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The first record of a subdivided nasal and frontoparietal in *Bombina bombina* (Anura, Discoglossidae)

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In one specimen of *Bombina bombina*, the right nasal is subdivided into five bones (N_{1-5}) which are interconnected via membrane. The right frontoparietal is subdivided into the anterior narrow portion (FP_1) and broader posterior portion (FP_2); the posterior portion being slightly longer. The posterior end of FP_1 is rounded, and the anterior end of the FP_2 is shallowly notched. However, both ends do not completely match with each other. These findings represent the first record of subdivided nasal and frontoparietal bones in adults of Recent anurans. They represent further support for the assumption that some exocranial bones of vertebrates are compound structures.

Key words: skull, subdivided bones, ontogeny, *Bombina bombina.*

Introduction

Subdivided dermal skull roof bones have been recorded in both extant and extinct fishes (e. g. WESTOLL, 1936; JARVIK, 1948; JESSEN, 1975; LONG et al., 1997; KEMP, 1999) and tetrapods (e. g. BOY, 1972; WERNEBURG, 1985; KLEMBARA, 1993a, KLEMBARA et. al., 2002). In Recent frogs, certain bones may ossify occasionally from several centres of ossification. For example, in *Ceratophrys cornuta* (L., 1758) the squamosal ossifies from three instead of the more usual two centres of ossification (WILD, 1997). LEBEDKINA (1979) found independent frontal and parietal centres of ossification of the future frontoparietal in the tadpoles of *Rana ridibunda* Pallas, 1771. So far, subdivisions of individual bones have not been recorded in adults of Recent anurans.

In his analysis of the phylogenetic history of dermal skull bones in vertebrates, JARVIK (1948) stated that a greater number of components are formed in the ontogeny of individual vertebrates than would be expected from the number of bones normally present in the adult. Sometimes ossification centres fail to fuse together early in ontogeny and, as a result, a particular bone may appear to be composed of more elements than normally appear in the adult. According to JARVIK (1948), these subdivisions indicate that the bones of the skull roof were originally numerous and only later in phylogeny did they fuse together forming large bones such as the parietal, frontal, nasal, etc. If so, subdivided bones indicate the recapitulation of the primitive condition (JARVIK, 1948, 1980; KLEMBARA, 1991, 1993a, b).

The aim of this paper is to report subdivided nasal and frontoparietal bones in specimen of *Bombina bombina* (L., 1761). This is the first documented example of subdivided exocranial elements in adults of Recent anurans.

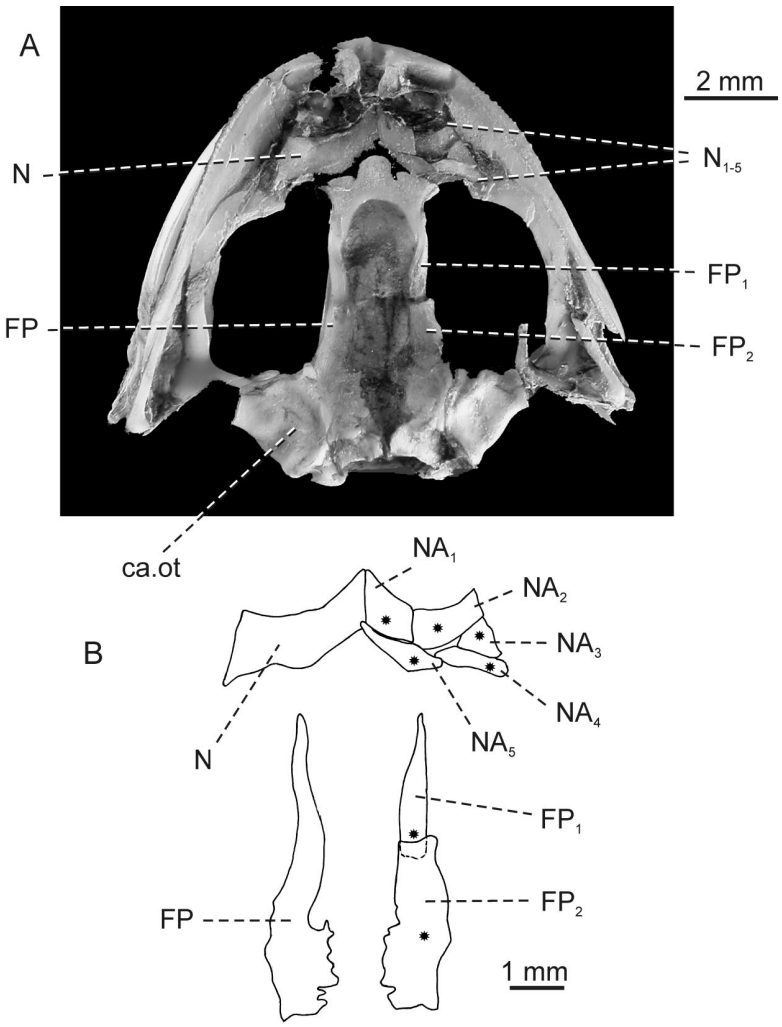

Fig. 1. A – *Bombina bombina* (C 2), photograph of skull in dorsal view. B – Outlines of unsubdivided (left side) and subdivided (right side) nasals and frontoparietals of the same specimen. The asterisk indicates approximate position of centre of ossification. ca.ot – otic capsule, FP – frontoparietal, N – nasal.

Sites, material and methods

The specimens of *Bombina bombina* are from two sites in W Slovakia: 1) Bratislava – Čunovo, specimens designated C 1 – C 62; and 2) Vysoká pri Morave, specimens designated VM 1–8. The material is deposited at the Department of Ecology, Faculty of Natural Sciences, Comenius University in Bratislava. All 70 specimens are subadults and adults. They were partially macerated in water in order to remove overlying soft tissues. The skull and fontanellae remained intact. Among these specimens, in one adult, C 2, the subdivisions of the exocranial bones are present. The length of the skull of C 2 is 11.5 mm.

Results

In specimen C 2, the following subdivisions of nasal and frontoparietal bones were recorded (Fig. 1).

Nasal. The right nasal is subdivided into 5 bones (N_{1-5}) of various size and shape. N_1 and N_2 are relatively large, mediolaterally elongate plates. N_4 and N_5 are anteroposteriorly short and mediolaterally long. N_3 is triangular and wedged between N_2 and N_4. As in the case of the left nasal, N_{1-5} are also surrounded by a membrane joining them with the surrounding ossifications. N_1 and

N_2 are the thickest in their approximately central and slightly medial portions; N_3–N_5 are the thickest in their lateral portions. Towards their margins, the bones become thinner. These thickenings represent the centres of ossification. All five $N_{1\text{-}5}$ are interconnected via a membrane, hence their independent intramembraneus origin is observable.

Frontoparietal. This is a paired bone; right and left halves are connected via the frontoparietal fontanelle. Each frontoparietal is an anteroposteriorly long plate that widens gradually in a posterior direction. The right frontoparietal is subdivided into an anterior narrow portion (FP_1) adjoining the dorsal margin of the anterior half of the lateral membraneous wall of the sphenethmoid and a broader and slightly longer posterior portion (FP_2). The anterior half of FP_2 adjoins the posterior half of the lateral membranous wall of the sphenethmoid and the posterior half of FP_2 adjoins the dorsal surface of the anteromedial portion of the otic capsule. The posterior end of FP_1 underlies slightly the anterior portion of FP_2. Both bones are connected through a membrane. The posterior end of FP_1 is rounded whereas the anterior end of FP_2 is shallowly notched. However, such extremities do not closely fit together. The ossification centre of FP_2 lies in its mid-length and slightly laterally. The ossification centre of FP_1 is not clearly distinguishable, however, the posterior part of the bone shows slight rugosity consisting of fine grooves and ridges on its dorsal and ventral surfaces. Such rugosity, however, is not visible on the neighbouring anterior portion of FP_2. Therefore, the rugosity on FP_1 probably marks the ossification centre of FP_1. All this indicates independent development of FP_1 and FP_2.

Discussion

The snout region of the osteolepiform ancestors of tetrapods is covered with numerous dermal elements called nasals, tectals and postrostrals. In various Devonian osteolepiform and porolepiform fishes, the snout region is often subdivided (JARVIK, 1948, 1980; LONG et al., 1997). Recently, subdivision of the nasals has been recorded in the Lower Permian discosauriscid tetrapod *Discosauriscus austriacus* (Makowsky, 1876) (KLEMBARA, 1993b, KLEMBARA et al. 2002). In one specimen of this tetrapod, the anterior portions of both nasals are subdivided into several small bones. In Recent urodeles, the nasal develops from two ossification centres (LEBEDKINA, 1979). According to ROČEK (1981), the nasal of *Pelobates fuscus* (Laurenti, 1768) represents a complex structure originated by fusion of the anterior tectal and several posterior tectals. The subdivided nasal in *Bombina bombina*, as described here, is the first record of the subdivision of this bone within adult Recent anurans and further supports the assumption that the nasal of anurans is a compound structure (see also JARVIK, 1967).

It is generally accepted that the frontoparietal bone in anurans is a composite structure originated by fusion of several exocranial elements (JARVIK, 1967; ROČEK, 1981). The frontal portions of the frontoparietal cover the orbitotemporal region of the neural endocranium, and there is a pineal foramen between their anteriormost portions in early ontogenetic stages of *Pelobates syriacus* Boettger, 1889 (JARVIK, 1967) as well as in the corresponding position in the adults of the Paleogene pipid frogs of the genus *Shelania* (for review see BAEZ & PUGENER, 1998).

Recently, ČIHÁK et al. (2003) described the developmental origin of the frontoparietal bone in *Bombina variegata* (L., 1758). They discovered that in early ontogenetic stages of this species, the ossification of the frontoparietal begins as three tiny areas of osteoid (uncalcified bone matrix) representing frontals 1–3 ($F_{1\text{-}3}$) that adjoin the orbital cartilage. Prior to calcification, the F_3 fuses with the F_2 and then this bone with the F_1. This compound structure, however, does not reach the prootic fissure posteriorly. With the beginning of calcification, the compound $F_{1\text{-}3}$ fuses with an additional element representing the F_4. After this, parietal ossification appears at the anterodorsal surface of the otic capsule. By comparing the topology of the subdivided frontoparietal of *B. bombina* presented here with that of *B. variegata* described by ČIHÁK et al. (2003) we conclude that the FP_1 of *B. bombina* corresponds to the $F_{1\text{-}2}$ in *B. variegata* and the FP_2 of the former corresponds to the $F_{3\text{-}4}$ plus parietal ossification in the latter form. By comparing the topology of the subdivided frontoparietal of *B. bombina* with that of *Rana ridibunda* (LEBEDKINA, 1979, Fig. 84b), it may be concluded that the FP_2 of *B. bombina* corresponds to the F_3 plus parietal centre of the latter form.

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