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Developmental patterns of the ethmoidal region of the anuran skull

Zbyněk Roček

Department of Paleontology, Charles University, CS-128 43 Prague 2, Czechoslovakia

Anurans are specialized, saltatorial amphibians whose general body structure has arisen as a result of adaptational processes that, as yet, are not well understood. The initial evolutionary changes involved in the origin of anurans seem to have centered on cranial modifications rather than morphological changes of the girdles and limbs for saltatorial locomotion. This is evidenced by *Triadobatrachus*, a Triassic fossil that generally is considered to resemble closely the hypothetical ancestor of modern anurans (Rage and Roček, 1986). The basic structural plan of the skull of *Triadobatrachus* is nearly identical to that of recent anurans.

The uniformity of the body structure among fossil and recent anurans is problematic to persons interested in systematics of these organisms. The similarity among adult anurans suggests that they are an homogeneous, monophyletic assemblage, but this hypothesis is less convincing when one also examines anuran larvae. These early ontogenetic stages conserve features inherited from ancestors to a greater extent than do adults. Thus, the larval characters may reflect phylogenetic relationships more accurately than features of the adult, some of which might represent adaptations acquired in later stages of ontogeny. While this observation generally is recognized, it often is overlooked.

Because anurans lived for most of their evolutionary history that comprises tens of millions of years in comparatively similar environments, one might reasonably anticipate that they would share certain morphological features in common. In other words, many shared structural characteristics of adult anurans may represent evolutionary convergences, whereas larval anatomical characters that are not associated with behavioral or ecological specializations (e.g., specialized mouthparts or modified caudal fins), may represent significant phylogenetic characters. Larval characters may be more useful in deducing anuran relationships than characters derived from the adults, which, in some cases, may lead to incorrect phylogenetic conclusions. In summary, this phenomenon makes it possible to determine relationships on the basis of early growth stages, whereas in many features the adults are so specialized and similar to one another that their affinities are not immediately obvious.

The ethmoidal region of the anuran skull shows few, if any, adaptive specializations; thus, this part of the skull is ontogenetically and phylogenetically conservative. In adult anurans, the basic structural scheme of the ethmoid area is the same (Fig. 1). The two nasal capsules are separated by a median partition, the septum nasi. The floor of the capsule, the solum nasi, is attached to the ventral part of the septum, and the roof of the capsule, the tectum nasi, is attached to the dorsal part of the septum. The anterior wall of the nasal

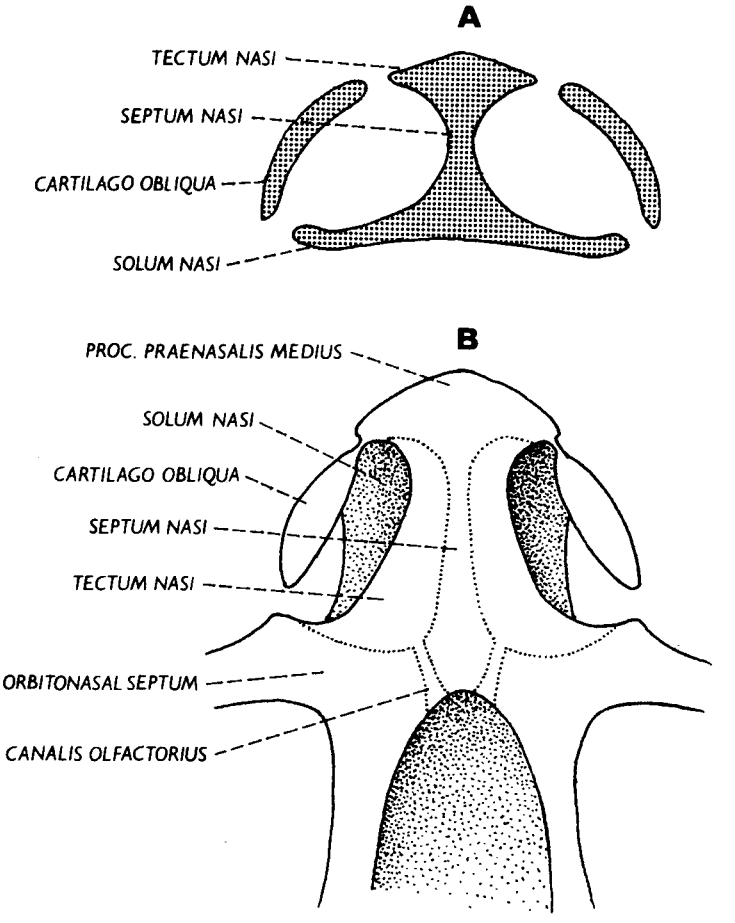

Fig. 1: Generalized anatomical scheme of the ethmoidal region of an adult anuran. A: Cross section at the level of the oblique cartilage. B: Dorsal view.

capsule is formed by the prenasal wall, and posteriorly, the orbitonasal wall separates the nasal capsule from the orbit. The orbitonasal wall is pierced by the canal for the olfactory tract. The basic structural plan describes the ethmoidal area of fossil crossopterygians (JARVIK, 1942), as well as such diverse anurans as ranids, pelobatids, and pipids.

In contrast to the similarity of the ethmoidal regions of adult anurans, the ethmoidal regions of anuran larvae are variable. In pelobatids, discoglossids, and ranids, the larval ethmoidal region consists of two cornua trabeculae that extend anteriorly from the lamina orbitonasalis [= larval postnasal wall]. Labial cartilages articulate with the anterior ends of the cornua trabeculae and serve as the upper jaws of the larvae. From this condition, the definitive ethmoidal structures of the adult anuran arise by the appearance of new cartilaginous tissue that connects the cornua medially (Fig. 2). This composite medial cartilage gives rise to the longitudinal, vertical wall separating the nasal capsules, the septum nasi. The septum, in turn, expands dorsally to produce the roof of the nasal capsule, tectum nasi, and ventrally to produce the floor, the solum nasi.

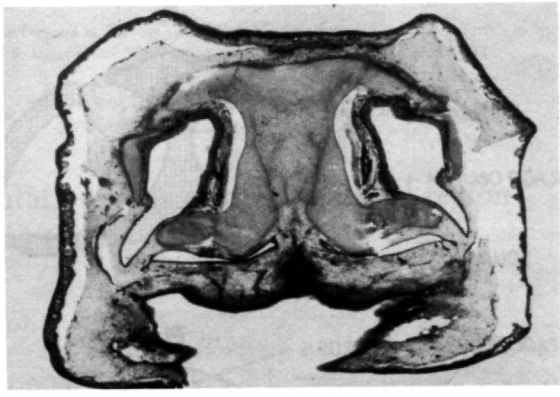

Fig. 2: *Pelobates fuscus*, cross section through the ethmoidal region of a tadpole in Stage 58 of Nieuwkoop and Faber (1967). Both cornua trabeculae are still clearly distinct from the new cartilaginous material between them. Taken from Roček (1981).

The developmental pattern of the ethmoidal region of pipids is completely different from that described for other anurans. In pipid larvae, the cornua trabeculae are absent. The ethmoidal region consists exclusively of a simple, horizontal plate called the planum internasale; the anterior edge of the planum serves as the larval upper jaw. The planum internasale disappears completely at metamorphosis, and all adult ethmoidal structures originate from new material located dorsal to the site of the planum.

Obviously, the development of the ethmoidal area in pipids is profoundly different from that of other anurans, but these differences are not evident in the structures of the adult skulls (Fig. 3). This phenomenon may be viewed as a case of morphological convergence in ontogeny, and an instructive example of why larvae and earlier ontogentic stages in general, should be included in systematic studies. It also should be noted that the planum internasale and the cornua trabeculae cannot be developed from one another; this is evident by tracing the origins of these structures through ontogeny. Thus, the planum internasale and cornua trabeculae are not homologous structures, and most probably had separate evolutionary origins.

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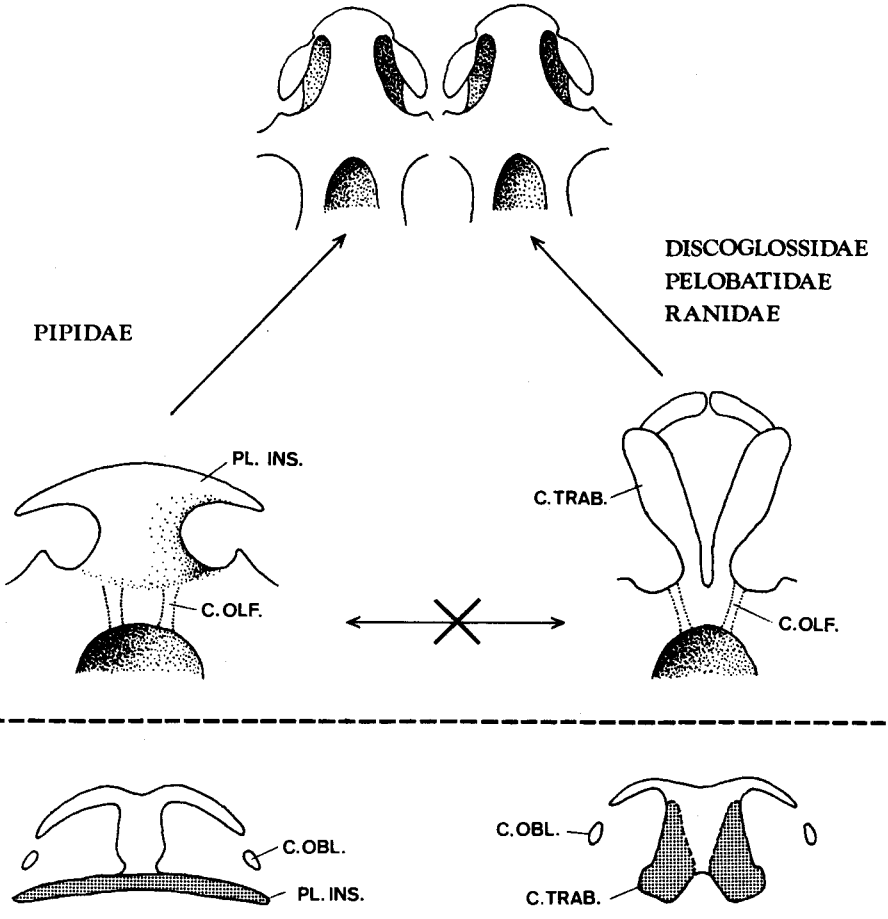

Fig. 3: Scheme of the ontogenetic development of the ethmoidal regions in pipids (left) and other anurans (right). Below the dashed line are cross sections of the larval ethmoidal regions. For explanation, see text. Abbreviations: C. OBL. = oblique cartilage; C. OLF. = olfactory canal; C. TRAB. = cornua trabeculae; PL. INS. = planum internasale.

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