11 August 2003
PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(2):337–340. 2003.

The hyopalatine arch of a 25 mm larva of *Synbranchus* and homology of the single pterygoid in the Synbranchidae (Teleostei: Synbranchiformes)

Ralf Britz, Sandra Favorito, and G. David Johnson

(RB) Division Of Fishes, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, U.S.A., and Lehrstuhl für Spezielle Zoologie, Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany, e-mail: britz.ralf@nmnh.si.edu;
(SF-A) Universidade de Sao Paulo, Museu de Zoologia, Caixa Postal 42594, Sao Paulo, SP, 04299-970, Brazil, e-mail: favorito@uniban.br;
(GDJ) Division Of Fishes, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, U.S.A., e-mail: johnson.dave@nmnh.si.edu

Abstract.—Identity of the single pterygoid bone in Synbranchidae is evaluated based on a 25 mm larva of *Synbranchus*. Two hypotheses have been proposed as to its homology: it is 1) the endopterygoid or 2) the ectopterygoid. We show that the bone in question develops in the position of the ectopterygoid and therefore represents the homologue of this bone in other teleosts. Thus synbranchids lack the endopterygoid, an observation that invalidates a previously proposed synapomorphy of this family and the channids (snakeheads).

Synbranchidae, or swamp eels, are a family of highly derived eel-like acanthomorphs, comprising 17 species (Bailey & Gans 1998) from fresh and estuarine waters of Middle and South America, Cuba, West Africa, Asia, and the Indo-Australian Archipelago (Nelson 1994). Several species are well known for their amphibious habits and the presence of accessory air breathing organs (see e.g., Rosen & Greenwood 1976, Liem 1987, Munshi et al. 1989) that enable them to undertake extensive overland excursions.

There are two hypotheses about the relationships of the Synbranchidae to other acanthomorph taxa: 1) synbranchids are the sister group of channids (Lauder & Liem 1983) and 2) synbranchids are the sister group of mastacembeloids (= mastacembelids plus chaudhuriids) (Travers 1984a, Johnson & Patterson 1993, Britz & Kottelat 2003).

One of the characters cited as support for Lauder & Liem's (1983) hypothesis is the presence of an enlarged endopterygoid in both, channids and synbranchids. The single pterygoid of synbranchids was considered an ectopterygoid by Regan (1912), Rastogi (1964), Rosen and Greenwood (1976), Gosline (1983), Travers (1984), and Britz (1996), and an endopterygoid by Lauder & Liem (1983). However, none of these authors specifically addressed the problem of the homology of this bone with respect to the ectopterygoid or endopterygoid of other teleosts. In the present paper we describe the hyopalatine arch of a 25 mm larval specimen of *Synbranchus* sp., to resolve the identity of the synbranchid pterygoid.

Material and Methods

A cleared and double stained larval *Synbranchus* sp. (USNM 372713) of 25 mm total length was studied. A Zeiss Tessovar was used to photograph the specimen. Additional comparative material comprised:

Mastacembelidae; all cleared and stained: *Mastacembelus erythrotaenia*: AMNH 42129 (1, 277 mm); *Mastacembelus* sp. (as

Macrognathus aculeatus) AMNH 097654 (1, 158 mm); *Macrognathus pancalus*: AMNH 217414 (8, 4.5–36 mm).

Synbranchidae; cleared and stained: *Macrotrema caligans*: MCZ 47107 (2, 172–178 mm), *Ophisternon aenigmaticum*: AMNH 31573 (1, 72 mm); *Synbranchus marmoratus*: AMNH 30213 (1, 142 mm), AMNH 74541 (1, 47 mm), MCZ 52376 (3, 65–140 mm; 1, disarticulated); *Monopterus albus*: AMNH 41579 (1, 167 mm); dry skeletons: *Ophisternon aenigmaticum* (as *Synbranchus marmoratus*): USNM 111347 (1, partial skeleton); *Monopterus* sp. (as *Synbranchus bengalensis*): AMNH 220023 (1, ca. 550 mm).

Terminology for the cartilaginous parts of the hyopalatine arch follows Arratia & Schultze (1991).

Results

The 25 mm larva of *Synbranchus* sp. still has a large yolk sac and prominent pectoral fins. The hyopalatine arch is largely cartilaginous (Fig. 1A). The hyosymplectic cartilage articulates with the otic capsule of the chondrocranium. In the area around the foramen for the hyomandibular branch of the facialis, there is a perichondral ossification, the hyomandibular, which bears a conspicuous process of membrane bone that extends ventrally between the body of the cartilage and the pars metapterygoidea of the palatoquadrate. A thin perichondral ossification, the symplectic, surrounds the anteroventral process of the hyosymplectic cartilage. The opercle, which articulates with a posterior process of the hyosymplectic cartilage, and the remaining three opercular bones are present as thin platelets of bone. The palatoquadrate comprises two unconnected parts, the posterior pars quadrata et metapterygoidea and the anterior pars autopalatina (Fig. 1A). The former is a roughly triangular cartilage, the ventral tip of which articulates with the lower jaw. Around this articulation and the lower third of the pars quadrata et metapterygoidea a perichondral ossification is present, the developing quadrate, with the usual posteroventral process of membrane bone. The developing metapterygpoid is present as a thin lamina of perichondral bone surrounding the posterodorsal corner of the pars quadrata et metapterygoidea. The pterygoid extends anteriorly as an elongate thin lamina of bone ventral to the anterodorsal corner of the pars quadrata (Fig. 1A, B). The elongate cartilage of the pars autopalatina sits more anteriorly in the roof of the mouth and bears a long anterolaterally directed process, the distal tip of which articulates with the lacrimal. Ventral to this cartilage is a small splint of bone, the developing dermopalatine (Fig. 1A). The lower jaw consists of the long Meckel's cartilage, its anterior part covered laterally by the dentary, which bears a few teeth, and its posterior part by the angular. The retroarticular is present as a small ossification at the most posterior tip of Meckel's cartilage, but the articular is not yet developed.

Discussion

In most actinopterygians, two dermal bones, the endopterygoid and the ectopterygoid, cover the medial face of the developing palatoquadrate between the pars quadrata and pars autopalatina (Arratia & Schultze 1991). Usually, the pars quadrata and the pars autopalatina are connected by a thin strip of cartilage during at least some period in early development. The endopterygoid ossifies dorsomedial to this cartilage and the ectopterygoid ventromedial to it (see e.g., Arratia & Schultze 1991:figs. 14, 15; Britz 1996:figs. 3–5; Britz & Johnson 2002:figs. 4, 5). Even when the cartilaginous connection between the pars quadrata and the pars autopalatina is resorbed during ontogeny, a small projecting tip on the anterodorsal face of pars quadrata usually remains for some time and can be used as a landmark. Such a stage is shown for a mastacembelid species in Britz (1996: Fig. 5). This landmark is also useful for taxa in

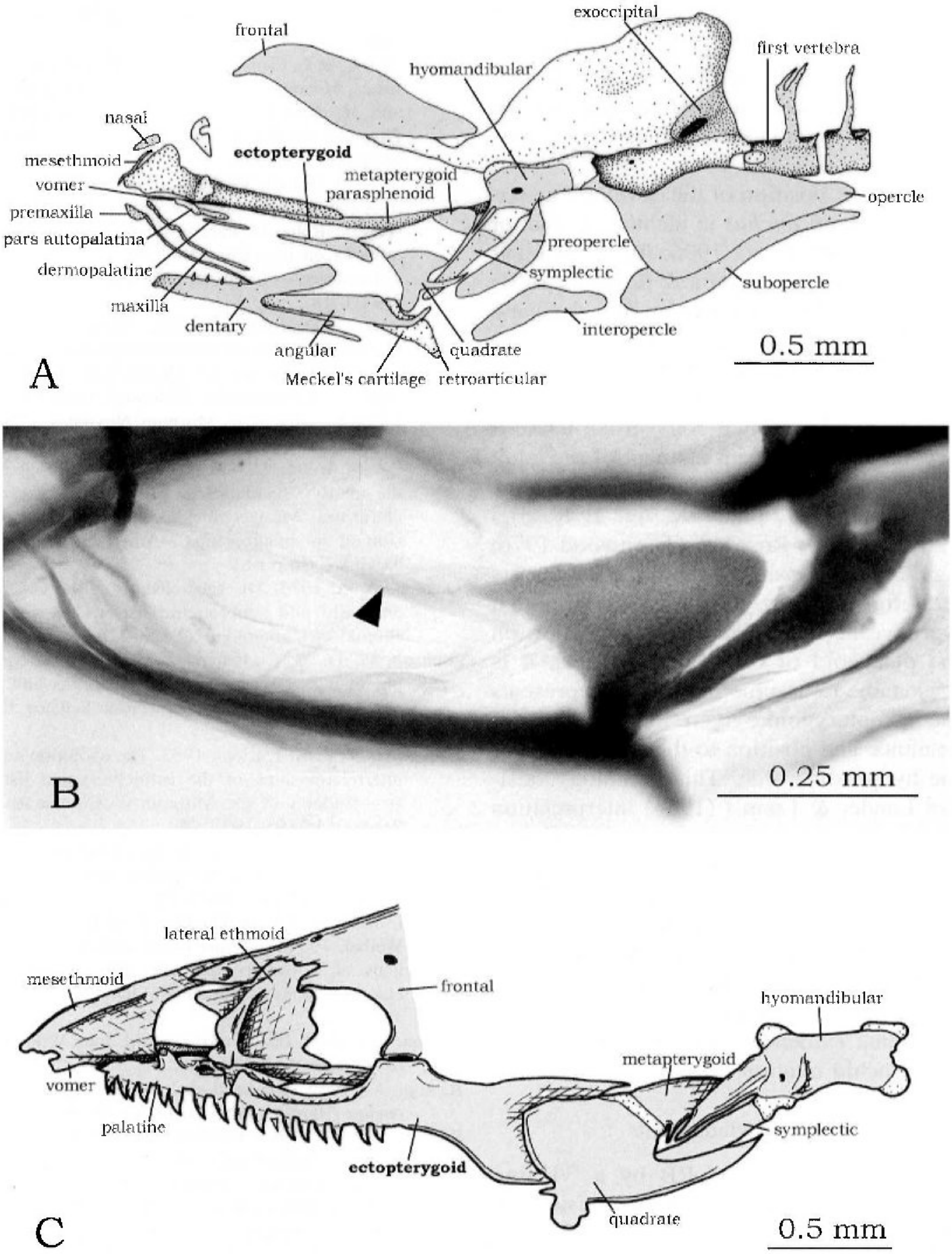

Fig. 1. *Synbranchus* sp., 25 mm: A, Skull and anterior two vertebrae, lateral view, cartilage white, bone light grey; B, Photograph of the hyopalatine area, lateral view, arrow points to ectopterygoid; C, *S. marmoratus*, 47 mm, hyopalatine arch and anterior part of neurocranium, lateral view, modified from Britz (1996), cartilage white, bone light grey.

which the pars quadrata and the pars autopalatina are never connected by cartilage.

The pterygoid bone of the 25 mm *Synbranchus* is located ventromedial to the projecting anterodorsal corner of the pars quadrata.

Thus, the position of the developing pterygoid in *Synbranchus* is identical to that of *Macrognathus* (Britz 1996: fig. 5) or other teleosts (see e.g., Arratia & Schultze 1991: figs. 14, 15; Britz & Johnson: figs. 4, 5) and clearly demonstrates its homology with this bone. During subsequent development the ectopterygoid of *Synbranchus* enlarges greatly and bears numerous strong teeth. It becomes the dominant element of the adult synbranchid palatoquadrate (Fig. 1C, see also Regan 1912:plate IX, fig. 1; Rastogi 1964:figs. 1–3; Rosen & Greenwood 1976: figs. 60, 61; Gosline 1983:fig. 3B; Travers 1984:fig. 10; Britz 1996:fig. 9C). Although we have no developmental information on the pterygoid of other synbranchids, it is reasonable to assume that it also represents the ectopterygoid, given its identical appearance and position to the other bones of the hyopalatine arch. This homology falsifies Lauder & Liem's (1983) interpretation of this bone as the endopterygoid and thus invalidates one of their putative synapomorphies uniting the Synbranchidae and the Channidae. The wider phylogenetic implications of our finding are beyond the scope of this paper and will be discussed in a forthcoming publication reevaluating the additional evidence for both hypotheses of synbranchid relationships.

Acknowledgments

Financial support of RB by a 'visiting scientist' fellowship of the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington D.C. is greatly acknowledged.

Literature Cited

Arratia, G., & H.-P. Schultze. 1991. Palatoquadrate and its ossifications: development and homology within osteichthyans.—Journal of Morphology 208:1–81.

Bailey, R. M., & C. Gans. 1998. Two new synbranchid fishes, *Monopterus roseni* from Peninsular India and *M. desilvai* from Sri Lanka.—Occasional Papers of the Museum of Zoology University of Michigan 726:1–18.

Britz, R. 1996. Ontogeny of the ethmoidal region and hyopalatine arch in *Macrognathus pancalus* (Percomorpha, Mastacembeloidei), with critical remarks on mastacembeloid inter- and intrarelationships.—American Museum Novitates 3181:1–18.

———, & G. D. Johnson. 2002. "Paradox Lost": Skeletal ontogeny of *Indostomus paradoxus* and its significance for the phylogenetic relationships of Indostomidae (Teleostei, Gasterosteiformes).—American Museum Novitates 3383: 1–43.

———, & M. Kottelat. 2003. Descriptive osteology of the family Chaudhuriidae (Teleostei, Synbranchiformes, Mastacembeloidei), with a discussion of its relationships.—American Museum Novitates (in press).

Gosline, W. A. 1983. The relationships of the mastacembelid and synbranchid fishes.—Japanese Journal of Ichthyology 29:323–328.

Johnson, G. D., & C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal.—Bulletin of Marine Science 52: 554–626.

Lauder, G. V., & K. F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes.—Bulletin of the Museum of Comparative Zoology 150:95–197.

Liem, K. F. 1987. Functional design of the air ventilation apparatus and overland excursions by teleosts.—Fieldiana 1379:1–29.

Munshi, J. S. D., G. M. Hughes, P. Gehr, & E. R. Weibel. 1989. Structure of the air-breathing organs of a swamp mud eel, *Monopterus cuchia*.—Japanese Journal of Ichthyology 35: 453–465.

Nelson, J. S. 1994. Fishes of the world. John Wiley & Sons, New York, 600 pp.

Rastogi, M. 1964. The head skeleton of *Amphipnous cuchia* (Ham.).—Acta Zoologica 46:283–292.

Regan, C. T. 1912. The anatomy and classification of the synbranchoid eels.—Annals and Magazine of Natural History, series 8, 9:387–390.

Rosen, D. E., & P. H. Greenwood. 1976. A fourth neotropical species of synbranchid eel and the phylogeny and systematics of synbranchiform fishes.—Bulletin of the American Museum of Natural History 157:1–69.

Travers, R. 1984. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part II: Phylogenetic analysis.—Bulletin of the British Museum of Natural History (Zoology) 47: 83–150.