine articulation in actinopterygians). A third connection of the anterior part of the palatoquadrate complex does not involve the *pars autopalatina* but rather is established between the dorsomedial process of the commissural lamina and the *crista suspendens* of the interorbital wall.

The anuran *commissura quadratocranialis anterior* was considered by Pusey (1938, 1943) as an homologue of the basal process that had moved anteriorly to fuse with the *trabecula* behind the nasal capsule. This view was rejected by Jarvik (1942), van Eeden (1951), and van der Westhuizen (1961). Jarvik (1942, 1954) considered the anterior quadratocranial commissure of anuran larvae (the subocular bar or *processus pterygoideus palatoquadrati* of adults) to be an homologue of the *pars autopalatina* and thus of the epipremandibular of osteolepiform fishes; he further suggested the suborbital ledge (intimately paralleled by the *crista suspendens*) as an homologue of the *trabecula*. The homology between the piscine suborbital ledge and the *trabecula* was confirmed by Bjerring (1977). Sedra (1950) maintained that the *commissura quadratocranialis anterior* and *commissura quadrato-orbitalis* respectively were homologous with the anterior and anterolateral parts of the *pars autopalatina* of the osteolepiform palatoquadrate. Van Eeden (1951) suggested that the *commissura quadratocranialis anterior* in larval anurans must be homologous with the connection between the palatoquadrate and the *crista suspendens*. He based this conclusion on his view that "the anuran connections concern only the dorsomedial surface of the *processus pterygoideus*". Supporting Jarvik's and van Eeden's views is the fact that in early anuran larvae the *commissura quadratocranialis anterior* intimately adjoins the part of the braincase wall that is derived from the *trabecula*, similarly to osteolepiforms in which the homologue of the *trabecula* (suborbital ledge with the *crista suspendens*) is in direct contact with the anteromedial portion of the palatoquadrate. Accordingly, the anuran *commissura quadratocranialis anterior* is not homologous either with the anteromedial (rostropalatine) ethmoidal articulation or with the posterolateral (ethmopalatine) ethmoidal articulation; both of these articulations join the *lamina orbitonasalis* that arises later in outogeny. The *commissura quadratocranialis anterior* joins the orbitonasal lamina only secondarily, after its detachment from the trabecular portion of the wall of the braincase.

A slightly different view was expressed by Swanepoel (1970) who pointed out that the *processus maxillaris posterior* chondrifies independently of the *lamina orbitonasalis* (also see van Eeden 1951; van der Westhuizen 1961; Roček 1993a) and that the whole subocular bar of the adult frog is in fact the *processus maxillaris posterior* fused to the rest of the commissure. This led him to the conclusion that the *processus maxillaris posterior* (which he regarded as an anterior part of the *commissura quadratocranialis anterior*) represents the *pars autopalatina palatoquadrati* and consequently is an homologue of the *processus pterygoideus* (epipraemandibular) of fishes. It may be inferred from its topographic relations with the postnasal wall, especially with the *lamina orbitonasalis*, that the *processus maxillaris posterior* is homologous with the lateral ethmoidal commissure of temnospondyls, and that the residual *commissura quadratocranialis anterior* is the *pars autopalatina*, and thus also the epipremandibular.

The comparatively robust palatoquadrate, located parallel to the wall of the braincase along the wall's entire length, may be hypothesized as an embryonic specialization of early larval anurans. It may be supposed that in anurans and, to a lesser extent also in osteolepiforms, this arrangement was associated with an anterior position of the quadratomandibular joint. Unfortunately, the known specimens of *Eusthenopteron* represent later developmental stages. Adult *Eusthenopteron* (Fig. 61) correspond approximately to a stage of labyrinthodonts represented by paedomorphic forms (*Dvinosaurus primus*). In living anurans, this stage cannot be recorded because at the time the *lamina orbitonasalis* appears, the *commissura quadratocranialis anterior* is already detached from the wall of the braincase, being attached to the postnasal wall either directly or via the *processus maxillaris posterior*.

The *processus oticus palatoquadrati* in primitive amphibians connected the anterolateral part of the otic capsule to the palatoquadrate, just as in the anurans. However, this connection does not correspond to any articulation in osteolepiforms, although the process itself was present in them immediately posterior to the *foramen trigemini*. In osteolepiforms the process was called the *processus paratemporalis* by Jarvik (1980a, his figure 107A) and the *processus oticus* by Shishkin (1973, his figure 78). Obviously, the articulation arose during the transition from piscine ancestors to amphibians. In Carboniferous amphibians, it was still merely a contact between the two elements that in later forms became modified into an osseous and ultimately a cartilaginous connection (Säve-Söderbergh 1936, his figure 15). Its most dorsal part was cartilaginous and could be considered homologous with the *crista parotica* (Shishkin 1973). It was located above the *truncus hyomandibularis VII*, posterior to the course of the trigeminal nerve, as in anurans. On the basis of comparisons of paedomorphic brachyopids with fully developed brachyopids, Shishkin (1973) could even distinguish that the larval otic connection (representing larval specialization) was interrupted in its posterior part, and that only its anterior part was maintained in adults. This condition obviously precedes replacement of the larval otic process by the adult commissure in anurans. According to van Eeden (1951), van der Westhuizen (1961), and Shishkin (1973), two seemingly different otic articulations in anurans (larval and adult) are in fact the same, the former only partly disintegrating during metamorphosis but re-establishing later as a consequence of the expansion of the *crista parotica*. Hence, there is no reason to consider the larval and adult otic connections as two diffrent articulations. This view is also supported by forms with direct development, such as *Leiopelma* and *Eleutherodactylus nubicola* (Lynn 1942) in which the otic process does not disintegrate during development (N. G. Stephenson 1951), and by the fact that in many anurans the otic articulation arises only at metamorphosis (Pusey 1938; Ramaswami 1940; Barry 1956).

Homology of the otic process in tetrapods is uncertain because there are two otic processes (*internus* and *externus*) in sharks and other primitive gnathostomes (Holmgren 1943). The larval anuran otic process was incorrectly considered by Parker (1871) to be the dorsal end of the hyoid arch ("suprahyomandibular") fused to the posterior side of the mandibular arch, whereas he believed the adult otic process to be a derivative of the ascending process. Gaupp (1893) considered the otic process as a larval specialization confined to the Anura. Pusey (1938) obviously considered larval and adult processes as parts of a single structure. Van Eeden (1951) maintained that the adult otic process (anterior portion of the *crista parotica* or *pars cartilaginea* [Gaupp 1896; also see de Villiers 1934; Swanepoel 1966, his figure 14]) originated from the palatoquadrate. According to Swanepoel (1970), the development of the otic process does not follow the same pattern in all Anura thereby implying that the structures described under that term are not always homologous. Van der Westhuizen (1961) considered both larval and adult otic processes as homologous and derivatives of the hind portion of the larval palatoquadrate (i.e., of the epimandibular). Also, he followed Allis (1914) and Holmgren (1940, 1943) in regarding the otic process to be homologous with the lateral commissure of fishes that, in turn, took its origin from the suprapharyngohyal or, according to Holmgren (1940, 1943), from the mandibular ray bars. In contrast, Shishkin (1973, his figures 77–78) considered the *processus oticus* to be homologous with the *processus temporalis* of the palatoquadrate of *Eusthenopteron*, although in that taxon the structure was not yet involved in articulations of the palatoquadrate; he believed such a connection to be a new acquisition in amphibians.

This new connection evolved in primitive amphibians apparently as a consequence of rotation of the mandibular portion of the palatoquadrate. In earlier developmental stages, the mandibular portion (*pars pterygoquadrata*) is located perpendicularly to the long axis of the neurocranium, so that the jaw joint is underneath the anterior margin of the otic capsule. Later, the mandibular portion rotates posteriorly so that in adults the jaw joint is farther posteriorly and below (or even behind) the otic capsule. This can be observed for instance by comparing young and old individuals of *Branchiosaurus* (Fig. 62) (Boy 1978, his figures 20b, 21). Also, in the paedomorphic brachyopid, *Dvinosaurus primus,* the palatoquadrate is suspended nearly vertically from the posterior part of the orbitotemporal region, whereas in fully-developed *Dvinosaurus egregius* it is directed posteroventrally, so that the quadrate is behind the posterior wall of the otic capsule (see Shishkin 1973, his figures 4, 17). It should be noted that in some paedomorphic labyrinthodonts (e.g., *Tupilakosaurus*, *Eobrachyops*), the anterior position of the palatoquadrate is associated with an unossified quadrate, which also indicates ontogenetic underdevelopment (Shishkin 1973).

The posterior part of the osteolepiform palatoquadrate (*pars pterygoquadrata palatoquadrati, epimandibulare*) is connected to the wall of the braincase by means of the

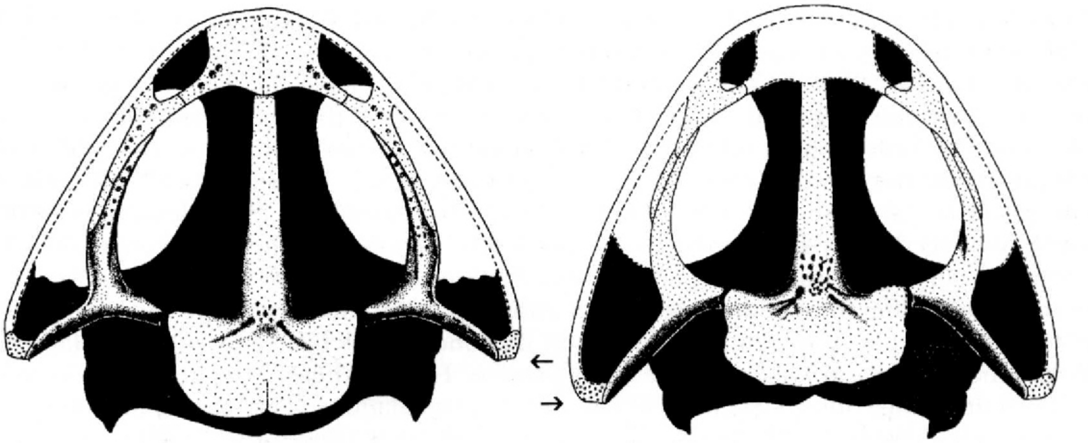


Fig. 62. Ventral view of the palate in young (left) and adult (right) individuals of *Branchiosaurus humburgensis*, showing different positions of the quadrate (arrows) caused by rotation of the palatoquadrate posteriorly. Drawings adjusted to the same size. From Boy (1978).

suprapterygoid commissure. The homologous portion of the anuran palatoquadrate is attached to the rudiment of the braincase (*pila antotica*) by the *processus ascendens*. Very little information is available about this connection in labyrinthodont amphibians because it was not in close contact with dermal bones and consequently did not imprint on their inner surface. Its hypothetical reconstruction in *Dvinosaurus* was published by Shishkin (1973, his figures 47, 49), and in some Triassic labyrinthodonts by Säve-Söderbergh (1936, his figure 15, 1944). The ossified *processus ascendens* is called the epipterygoid in temnospondyl amphibians (Shishkin 1967). This process is consistently associated with the branches of the trigeminal nerve and with the *vena capitis lateralis* (Swanepoel 1970). The *processus ascendens* was considered by Jarvik (1954) to be a fusion of the suprapharyngomandibular with the epimandibular (posterior part of the palatoquadrate). Since it disappears during metamorphosis in the majority of anurans, the *suprapharyngomandibulare* is mostly absent in the skulls of adults.

In the Anura, the basipterygoid articulation, also called the "basal articulation" and the "palatobasal articulation" (Shishkin 1967), is a connection either (1) between the *processus basalis palatoquadrati* and the basipterygoid (or basitrabecular) process of the *trabecula cranii*, or (2) of the *processus basalis* directly with the base of the otic capsule. This connection was originally developed in osteolepiforms as a potentially movable joint. By contrast, in some temnospondyls it also involved the parasphenoid and the pterygoid. These two dermal bones came into contact, thereby causing immobility in the articulation. Consequently, the primary articulation between the *processus basalis* and the neurocranium became vestigial, with the basipterygoid process of the otic capsule being dominant (and ossified) but the basal process only weakly developed or entirely absent (as in Triassic capitosaurids [Shishkin 1973]). Shishkin and Ochev (1966) and Shishkin (1967) observed that in some capitosaurids (*Parotosaurus*) the basitrabecular process arose independently from the basisphenoid. This was interpreted to be arrested development at an early developmental stage in which the basitrabecular process originates independently of the basisphenoid. This condition is similar to that in advanced metamorphic stages of anurans and confirms the view that the basitrabecular process is also a viscerocranial (i.e., neural crest) derivative.

In the Anura, the basipterygoid process is usually considered to be absent (see E. M. Stephenson 1951) and the basal process well-developed (Fig. 63). As noted above, the basal process is attached to the otic capsule behind the *ramus palatinus VII* and not anteriorly as in fishes and other vertebrates. In most anurans, it appears only in the course of metamorphosis, and originates from an independent cartilage that develops between the palatoquadrate and the otic capsule. Differences in the position and origin of the basal process led de Beer (1937) to consider it not to be homologous with the *processus basalis* of osteolepiforms and this opinion was widely accepted for a certain period of time (Pusey 1938; van der Westhuizen 1961). Slabbert and Maree (1945) and van Eeden (1951) observed that the position of ganglion VII is unstable in the Anura and consequently not suitable as a criterion of homology. Accordingly, Shishkin (1973) criticized distinguishing between the basal process of *Ascaphus* and the "pseudobasal" process of other anurans and such a distinction is not generally accepted now. Also Sedra (1950) considered the basipterygoid articulation of *Ascaphus* and *Discoglossus* to be a true basal process, homologous with that of osteolepiforms.

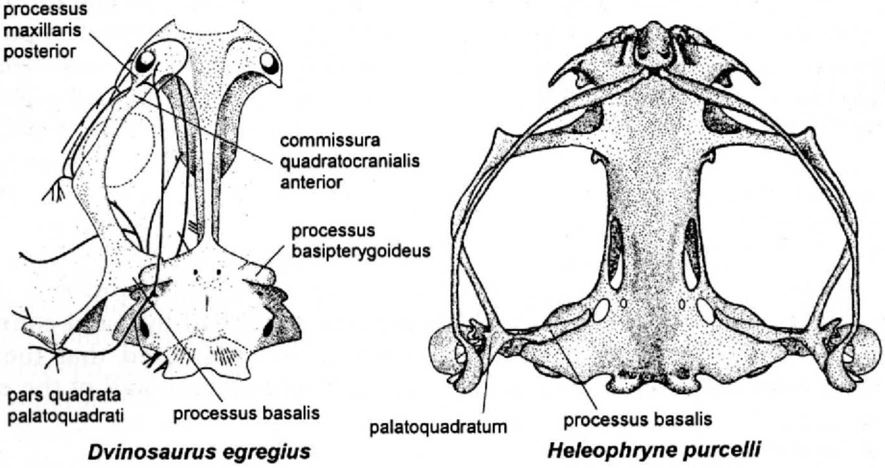


Fig. 63. Ventral views of endocrania showing the basipterygoid articulation in labyrinthodonts (left) and anurans (right). Restoration of the skull of *Dvinosaurus* includes nerves; left part of the skull omitted. From van der Westhuizen (1961) and Shishkin (1973).

It is therefore highly probable that the basal process represents the true *processus basalis* of primitive gnathostomes. Huxley (1875) regarded the basal process as the pharyngomandibular and Sewertzow and Disler (1924) considered it to be the pharyngohyal (not further specified because they did not distinguish between the suprapharyngobranchials and the infrapharyngobranchials), because it develops independently of the palatoquadrate and of the otic capsule and only secondarily fuses with the palatoquadrate (also see Kruijtzer 1931) or with the ventral articular head of the epimandibular (Jarvik 1954; van der Westhuizen 1961).

As noted above, Shishkin (1973, his figure 74) considered the *processus basalis* in anurans to be homologous with the *processus basitrabecularis* (*basipterygoideus*) of labyrinthodonts; it follows from this interpretation that the anuran *processus basalis* is the infrapharyngomandibular. It should also be mentioned that Pusey (1938) believed the basal process to be the outer end of the basitrabecular process which had first become separated from the cranial floor by the destruction of its root and had then become fused with the palatoquadrate; a joint was then secondarily formed between the basal process and the otic capsule. According to Pusey, the original basal process, and the basipterygoid (basitrabecular) process was preserved only in *Ascaphus*.

Another view, expressed by E. M. Stephenson (1951) and N. G. Stephenson (1951), was that the basal process of anurans is of hyoid origin and that it took part in the origin of the columella. This opinion was based on a presupposition that in *Leiopelma* the rudiment of the columella is pierced by the *arteria stapedialis*. However, that is not the case; rather, the artery is the *arteria quadratomandibularis* (Shishkin 1967).

According to Jarvik (1954), van der Westhuizen (1961), and Shishkin (1973), the *processus basipterygoideus* is the infrapharyngomandibular that disappeared in adult (and probably in larval) Anura. Only van Eeden (1951) maintained that the otic ledge in *Ascaphus* represents a retention of the basitrabecular process. If this homology were correct, then the palatobasal articulation would be the intra-arcual one representing the original articulation between the infrapharyngomandibular and the top of the epimandibular, i.e., the basal process. Because of variation in the course of nerves, and because of the fact that an independent chondrification has been observed in some primitive amphibians between the palatoquadrate and the otic capsule (which is also true for the basal process in chondrichthyans [de Beer 1926]), it can be accepted that the basal articulation in anurans is homologous with the basipterygoid (basitrabecular) articulation of osteolepiforms and labyrinthodonts respectively (Shishkin 1967, his figures 1, 2, 1973, his figure 74).

The otic (otohyoid) ledge of some Anura (*Leiopelma*, *Breviceps*) deserves special mention. This is a structure that develops independently of both the palatoquadrate and the otic capsule and which fuses with the floor of the otic capsule; it is, however, connected to the palatoquadrate by a strip of connective tissue. A similar structure in *Eusthenopteron* is also called the otic ledge, and is considered to be a derivative of the infrapharyngohyal (Jarvik 1954). Thus, there seems to be an additional type of connection between the palatoquadrate and the otic capsule that involves an element of hyoid origin. According to Swanepoel (1970), the otic ledge and the basal process together represent the infrapharyngohyal. He extended this conclusion to all Anura and because of the hyoid origin of these structures, he proposed to discard the term "otic ledge" in favour of "otohyoid ledge" (*sensu* E. M. Stephenson 1951) and "basal process" or "pseudobasal process" in favour of "hyobasal process" (*sensu* E. M. Stephenson 1951). However, it is not clear whether the basal and hyobasal connections are homologous. As noted above, van der Westhuizen (1961) suggested that the otic ledge represents the infrapharyngohyal incorporated into the ventrolateral wall of the otic capsule.

D. *Fissura Prootica*

The larval *fissura prootica* separates the *pila antotica* from the otic capsule (Fig. 64). The only (and rather weak) connection between the orbitotemporal and otic regions of the braincase is the posterior part of the *trabeculae*. In some anurans (e.g., *Xenopus*) the space between the posterior ends of the *trabeculae* (bottom of the braincase) consists of a thin layer of mesenchyme that to some extent renders this connection movable, unless movement is prevented by viscerocranial elements, especially the palatoquadrate extending between the ethmoidal and the otic capsule. Later, the *fissura* is closed dorsally by the orbital cartilage that extends posteriorly and fuses with the *taenia tecti marginalis*, to form the *foramen prooticum*.

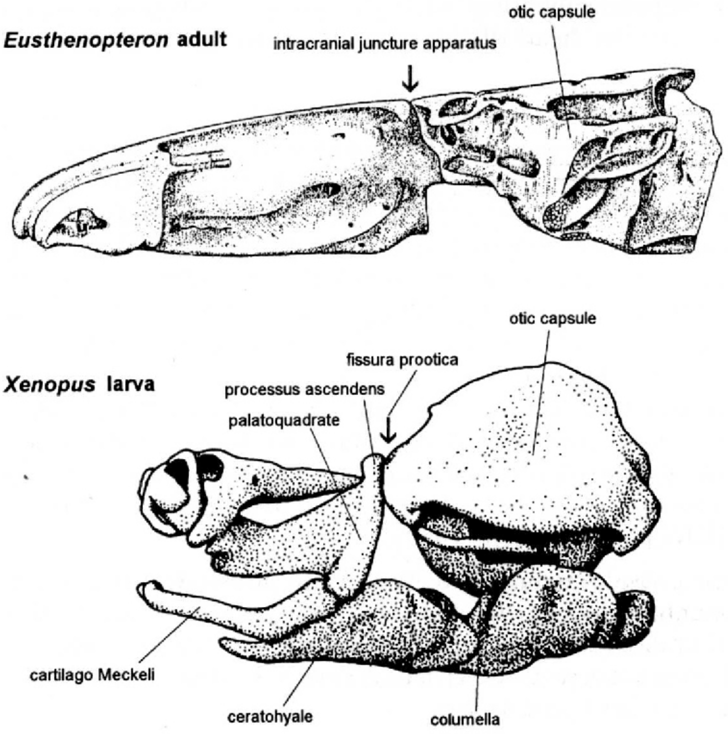


Fig. 64. Left lateral views of the neurocranium of an adult osteolepiform fish (*Eusthenopteron*) and the chondrocranium of a larval pipid (*Xenopus*). *Eusthenopteron* has its lower jaw and hyobranchial skeleton removed. *Xenopus* is at a developmental stage in which the part of the floor of the braincase that develops from the posterior part of the *trabeculae* consists exclusively of mesenchyme and the braincase is divided into orbitotemporal and otic parts. From Roček (1986).

A similar division of the neural endocranium is found in osteolepiform fishes, where it is represented by a complex articulatory system separating the orbitotemporal and otic regions of the endocranium. This articulation is called the intracranial joint (*sensu* Romer 1937) or the intracranial juncture apparatus (*sensu* Bjerring 1978). Osteolepiforms seem to be the only vertebrates that have the adult skull divided into anterior and posterior moieties.

In osteolepiform and porolepiform fishes the apparatus lies at the level of the anterior tip of the notochord, either between the posterior margin of the frontal and the anterior margin of the parietal, or underneath a compound bone of which the frontal and parietal are dominant elements. In coelacanthiforms the location of this apparatus is rather different, and hence it cannot be considered homologous with that of the other groups (Bjerring 1978). The topographic relations of the apparatus is exemplified by *Eusthenopteron*, the best known representative of the osteolepiforms. In this animal, the division runs through (or close in front of) the trigeminal exit, at the level of the anterior tip of the notochord.

The question arises as to whether it is possible to homologize the *fissura prootica* in tadpoles with the "intracranial juncture apparatus" of the osteolepiform fishes. Evidence supporting this homology derives from the fact that both slots lie at the most anterior level reached by the notochord in the course of ontogeny. The same holds true for their topographic relation to the ossification centres of the frontal and parietal. The main difference between the two slots is that in the osteolepiforms the *nervus trigeminus* passes through a separate foramen that lies posterior to the intracranial juncture, whereas in tadpoles it passes through the *fissura prootica*. However, this difference may be due to the fact that in most anurans (except for the Leiopelmatidae and Discoglossidae) there is a single relatively large trigeminofacial ganglion instead of separate trigeminal and facial nerves. The relatively large size of this ganglion, together with a considerable shortening of the anterior part of the otic region (Shishkin 1973, his figure 68), could have brought about the fusion of an originally separate foramen with the *fissura prootica*. The notion that the intracranial juncture and the prootic fissure are homologous is also supported by the topographic relations of the posterior part of the palatoquadrate with the neural endocranium.

It follows from the above that the intracranial joint apparatus found in adult osteolepiforms is present as the *fissura prootica* in metamorphosing tadpoles. The structural changes that occur during the concluding stages of metamorphosis are additions acquired during the phylogenetic transition from the Devonian osteolepiform fishes to anurans.

E. Otic Region

Van Wijhe (1922) found six metotic somites in the Selachii whereas in the Amphibia only three can be recognized during ontogeny. As already pointed out by Elliot (1907), this may be caused by some reduction of the otic somites in the otic region of the Anura, a phenomenon that is morphologically well recognized (Shishkin 1973, his figure 68). However, recent authors accept the view that much of the original segmentation of the axial part of the otic region, as represented by the parachordals (of sclerotomal origin) has been obscured, and that the segmentation is distinct only during the early development of the myotomes (Bjerring 1977). The same may be true for the preotic mesoderm that is retained only as muscular derivatives associated with oculomotor function (Gans 1993). Since it is highly probable that the arrangement of the hyobranchial muscles corresponds to the original segmentation of the somites in the otic region, it can be inferred that the original number of otic somites (not including the occipital one) in the Anura was five (compare Fig. 65 with Bjerring's [1977] figure 14).

Little can be said about the otic capsule except that the cartilaginous edge of the *crista parotica* is a derivative of the palatoquadrate (de Villiers 1934; van der Westhuizen 1961; and others). Swanepoel (1970) claimed that the posterior part of the *crista parotica* is probably the *suprapharyngohyale*. If this is correct, the *crista parotica* is of dual origin, being derived both from the mandibular and the hyoid arches.

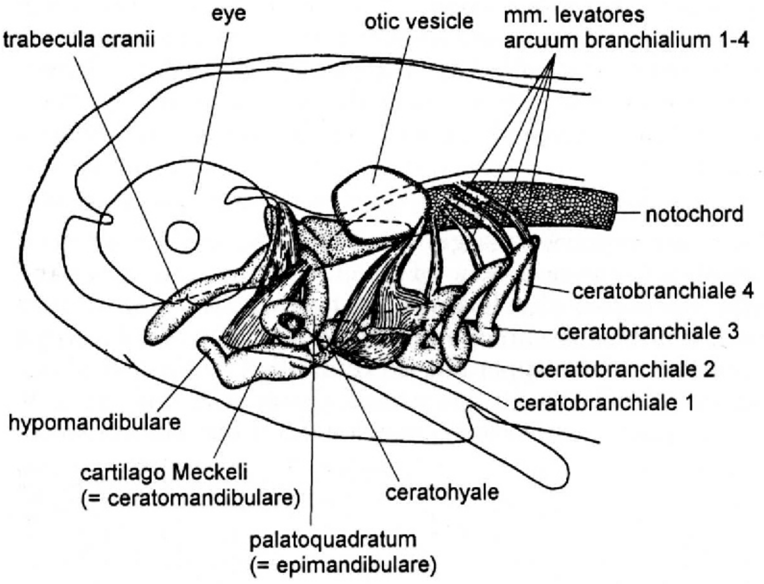


Fig. 65. Reconstruction of the left side of the head skeleton of an embryo of *Hynobius keyserlingi* (total length 11 mm), showing segmentation of the branchial muscles associated with the posthyoid branchial arches. The head skeleton at this stage consists mostly of rudiments of the viscerocranium derived from the neural crest. From Schmalhausen (1955).

F. Middle-Ear Structures

Whereas development of the anuran ear ossicle is satisfactorily known, its evolutionary origin is still a matter of discussion and the homologization of its constituent parts with those of other vertebrates is difficult. The problem is whether or not the dual developmental origin of the ossicle reflects in some way its evolutionary history. In addition to the following account, reviews of this topic have been presented by Reinbach (1950a) and Barry (1956).

Since early in the 20th century (Gaupp 1899, 1913; Fuchs 1905; Dombrovsky 1917, 1918) it has been agreed that the anuran tympanic cavity is homologous with the spiracular cavity derived from the gill slit between the mandibular and hyoid arches of amphibian piscine ancestors. The original spiracular cavity is retained as the tympanic cavity and Eustachian tube in most anurans, and may vary in size according to the age of individual frogs (Ecke 1935, his figure 2).

By contrast, there is no unequivocal agreement regarding the origin of other middle-ear structures. Parker (1876) considered the *operculum* (which he called the stapes; see figures 8 and 9 of his plate 54) as "a new thing in the Amphibia, not existing in the Fishes". Gaupp (1893) observed that the *operculum* of *Rana* develops from tissue occluding the *fenestra ovalis*. Various opinions have been expressed about the origin of this tissue. Barry (1956) believed it to be derived from the perichondrium of the erstwhile solid wall of the auditory capsule. The capsular origin of the *operculum* was also confirmed by Swanepoel (1970) for *Breviceps*. Van der Westhuizen (1961) observed that cells liberated from the ventral rim of the *fenestra ovalis* accumulated on the outer surface of the opercular membrane. He concluded that the infrapharyngohyal portion of the hyoid arch becomes incorporated into the floor of the otic capsule and that the *operculum* is derived from this visceral element. At present it can be taken as fully established that the operculum chondrifies within membranous tissue of the *fenestra ovalis*. It seems highly probable that this membrane is of capsular origin.

The ear ossicle (*columella auris*) is generally believed to be entirely homologous with the hyomandibular of the piscine ancestors of the Amphibia (Gadow 1889; Kingsbury and Reed 1909; Gregory 1915; Schmalhausen 1923, 1953, 1956a,b, 1957b, 1968; Gazagnaire 1932; Eaton 1939b; Westoll 1943a). Gazagnaire (1932) was of the opinion that the entire plectrum in *Rana temporaria* was derived from the hyoid arch. Also Kruijtzer (1931) suggested that the entire plectrum represents the hyomandibular (i.e., *epihyale*). Swanepoel (1970) came to the same conclusion as Kruijtzer and homologized the whole anuran plectrum with the *epihyale*.

According to most of these views the hyomandibular in lobe-finned fishes was connected both to the mandibular arch and to the opercular apparatus (if such was already developed) and its principal function was to correlate motion of the opercular apparatus with the jaws. Beginning with the crossopterygians it gradually lost its mobility, which, according to Schmalhausen (1953), was associated with a transition to another kind of food; as a consequence, this led to autostyly in the early amphibians. The hyomandibular was gradually reduced in size, and took over its new function as a sound-conducting apparatus.

Eaton (1939b) maintained that the hyomandibular in the rhipidistian crossopterygians was connected by its *processus opercularis* (*sensu* Eaton [1939b]; "*processus externus*" and "*processus extrastapedialis columellae*" of Shishkin [1973]; "tympanic process" of Jarvik [1980b, his figure 90A,B]) to the exocranial dermal bone, the *operculare*. In the course of further evolution, the opercular bone was reduced and then replaced by the tympanic membrane (also see Thompson 1966; Jarvik 1980b); the *processus opercularis* (which at this stage of evolution is called the *processus tympanicus* or *processus extrastapedialis columellae*) changed into the *pars externa plectri* (extracolumella). Another outgrowth of the crossopterygian *hyomandibulare*, the *processus ventralis* ("otic process" of Lombard and Bolt [1979, their figure 4b]; "ventral articular head" of Jarvik [1954, his figure 16A]) gave rise to the main part of the ossicle, the stapes, i.e., *pars interna* and *pars media* (stylus, *sensu* Jarvik [1980b, his figure 90C]). Then, according to Eaton (1939b), the ossicle made contact with the braincase by means of the *processus dorsalis (ascendens;* also see Jarvik [1980b, his figure 90C]) of the hyomandibular. However, Shishkin (1973) and Tatarinov (1962) maintained that the *processus ascendens* is a secondary structure that arose during the course of evolution from labyrinthodonts to anurans.

According to Westoll (1943a), the opercular process of the hyomandibular (located below the *operculare*, posterior to the squamosal) is presumed to be homologous with the *pars externa plectri* (his *processus externus columellae* or *processus extrastapedialis columellae*). During the transition from fish to tetrapods, the palatoquadrate shifted anteriorly and the ceratohyal moved behind the hyomandibular. Consequently, the slot between the palatoquadrate and the hyomandibular enlarged and occupied a tympanic diverticle, rimmed by the squamosal anteriorly and by the *processus quadratus* (= *internus*) *columellae* posteriorly. The resulting tympanic cavity is located in a dorsal position, similar to the placement in fishes. These topographic changes also supposedly involved the migration of the *processus externus* and the bifurcation of the *ramus hyoideus* and *chorda tympani*, the latter finally running posterior to the process. The route of the *chorda tympani* behind and below the tympanic cavity in anurans is different from the condition in fishes. De Beer (1937) interpreted the anuran condition as secondary, and as having arisen through a shift of the mandibular and hyoid arches far forward in anuran larvae.

Westoll's view was criticized by Shishkin (1973) on the basis of data from paedomorphic temnospondyls. Shishkin (1973, his figure 82a-d) (also see Fig. 66) argued that the primitive tympanic cavity of labyrinthodonts evolved directly from the spiracular cavity of osteolepiforms. In the course of evolution from the temnospondyls to anurans, the middle ear maintained its original structure, but the ventral connection of the hyomandibular (*processus infrastapedialis* in Fig. 67) was lost; the same is true of the dorsal articular head. In agreement with Eaton (1939b), Shishkin homologized the opercular process of the hyomandibular with the *processus externus* (= *extracolumellaris*) *columellae*, whereas the *pars interna plectri* ("footplate") maintained its original position within the *fenestra ovalis*. Jarvik (1980b) assumed that an extended part, usually called the footplate ("pseudooperculum" *sensu* Gaupp [1896, his figure 20]), in the proximal part of the labyrinthodont and anuran columella, represents the peculiar tongue-like lamina of osteolepiform fishes. This structure maintains a close relationship with the *cornua hyoidei* as indicated by the observations of Litzelmann (1923), who described fusion of the columella with the *cornu hyoidei* in *Bombina*.

Investigation of the detailed morphology of the hyomandibular revealed that the anuran columella is only partly homologous with its piscine counterpart. There are several reasons for adopting this view.

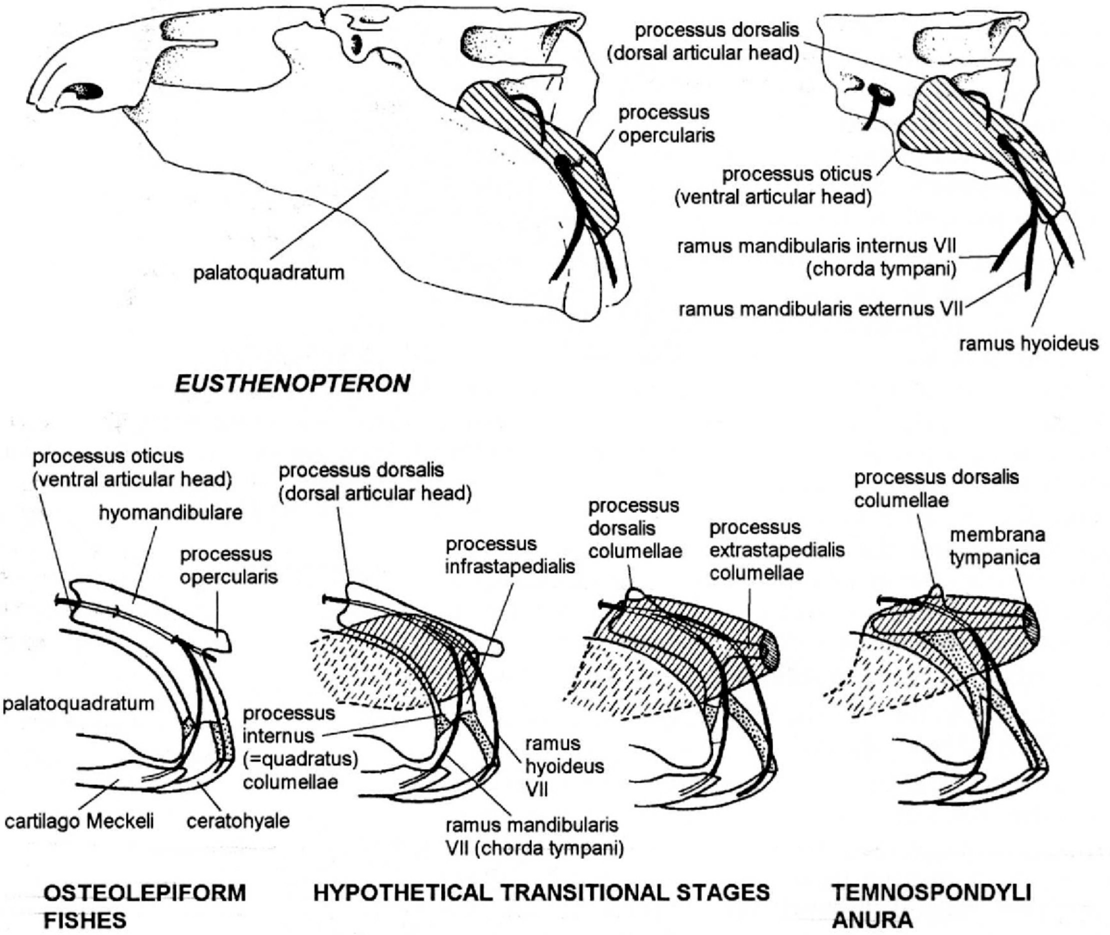


Fig. 66. Evolution of the anuran ear ossicle from the hyomandibular of osteolepiform fishes. Drawings are of the left lateral view. Upper: The skull of *Eusthenopteron* with its palatoquadrate intact (left) and the otooccipital region with the palatoquadrate removed. Hatching indicates the hyomandibular. Lower: A series of evolutionary changes illustrating Westoll's hypothesis. Hatching indicates the tympanic cavity and the *tuba auditiva*. From Shishkin (1973) and Lombard and Bolt (1979).

Salvadori (1928) found a transient ligament between the primordia of the *ceratohyale* and the future *plectrum* in *Bufo* and *Rana*, and considered the *pars interna* (as well as the operculum) to be of capsular origin, and the *pars media* (and *pars externa*) to be derived from the hyoid arch. Barry (1956) expressed the opion that because the *pars interna* develops in the same mesenchymatous tissue as the operculum, it (including the *pars media*) should be considered capsular in origin. Barry followed Reinbach (1950a) who even proposed the term *"pars otica columellae"*. Van der Westhuizen (1961) believed the *pars interna* (as well as the operculum and some other structures) to be a derivative of the *infrapharyngohyale*. However, it is now generally agreed that the *pars interna plectri* is a derivative of the hyoid arch.

By contrast, the distal part of the plectrum (i.e., *pars externa plectri*) and the *annulus tympanicus* develop in Anura from the palatoquadrate. Thus, an hyoid origin is restricted to the *pars interna* (including an ossified part termed the *pars media*). Since both the *annulus tympanicus* and the *pars externa* are undoubtedly derived from the *pars quadrata* of the palatoquadrate, they are derivatives of the mandibular arch. This condition derives from hyostyly, i.e., from the connection of the posterior part of the palatoquadrate to the neurocranium through the *hyomandibulare* (Fig. 66). It should be noted, however, that van der Westhuizen (1961) believed the *pars externa plectri* to be a derivative of the *epihyale*.

The comparative anatomical and developmental evidence is in agreement with Shishkin's (1973) view that the opercular bone cannot be homologous with the tympanic

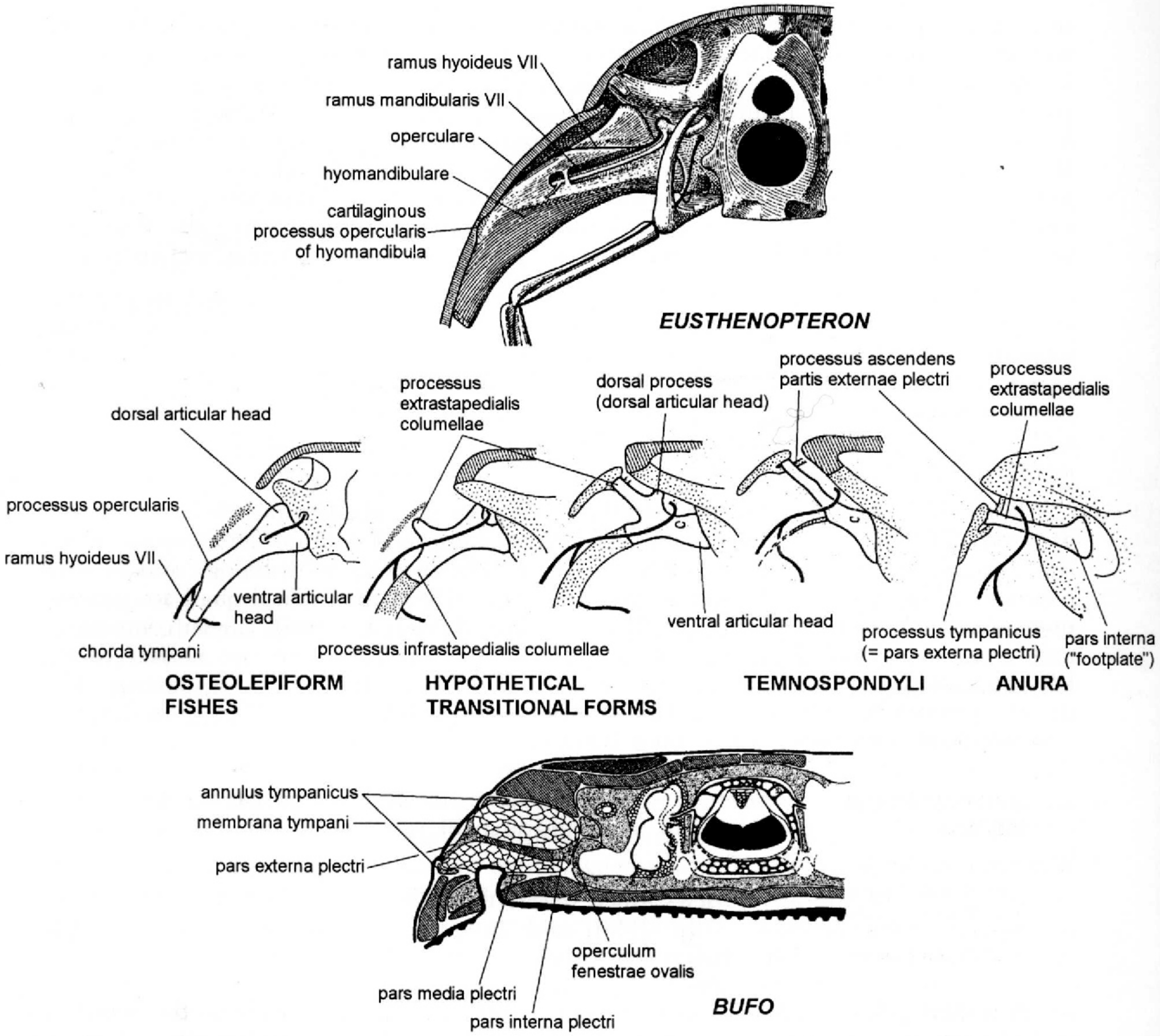


Fig. 67. One of the several schemes explaining the evolution of the anuran ear ossicle from the hyomandibular of osteolepiform fishes, as exemplified by *Eusthenopteron*. Drawings are of the left part of the skull in posterior view. The anuran condition is illustrated by a cross-section through the otic region of a metamorphosed *Bufo*. From Ecke (1935), Jarvik (1954), and Shishkin (1973).

membrane because of its location behind the spiracular cavity in fishes (predecessor of the *cavitas tympanica* of tetrapods). Rather, it could be a derivative of the gill rays of the palatoquadrate (Swanepoel 1970). Reinbach (1950a) suggested that the *pars externa* (= extracolumella) was derived from fish spiracular cartilages originating from the palatoquadrate.

Tatarinov (1962, his figure 2) suggested that the *processus ascendens plectri* evolved as an organ restricting the range of vibrations of the *pars externa plectri* and tympanic membrane. The *cartilago paraarticularis* found in adult *Bombina* is a vestige of the *pars externa plectri* (Stadtmüller 1931c).

Several authors have re-analysed the relationship between the processes of the osteolepiform hyomandibular and their equivalents in anurans. Lombard and Bolt (1979) confirmed that the original otic process ("ventral articular head" of Jarvik [1980b]) of the hyomandibular inserts in, and attaches to, the rim of the *fenestra ovalis* of the otic capsule in adult anurans. Similarly, the original opercular process on the hyomandibular articulates with the tympanic membrane in adult frogs. In this conclusion they agreed with Shishkin. However, according to Lombard and Bolt (1979), "the cartilaginous connection to the palatoquadrate in larval anurans" is homologous with the original *processus quadratus hyomandibulae*. Furthermore, a blastematous connection of the rudimentary columella to the ceratohyal in anuran larvae (persistent as a ligament in some adults) may correspond to the original *processus hyoideus hyomandibulae*. Thus, Lombard and Bolt believed that during ontogeny evidence of all primitive hyomandibular connections occurs in some frogs, with the connections of the quadrate and hyoid disappearing prior to, or during, metamorphosis.

In the earliest tetrapods (*Acanthostega*), the ear ossicle is still robust, with its proximal part (footplate) large and presumably abutting on to the otic capsule at the *fenestra ovalis*, whereas its distal part is pointing into the otic notch bordered by the tabular. As in other primitive amphibians, the ossicle, because of its large size, was still unable to conduct vibrations from the tympanum to the otic capsule (Tatarinov 1962); most probably, it was still involved in kinetic movements of the palate and cheek, as was its predecessor in osteolepiform fishes (Clack 1989).

Bolt and Lombard (1985) compared the footplate (i.e., the *pars interna plectri*), as well as some other features, of temnospondyl labyrinthodonts and anurans, and concluded that these structures are similar in the two groups, both in their morphology and in their function. They derived the anuran tympanic annulus from the "dorsal quadrate process" of dissorophoids, such as *Cacops*. Also, Tatarinov (1962, his figure 1) made similar comparisons and concluded that among extant amphibians, the anurans are the closest to the labyrinthodonts in terms of the structure of their sound-conducting apparatus. It is therefore not astonishing that in *Triadobatrachus*, a pro-anuran amphibian from the early Triassic (Rage and Roček 1989, their figure 2), the columella is reminiscent of that of *Doleserpeton* (Bolt and Lombard 1985, their figure 2) which, in turn, does not differ much from that in anurans. However, this does not solve the problem of whether the anuran ear ossicle is derived entirely from the hyoid arch or whether it also includes material from the mandibular arch.

In contrast to the above views which derive the anuran ear ossicle exclusively from the piscine hyomandibular, Villy (1890) and Tumarkin (1955) emphasized the dual developmental origin of the anuran ear ossicle and claimed that it is only partly, or not at all, homologous with the osteolepiform hyomandibular. It should be noted that in the evolution of the Amphibia the transmission of sound via tympanum → ear ossicle → *fenestra ovalis* is not the only mechanism known. In the early Amphibia, sound reception was via *squamosum* → ear ossicle → *fenestra ovalis* (e.g., in *Mastodonsaurus* [see Schoch 2000]). Another method was that sound vibrations were transmitted via the anterior limb → pectoral girdle → *operculum fenestrae ovalis*; this was later taken over by the Caudata and some Anura. The hyomandibular was not involved in the last method and consequently this element became reduced or disappeared. In contemporary Caudata it disappeared probably as a consequence either of an aquatic, or according to Schmalhausen (1957b), a subterranean way of life. In the Anura, it either was only partly reduced or, according to Tumarkin (1955), its proximal part arose as a new structure. This would explain the fact that in the Anura the plectrum arises only after the operculum. If Tumarkin's hypothesis is correct, then the ear ossicles of the Anura and Caudata are not homologous. Also, de Villiers (1936) denied the hyoid origin of the plectrum and operculum, as well as the ontogenetic continuity between these two structures and the palatoquadrate. For another mechanism of reception of sound in frogs and some fossil amphibians see Bjerring (1997).

In order to resolve developmental peculiarities found in anurans, the theory that the anuran columella is strictly homologous with the *hyomandibulare* of osteolepiform fishes and primitive amphibians was modified by Schmalhausen (1923, 1953). He, followed by van der Westhuizen (1961), maintained that only the *pars externa* is homologous with the *hyomandibulare* (*epihyale*) which was secondarily incorporated in the palatoquadrate, whereas had already been lost by all paedomorphic temnospondyls related to anurans. Further modification of the hyobranchial apparatus of temnospondyl larvae led to the hyobranchial skeleton of modern anuran tadpoles.

The *commissurae terminales* that unite the posterior ends of the ceratobranchials develop after the branchial arches have already formed and hence are new structures. These elements are unique to larval amphibians and hence are not homologous with the epibranchials of fish (Severtzov 1970). The entire hyobranchial skeleton acquired an oblique position relative to the longitudinal axis of the body. Severtzov maintained that the transformation of the hyobranchial apparatus in anuran tadpoles took place not as a result of direct adaptation to food of a different type, but indirectly because of changes in other organs.

The *hypohyalia* do not change their position but spread out and fuse, forming the *pars reuniens*, a structure that remains procartilaginous throughout larval life. According to Severtzov (1969, 1970) the *copula anterior* arose anew during evolution of the larvae of frogs and has no homologue among the ancestors of the Anura (but see below). The medial parts of the ceratohyals increased in size, and the hypohyals fused to form the *pars reuniens* (de Beer 1937; Severtzov 1980a; Haas 1997). Similarly, the hypobranchials drew together and fused into the *planum hypobranchiale*. Collectively these changes resulted in the formation of a broad disk that functioned in the pumping movements of the hyobranchial skeleton.

Severtzov (1969, 1970, 1980a) postulated the anterior copula to be a new formation characteristic only of anuran larvae, whereas Jarvik (1963, 1967a) maintained it to be an homologue of the sublingual pivot of the Devonian osteolepiform fish *Eusthenopteron*. Jarvik considered the posterior copula to be homologous with *basibranchiale I* of the Caudata and the posterior extension on the copula (called the *urohyale* by Severtzov [1980a, his figure 1A]) to be homologous with the *processus urobranchialis* of salamanders' basibranchial I. Haas and Richards (1998), following earlier authors (e.g., Stöhr 1882), considered the posterior copula to be homologous with the *basihyale*.

It should be recalled that the basibranchials are of mesodermal origin (Fig. 5) and that they may represent ossified muscles of primitive aquatic gnathostomes.

The *ceratohyale*, half of the *pars reuniens* (the *hypohyale*) and the *basihyale* (anterior copula) constitute the lower part of the hyoid arch, whereas the posterior copula, *planum hypobranchiale* (the *hypobranchialia*) and constituent parts of the branchial basket (the *ceratobranchialia*) make up the lower parts of the posthyoid branchial arches (also see Severtzov 1980b).

In adult amphibians, the hyobranchial apparatus transforms into the hyoid, a skeleton on which the muscles of the floor of the mouth insert (Fig. 35). Although the apparatus no longer serves in support of gills, as it did in fishes, the amphibian hyoid is still involved in respiration. In the absence of ribs, breathing in anurans relies on pumping by the floor of the mouth. The dorsal/ventral movements of the hyoid accomplish this and are in fact respiratory movements (Severtzov 1971 and references therein). The entire hyoid complex was profoundly transformed from the condition occurring in adult temnospondyls and caudates. There was further loss of distal elements (ceratobranchials). In the hyoid of adult anurans, the proximal section of the *cornu anterior* is an homologue of the piscine *hypohyale*, whereas its distal part (separate from the proximal part in the Pelobatidae and the Megophryidae [Severtzov 1971]) is homologous with the *ceratohyale*. The *processus posterolateralis* represents the former *hypobranchiale I*, and the *processus posteromedialis* (*cornu posterior* of Severtzov [1980a]) is an homologue of *hypobranchiale II*. The *processus anterolateralis* is a new structure.

H. Frontoparietal Complex

In primitive living actinopterygians (*Amia*, *Polypterus*), and also in some Teleostei (e.g., *Esox*), the frontal bone arises on the dorsal margin of the lateral wall of the braincase, i.e., in a location similar to that of the frontal in anurans. It forms from several ossification centres along different neuromasts of the supraorbital sensory line (Fig. 68). In *Amia* and *Esox*, there are three ossification centres, termed by Lebedkina (1979, her figures 81, 82) in accordance with Pehrson (1922, 1940, 1944) as f^1, f^2, and f^3 (abbreviations for *frontale 1*, *frontale 2*, and *frontale 3*). These centres soon fuse into a single bone. The fusion begins with f^1 and f^2; later f^3 is incorporated and if an f^4 is present it fuses as well. On the basis of the topographical relationship of these ossification centers to the brain and to underlying endocranial structures, Lebedkina (1979) concluded that the first two frontals adjoin the *cartilago orbitalis* anterior to the level of the foramen for the optic nerve. The third frontal adjoins the posterior part of the *cartilago orbitalis*, behind the level of the *foramen opticum*. The same situation occurs in primitive caudates, e.g., *Ranodon* (Fig. 69). In anurans (Fig. 42) the sequence is different in that the earliest ossification centre to form is homologous with *frontale 3*, not with *frontale 1*.

The *parietale* arises in fishes from one or two ossification centres on the *canalis semicircularis anterior*. These centres either fuse together, or remain separate as two parietals even in adults (e.g., Devonian *Osteolepis* and extant *Polypterus* [Jarvik 1947, 1948, 1967b]).

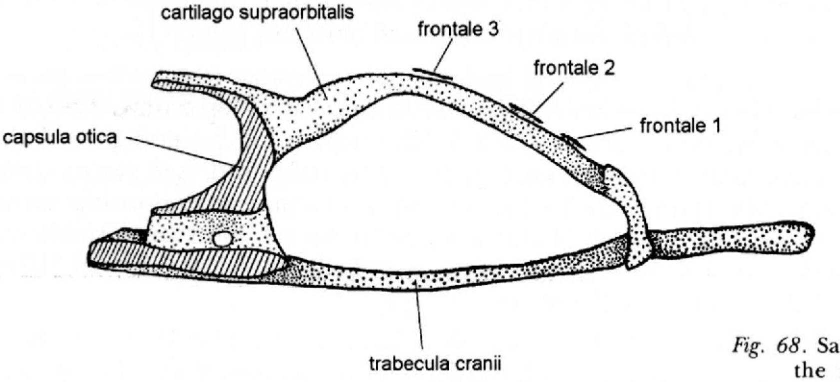


Fig. 68. Sagittal section of an embryo of the fish *Esox lucius* (total length 13 mm) showing the rudiments of three frontals which later fuse. From Lebedkina (1979).

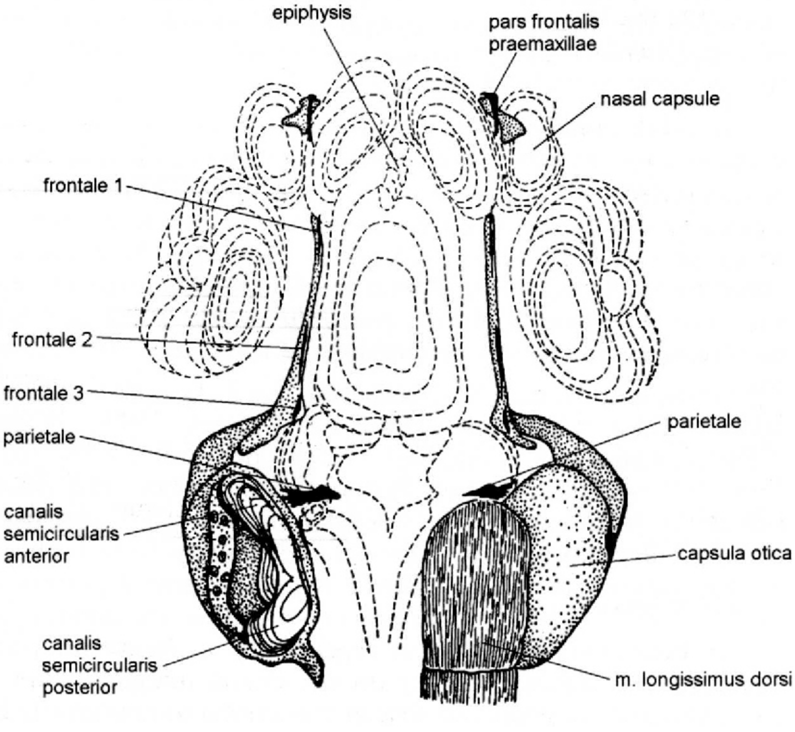


Fig. 69. Dorsal view of the skull of an embryo of the primitive caudate *Ranodon sibiricus* (24 mm total length), showing three ossification centres of the frontal. Part of the left otic capsule has been removed. The brain, bottom of the braincase, nasal capsules and eyeballs appear in dotted outline. From Lebedkina (1979).

Lebedkina (1979) used the spatial relationship of the ossification centres to the underlying endocranium as a criterion of homology in comparing the Caudata and the Anura. She concluded that in the Caudata the frontal of adults is a composite bone resulting from the fusion of three original frontals, whereas in anurans it corresponds only to frontal 3. If this is true, the conclusion by Sedra (1949), Eaton (1942), and Ramaswami (1956) that the frontoparietal of anurans is represented only by the frontal appears to be incorrect.

Of the supplementary ossifications found in some Pelobatidae, only those that are topographically stable and occur in all individuals are considered true ossification centres of dermal bones. Some of these ossifications arise on the dorsal margin of the orbital cartilage and can be homologized with the frontals; when the ossification extends on to the roof of the otic capsule it is homologous with the frontoparietal. A similar, regular ossification occurs in *Eopelobates* and *Pelobates* as an unpaired median element adjoining the *tectum synoticum*. Undoubtedly, it is homologous with a similar element in a fossil anuran from the Green River Formation. Also, the part of the frontoparietal in *Pelobates* that arises lateral to the *arteria occipitalis* is stable and thus fulfills the above criteria. These regular and topographically stable ossifications were identified as the supratemporals (Reinbach 1939b; Jarvik 1967b) or postorbitals (Griffiths 1954a). In *Pelobates cultripes* separate ossifications within the parietosquamosal arch may represent original, independent dermal bones of the temporal cranium of temnospondyls (Smirnov 1999, his figure 4).

When the frontoparietal of anurans is traced back to their ancestors (the back-sequence is *Triadobatrachus* → temnospondyls → osteolepiform fishes), it is essential that only homologous elements are compared. Various criteria for establishing homologies of the frontal and parietal bones in fishes and tetrapods have been proposed (see Roček 1987 for a brief review). Among them, the criterion of exocranial-endocranial relationship seems to be reliable (at least for cranial roofing bones) because certain endocranial structures provide a substrate on which condensation of osteogenic mesenchyme occurs (Leibel 1976). However, additional factors may be active in dermal osteogeny.

When these criteria are applied, one can assume that the bone designated as the frontal in labyrinthodonts (Bolt 1969, his figure 2, 1977, his figure 12) corresponds to the element of the same name (*sensu* Jarvik 1980a, his figure 120) in osteolepiform fishes, and that it bears the same spatial relationship to the neural endocranium in those groups as does the anterior part of the frontoparietal in anurans (Fig. 70). The following discussion compares the frontal and parietal bones among the evolutionary stages represented by osteolepiform fishes, Palaeozoic amphibians, and anurans.

In the late Devonian fish *Eusthenopteron* and the early Permian rhachitomous dissorophoid *Doleserpeton*, the frontals adjoin the orbitotemporal region of the neural endocranium dorsally; they extend approximately from the level of the foramen for the *ramus medialis nervi ophthalmici* to slightly in front of the *foramen nervi trigemini*. In *Eusthenopteron* the parietals occupy the space posterior to the level of the foramen for the trigeminal nerve up to the level of the vagus, but reach only the *tectum synoticum* in *Doleserpeton*. Thus, the only noticeable difference between these two forms is the lateral extent of the frontals and the posterior extent of the parietals. These differences seem to be related to changes in proportions of the neural endocranium.

In the early Triassic *Triadobatrachus*, an intermediate between Palaeozoic amphibians and anurans, the frontals and parietals fused together (Fig. 71), giving rise to the frontoparietal complex. Eaton (1942) and Sedra (1949) believed that the parietals disappeared during the course of evolution between Palaeozoic amphibians and *Triadobatrachus* and that the bone called the frontoparietal in *Triadobatrachus* and all anurans is actually only the frontal. However, Griffiths (1954b) demonstrated this view to be highly improbable. Although a slight median suture can still be traced within the parietal portion of the frontoparietal complex in *Triadobatrachus*, both halves fuse completely in the anterior part. The posterolateral extent of the bone is remarkable; it reaches the *crista parotica*. This is a unique character in *Triadobatrachus* because neither the parietal in osteolepiforms or in labyrinthodonts nor the parietal portion of the complex in anurans extend so far laterally.

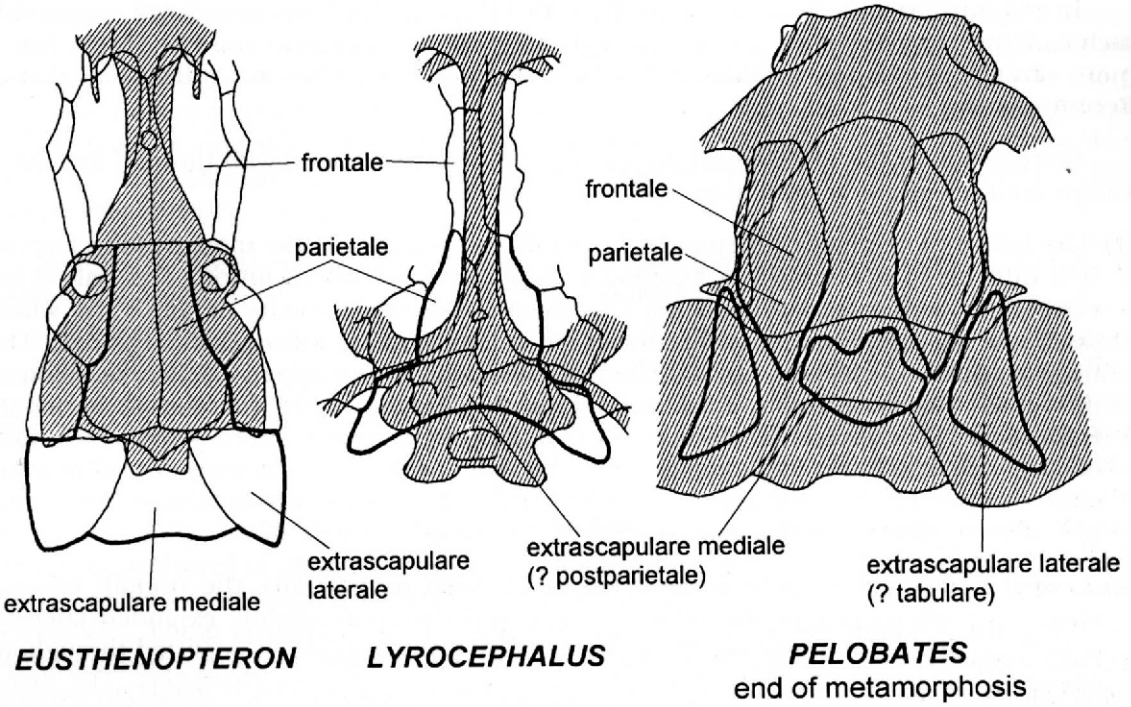


Fig. 70. Comparison of the posterior part of the dermal skull roof of representatives of adult osteolepiform crossopterygians (*Eusthenopteron*), adult temnospondyls (*Lyrocephalus*) and larval anurans (*Pelobates*). Hatching indicates the endocranium. From Roček (1987).

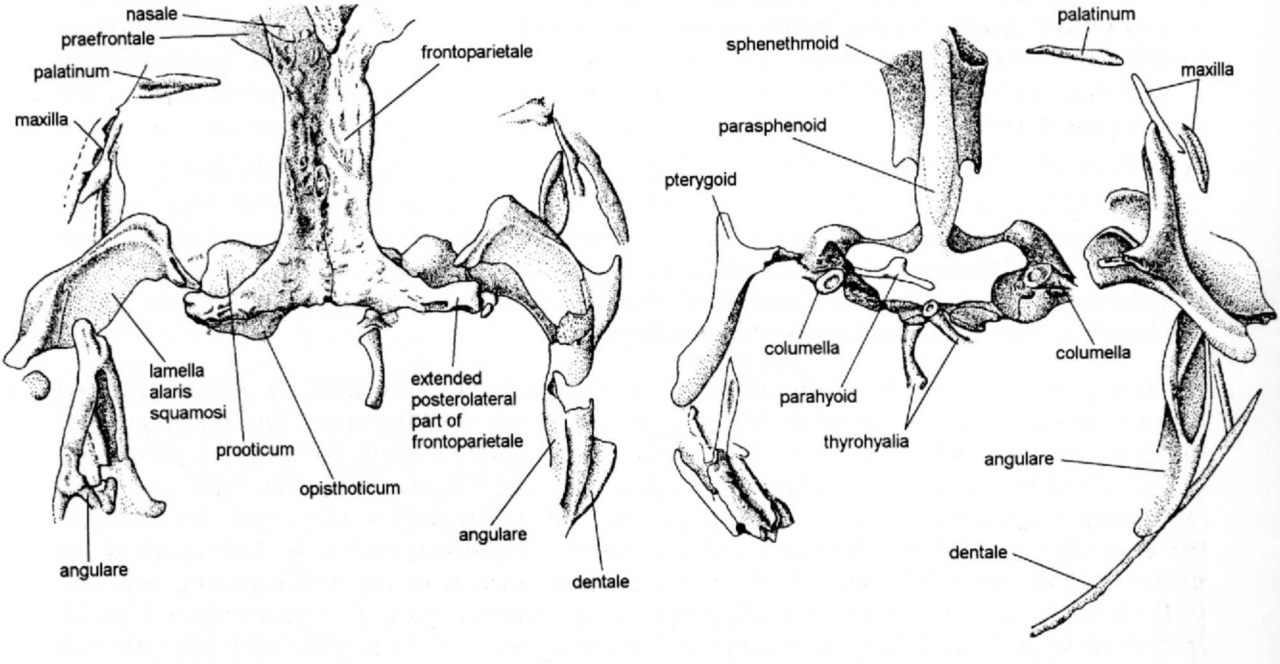


Fig. 71. Dorsal (left) and ventral (right) views of the skull of *Triadobatrachus massinoti*, an anuran from the early Triassic. The lower jaw is reflected back against the ventral face of the thorax. From Rage and Roček (1989).

In the earliest known anurans in which the frontoparietal is satisfactorily preserved, such as *Vieraella*, *Notobatrachus*, and *Eodiscoglossus*, and discoglossids from Las Hoyas, Spain (pers. obs.), the variation in shape and extent of this element does not differ from that of Recent anurans.

Comparison of the frontals and parietals at the pre-anuran level with those of the oldest known anurans allows several assessments to be made:

(1) The fusion of originally independent frontals and parietals is the most striking feature. It is difficult to hypothesize a functional significance for such a fusion. The only other vertebrates with frontoparietals are Cretaceous pachycephalosaurs in which the whole skull was strengthened, supposedly as an adaptation to intraspecific combat. The frontoparietal complex was one of the earliest characters to appear in the evolution of the Anura. However, fusion of the two sides of the complex versus retention of a separate frontoparietal on each side seems to occur quite irregularly in anuran phylogeny. Whilst entirely or partially fused frontoparietals (the more derived condition) occurred in some early forms (*Triadobatrachus* and Cretaceous pipids), separate frontoparietal bones (the primitive condition) persist in many Recent anurans.

(2) Owing to changes in both endocranial and orbital proportions, the frontals became elements participating in the orbital border, and they only slightly extended laterally over the walls of the braincase. Once this condition was attained, it persisted throughout anuran phylogeny, regardless of the states of other frontoparietal characters. The shape of the frontal part of the complex (viewed dorsally) always corresponds to the shape of the orbitotemporal section of the braincase. The extent of the frontals both anteriorly and medially varies with degree of ossification, so that the frontoparietals may not contact each other medially and/or may not contact the nasals anteriorly; consequently, the median fontanelle may remain open.

(3) The parietal portion of the complex in anurans adjoins the neural endocranium to approximately the same extent as it does in osteolepiforms and labyrinthodonts. Leibel (1976) determined experimentally that differences in the shape of the parietal portion are due to anteroposterior shortening of the otic capsules and their lateral expansions. However, in *Triadobatrachus* the posterolateral wings of the frontoparietals reach the level of the *crista parotica*, a condition not found in osteolepiforms, labyrinthodonts, or anurans. The extent of the posterior part of the frontoparietal already varied considerably in Jurassic forms (compare *Notobatrachus* with the discoglossids from Las Hoyas).

(4) Although most fossil and extant adult anurans have a frontoparietal formed by fusion of parietals and frontals only (see below), there may be some forms that include additional elements within the complex. These include an unpaired median element that can be distinguished in tadpoles (*Eopelobates*, *Pelobates*) or even in adults (the pelobatid from the Eocene Green River Formation; Roček and Rage [2000b]) and paired elements adjoining the prootics anterodorsally.

Some elements similar to the unpaired median element adjoining the *tectum synoticum* in some anurans may be found in labyrinthodonts or fish. Examples are the "*centroparietale*" in *Aphaneramma* (Temnospondyli, Trematosauridae) (Wiman 1915; Broili 1917, his figure 6; Säve-Söderbergh 1935, his figure 56, 1936, his figure 24, 1937, his figure 8A), the "parieto-extrascapular" in *Ichthyostega* (Jarvik 1980a, his figure 171) and the "median extrascapular" in osteolepiforms, many porolepiforms, and primitive actinopterygians. In most labyrinthodonts the pertinent space is occupied by a pair of postparietals that may fuse into an unpaired interparietal. According to Jarvik (1967b) this element may be homologized with the median extrascapular of the osteolepiforms and, consequently, with the postparietals or interparietal of primitive labyrinthodonts. In evolutionarily more advanced vertebrates a similar unpaired element may also occur. It is found in most reptiles where it is called the "postparietal", "interparietal", or "dermal supraoccipital" (Romer 1956). Although the parietal region of the skull of some reptiles is considerably modified, this bone maintains remarkable constancy (see Brink 1982). In those mammals in which this element occurs (mainly called the "interparietal"), it is always of paired origin although it later fuses during ontogeny; in some cases (Rodentia, Ruminantia) it even fuses with the parietals (Maggi 1898; Huene 1912; Watson 1913; Säve-Söderbergh 1935; Stadtmüller 1936).

Sewertzow (1891) incorrectly considered the unpaired dermal element in anurans as homologous with the *supraoccipitale* of labyrinthodonts.

Two explanations of the occurrence of the median element in *Eopelobates* and *Pelobates* may be proposed. First, it might represent an evolutionary neomorph arising within the posterior section of the interparietal suture during evolution from the level of *Triadobatrachus*. Second, it might represent an inheritance from ancestors. Whereas the first explanation is purely hypothetical, the second seems to be supported by the latent capacities of some anurans (e.g., pipids) to realize a morphogenetic programme normally abbreviated by paedomorphosis (Smirnov 1993). Supposing this, it is quite possible that the median element of anurans is homologous with those termed the postparietals (Smirnov 1997), parieto-extrascapulars, median extrascapular, or interparietal in various other vertebrates. These elements (either paired or unpaired) could disappear in the course of evolution from anuran ancestors to *Triadobatrachus*. This conclusion is contrary to the opinion of Hecht (1962) who maintained that the frontoparietal in *Triadobatrachus* does include postparietals and even tabulars, and to the view of Säve-Söderbergh (1936, his figure 67) who believed the frontoparietal of *Rana* to include the equivalents of the frontal, frontoparietal, and parieto-extrascapular bones.

Unlike the element just discussed, the ossifications arising lateral to the *arteria occipitalis* are not restricted to pelobatids. In *Triadobatrachus*, there is no fossilized trace of the *arteria occipitalis* and it probably extended between the endocranium and the exocranial layer, as occurs in osteolepiforms and very probably in labyrinthodonts. In adult pelobatids and many other fossil and extant anurans, this artery extends through a canal in the posterior part of the frontoparietal. The canal is a remnant of an earlier developmental stage in which a space is present between the main body of the frontoparietal and its posterolateral portion (e.g., Reinbach 1939b, his figures 2a,b, 3, 4). The connection between these two parts first arises beneath the artery and later above it. This condition seems to be retained in *Notobatrachus*, and in some extant anuran taxa as well. The artery may extend entirely above the frontoparietal, leaving no trace of its course on the bone surface, or it may course lateral to the bone if the bone is represented merely as a narrow strip along the median suture. The latter condition occurs in ranids.

Examination of the labyrinthodonts and osteolepiforms shows that they have a lateral extrascapular (called the "supratemporal" by some early writers [see Allis 1899] or the "tabular" by others]) represented by a lateral ossification on the corresponding area of the endocranium of anurans. Sewertzow (1891) considered both lateral bones above the otic capsules to be postfrontals. Reinbach (1939b) called this element the "*os supratemporale*"; however, this was proven to be incorrect by Griffiths (1954a) who considered it an homologue of the postorbital. If Reinbach's supratemporal and Griffiths' postorbital are indeed homologous with the corresponding bones in osteolepiforms and temnospondyls, they trace a peculiar evolutionary trend. Whereas in osteolepiforms these bones are almost without contact with the neural endocranium, and most probably arose in association with the supratemporal commissural canal and the postotic sensory canal (two branches of the lateral-line system in the head of lobe-finned fishes), in labyrinthodonts they already adjoin (at least in part) the posterolateral section of the otic capsule. Continuation of this trend into the anurans would result in involvement of the part of the frontoparietal lateral to the course of the *arteria occipitalis*. It is obvious that this element is not included in the frontoparietal of some anurans; it is lost, for instance, in ranids.

I. *Squamosum*

The dual developmental origin of the squamosal both in anurans and in caudates (see Lebedkina 1979, her figures 24, 25), and the variation in the dermal bones of the temporal region in labyrinthodonts stimulated a prolonged discussion of the homology of the squamosal; the issue is still not unequivocally resolved. Correct assessment of the transformations of this bone in the course of evolution from piscine ancestors to anurans requires clarification of homologies. In other words, the question arises whether or not the *squamosum* in osteolepiforms, labyrinthodonts, and anurans is the same bone.

The term "*squamosum*" was introduced by Cuvier (1822 ex Lebedkina 1979) for a mammalian bone. Later Huxley (1864) suggested that it might be homologous with a piscine dermal bone called the *supratemporale* (*sensu* Bakker [1822] ex Lebedkina [1979]; "*dermopteroticum*" of Parker [1873]; "*prosquamosum*" of Baur [1896]) located on the dorsolateral part of the otic capsule, i.e., on the lateral (horizontal) semicircular canal, as in anurans. However, when Gaupp (1892) observed that in amphibians this bone arises on the palatoquadrate and not on the otic capsule, the homology of this bone with the mammalian *squamosum* and with the *supratemporale* or *dermopteroticum* in fishes was doubted. Gaupp (1894) introduced another term, the "*paraquadratum*", which was accepted by some authors (e.g., de Villiers 1936). However, when it was discovered (Thyng 1906) that the bone called the *squamosum* in mammals also develops in association with the palatoquadrate (namely with its quadrate portion in amphibians; incus in mammals), Gaupp's reasons for doubting the homology between the anuran and mammalian squamosals became invalid and the term *squamosum* was reinstated for anurans.

Information accumulating since the beginning of the 20th century revealed that in labyrinthodonts, the otic region (in which the squamosal is located in adult anurans) is occupied by two bones, not just by one. Some early authors applied the term "*squamosum*" to the bone on the dorsal surface of the otic capsule. However, the majority agreed that the developmental topographic origin (in relation to the chondrocranium) is decisive for establishing homologies, and concluded that the term *squamosum* should be used for the bone that develops on the lateral surface of the palatoquadrate. The question then arose as to the identity of the dorsal bone; if the situation in osteolepiforms was taken as the key for establishing homology, again two bones were involved. They were called the "*intertemporale*" and "*supratemporale*" by Säve-Söderbergh (1933), the "*dermopteroticum anterior*" and "*dermopteroticum posterior*" by Stensiö (1947), and the "*supratemporale*" and "*tabulare*" by Parrington (1967). Since it was obvious that during the transition to terrestrial tetrapods (and later to anurans) the otic region was compressed antero-posteriorly, undoubtedly in connection with separation of the pectoral girdle from the skull and with the reduction of the branchial arch system, it was agreed that either only one of these two bones was retained, or that the two fused together. Whichever occurred, the bone remaining is usually called the *supratemporale*.

These considerations led early authors to believe that the anuran squamosal evolved from two ancestral bones (still before the actual dual developmental origin of the squamosal was discovered). The dorsal of the two ones was called the *supratemporale* ("*l'os tympanique*" of Cuvier [1824]; "*tympanicum*" of Bayer [1884, his plate I/l]; "*squamosum*" of Reinbach [1939a]), and the ventral one was called the "*squamosum*" ("symplecticum" of Bayer [1884, his figure I/l]; "*tympanicum*" and "*paraquadratum*" of Reinbach [1939a]). Nevertheless, the whole bone is still called the *squamosum*, although the more appropriate term "*supratemporo-squamosum*" was proposed by Reinbach (1939a).

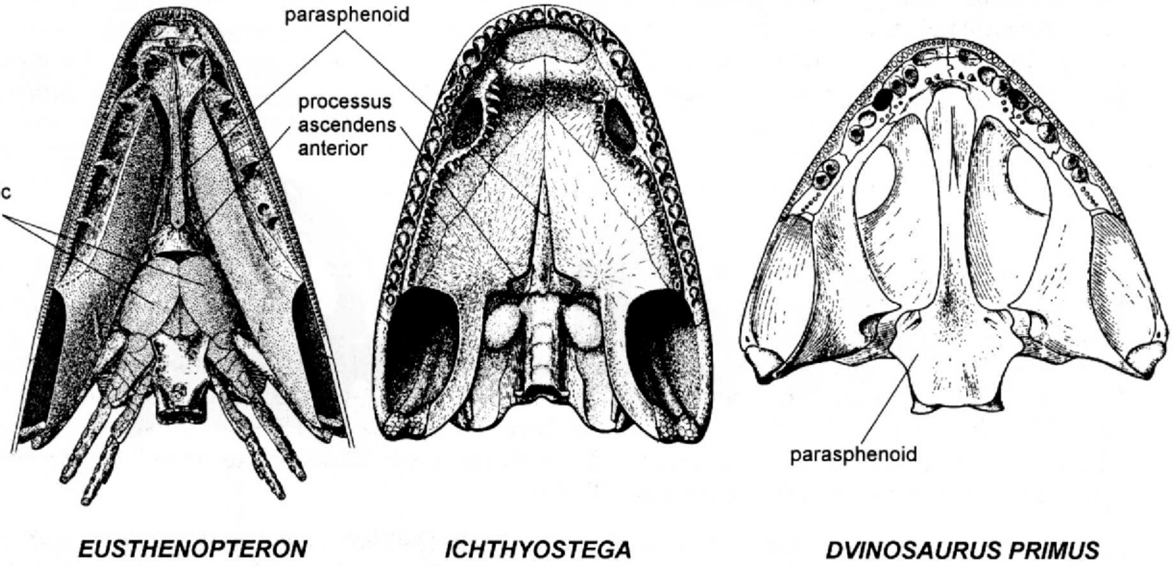
Another source of confusion was that Reinbach (1939a) and Jarvik (1967b) did not distinguish the lateral ossification in *Pelobates* (next to the *arteria occipitalis* and later entering into the frontoparietal complex) from the dorsal ossification centre of the squamosal; they called both of them the "*supratemporale*". Some authors, e.g., Stadtmüller (1936), denied the existence of the *supratemporale* in extant amphibians.

J. Parasphenoid

In osteolepiform fishes (Fig. 72), the parasphenoid is represented by a long, narrow bone extending anteriorly beneath the ethmoid region to the level of the vomers, and posteriorly reaching the intracranial joint apparatus (Jarvik 1954, 1980a). This bone is provided with a *processus ascendens anterior* which, according to Jarvik (1954), was formed by modified infrapharyngeal dental plates of the mandibular visceral arch. The floor of the otic region, including part of the otic capsules, is joined by the paraotic dental plates. In *Ichthyostega*, the parasphenoid reaches posteriorly to the *fissura preoticalis* (Jarvik 1996, his figure 25), which is homologous with the osteolepiform intracranial joint apparatus and with the *fissura prootica* of anurans. Also, the small anterior ascending process was retained in this early tetrapod, and the same holds for post-Devonian labyrinthodonts. In all of them the process ensheaths the basipterygoid process (Romer 1947), thereby constituting a convenient criterion of its homology. However, in post-Devonian labyrinthodonts, the parasphenoid extended posteriorly beneath the otic region, and even beneath the occipital region. This supposedly resulted from incorporation into the parasphenoid of some originally independent dental plates homologous with the infrapharyngeal dental plates of the hyoid arch (Jarvik 1954). The lateral process of the parasphenoid beneath the otic capsule is called the *processus ascendens posterior*. The evolutionary extension of the parasphenoid into the otic region seems to be evidenced by the fact that in fetalized post-Devonian labyrinthodonts the parasphenoid developed from several parts (Shishkin 1973). In *Triadobatrachus*, the parasphenoid is well developed, extending over a considerable part of the floor of the otic capsule (Rage and Roček 1989, their figure 2). It may be of some interest that in *Xenopus*, the parasphenoid develops a pair of acuminate lateral flanges, one on each side, beneath (and apparently slightly behind) the prootic foramina, and directed toward the base of the prootic (Trueb and Hanken 1992, their figure 8). These flanges have the same position as the paraotic dental plates in osteolepiforms, and as the posterior ascending process in actinopterygians (see Jarvik 1954, his figure 30).

K. Additional Ossifications

A dermal ossification (called the "*internasale*") is occasionally found between the nasals in the primitive Devonian amphibians *Ichthyostega* and *Acanthostega*, and in the middle



EUSTHENOPTERON **ICHTHYOSTEGA** **DVINOSAURUS PRIMUS**

Fig. 72. Roof of the mouth cavity in osteolepiforms (*Eusthenopteron*), an early tetrapod (*Ichthyostega*), and a paedomorphic late Permian temnospondyl amphibian (*Dvinosaurus primus*), showing the progressive expansion of the parasphenoid into the otic and occipital regions. Skulls not drawn to the same scale. *Eusthenopteron* from Jarvik (1954), *Ichthyostega* from Jarvik (1996), and *Dvinosaurus* from Shishkin (1973).

Carboniferous *Loxomma*, *Megalocephalus* (Beaumont 1977), and *Orthosauriscus* (Watson 1926, his figure 6). An ossification between the frontals and called the "interfrontal", "internasofrontal" or "nasofrontal" has been described in the temnospondyls *Osteophorus romeri* and *Eryops megacephalus* (Eryopidae), *Trematosaurus sobeyi* (Trematosauridae), *Batrachosaurus browni* (Brachyopidae) (Broom 1913, his figure 11; Sawin 1941, his figure 1; Broili 1917, his figures 15, 16; Säve-Söderbergh 1935, his figures 18, 19, 21; Westoll 1943b; Romer 1947, his figure 23), *Trematosuchus* (Orlov 1964, his figure 68) and *Branchiosaurus* cf. *petrolei* (Branchiosauridae) (Boy 1972, his figure 29), and in the microsaur *Ricnodon* (Hapsidopareiodontidae) and in *Mordex* (Steen 1938, her figures 13, 42). Similar ossifications were recorded for the temnospondyls *Kestrosaurus dreyeri* (Brachyopoidea) (Welles and Cosgriff 1965, their figure 25), *Batrachosauroides impressus* (Novikov 1994 ex Smirnov 1997), and *Sclerocephalus joginschneideri* (Werneburg 1992).

An ossification between the frontals can also be found in living caecilians. However, as von Meyer (1859 ex Broili 1917) early pointed out, this ossification in caecilians is, in fact, the exposed sphenethmoid.

In one specimen of *Benthosuchus sushkini*, an unpaired extra bone was recorded between the posterior margins of the frontals and the anterior margins of the parietals (Bystrow and Efremov 1940). Klembara (1993) found a similar extra bone, called the "median frontal" in *Discosauriscus austriacus*.

An additional median bone occasionally develops behind the frontoparietal in *Bombina* (Smirnov 1999, his figure 3a) and may be homologous with that between the posterior parts of the parietals (called the "interparietal", "interpostparietal", or "centroparietal") in *Apateon flagrifer* (Branchiosauridae) (Werneburg 1986, his figures 1a, 6c, 8a, 9a, 10a, 1989, his figure 4). A similar bone was found in other temnospondyls: *Lydekkerina huxleyi* (Lydekkeridae) (Shishkin *et al.* ex Smirnov 1997), and in *Wetlugasaurus angustifrons* (Smirnov 1997).

A dermal ossification above the otic capsule in aged *Discoglossus* (Smirnov 1999, his figure 3a,b) may represent one of the bones within the postorbital part of the exocranium in temnospondyl amphibians. Also, Stadtmüller (1931b) described an additional ossification in the occipital region of *Bombina bombina*, that he called the "*pleurooccipitale*".

L. Ossification Sequence

The sequence in which bones ossify has been compared between larval temnospondyls (Boy 1974, his table 1; Schoch 1998, his figure 8) and anurans. Ossification in temnospondyls proceeds through several well-distinguished stages (Fig. 73). The first involves only the bones of the jaws and palate, namely the premaxilla, maxilla, dentary,

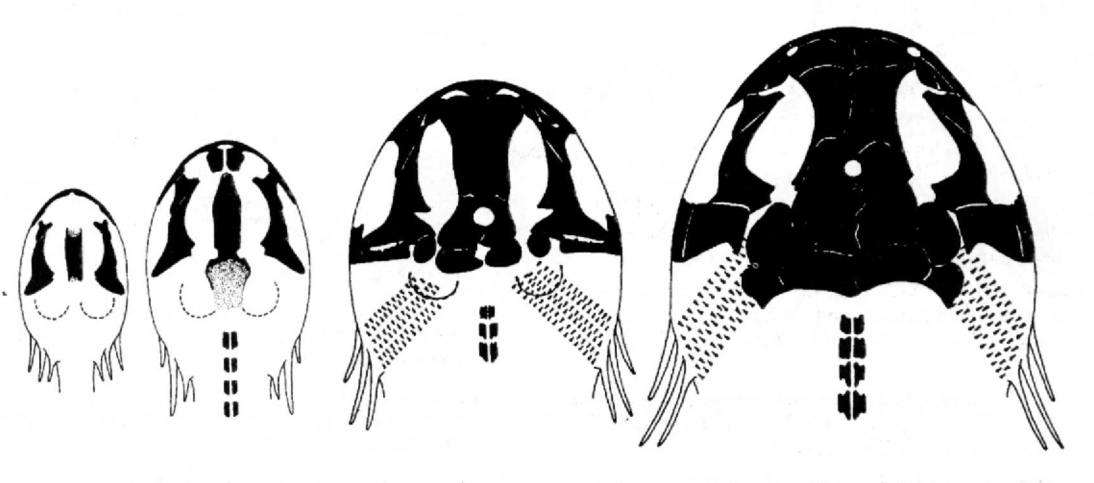


Fig. 73. Ossification sequence in the dermal skull (as seen in dorsal view) of *Branchiosaurus* from the early Permian of Europe. Drawings not precisely to scale. From Boy (1974).

prearticular, parasphenoid, palatine, pterygoid, and somewhat later the vomer. In the next stage the bones of the dermal skull roof ossify nearly simultaneously with each other. These are the nasals, frontals, parietals, postparietals, lacrimals, and squamosals. These are followed by the supratemporals, tabulars, postfrontals, prefrontals, and others. All larvae are ossified as early as at the beginning of metamorphosis, which is a striking difference from anurans in which ossification is completed much later. In branchiosaurs and anurans, the last structure to develop is the hyobranchial skeleton; besides the braincase and the sclerotic ring, these are the only structures in branchiosaurs to ossify after metamorphosis.

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