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The erectile cheek-spine apparatus in the bristlenose catfish *Ancistrus* (Loricariidae, Siluriformes), and its relation to the formation of a secondary skull roof

Tom Geerinckx*, Dominique Adriaens

Evolutionary Morphology of Vertebrates, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

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Abstract

In the South American catfish family Loricariidae, the opercle has been decoupled from the lower jaw, and has also lost its function in expiration. While many loricariid species have a small and slightly mobile opercle with reduced opercular musculature, within the hypostomine subfamily a novel opercular mechanism has developed that erects a tuft of enlarged odontodes anterior to the opercle. This defensive mechanism is examined in *Ancistrus* cf. *triradiatus*. The opercle has a prominent anterior process and the orientation of the reinforced articulation hinge to the hyomandibular bone has shifted. The opercular musculature is well developed, with a hypertrophied dilatator operculi that extends deep inside the skull roof bones and toward the midline, over the brain, but below the superficial skull roof. Hence the frontal, sphenotic, parieto-supraoccipital and compound pterotic bones consist of a dorsal, superficial part and a deeper part separating the brain from the muscle: two functional skull roofs are thus formed. The impact on the path of the cranial sensory canals is substantial, moving canals away from the skull surface. Hypertrophy of cranial muscles is known from many teleosts, but the invasion of such large muscles into the skull, which is drastically modified and literally hollowed out, has never been described before. These cranial modifications are greater in males than in females, related to the territorial behavior of the former, in which the erectile spines are usually used.

Keywords: Suckermouth armored catfishes; Defensive mechanism; Opercular musculature; Muscle hypertrophy; Skull roof

Introduction

Among the Neotropical fish taxa, the suckermouth armored catfishes or Loricariidae are remarkable for their atypical catfish morphology, specialized feeding apparatus and high species and shape diversity. Their armor, covering almost the whole body, is formed by numerous dermal bone plates carrying odontodes, tooth-like structures composed of dentine, covered by a hypermineralized (enameloid) substance. These are firmly ankylosed to the bone or anchored by connective tissue fibers (Bhatti, 1938; Sire and Huysseune, 1996). This spiky external skeleton might well be an effective protection against predation. Odontodes are thought to have evolved independently in the loricarioid lineage (Bhatti, 1938; Reif, 1982), and are also found in e.g. callichthyids, scoloplacids, and the almost naked astroblepids, related loricarioid families (Schaefer et al., 1989; Sire and Huysseune, 1996; Schaefer and Buitrago-Suárez, 2002).

In some loricariid genera, the tuft of large, spiny odontodes anterior to the opercle can be erected.

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*Corresponding author.
E-mail address: tom.geerinckx@ugent.be (T. Geerinckx).

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Alexander (1965) and Howes (1983) mentioned the role of the dilatator operculi muscle in the erection of the odontodes. In *Ancistrus*, where this mechanism is most developed, both authors noted the impressive size of this muscle, reaching toward the dorsal midline of the skull, between the braincase and the dermal roof of the skull.

All loricariid odontodes, including the erectile ones, can be shed; marks on the dermal ossicles of *Ancistrus* cf. *triradiatus* and *Chaetostoma* sp. provide evidence of odontode loss or shedding (Howes, 1983; Geerinckx, pers. obs.). The fixed cheek odontodes of *Loricaria uracantha* develop in ca. 48 days and are shed after ca. 148 days (Moodie and Power, 1982). The number of erectile spines of the cheek-spine apparatus in *Ancistrus* and related genera is taxonomically informative (Eigenmann and Eigenmann, 1890; Muller, 1989; Miquilarena et al., 1994; Ceas and Page, 1996; Fisch-Muller et al., 2001). Their movements, however, have not yet been studied.

The present paper aims to describe the morphology, function, and use of the opercular odontode-erecting apparatus in *A.* cf. *triradiatus* Eigenmann, as well as discuss the seemingly indeterminantly growing opercular musculature and its drastic impact on the spatial design of the skull roof bones.

Material and methods

Specimens of *A.* cf. *triradiatus* and other loricariid species (see below) were commercially obtained. Live observations of the fast movements of the mechanism were aided by the use of high-speed filming from different perspectives (using a Redlake Motionscope digital high-speed camera set at 200 frames s^{-1}). Muscle dissections were performed on several subadult to adult specimens (maturity is reached at 5–6 cm standard length). The clearing and staining method of Taylor and Van Dyke (1985) was applied for the osteology. One subadult specimen was selected for serial sectioning, using a Technovit 7100 plastic embedding, a Reichert-Jung Polycut microtome, and toluidine blue stain for visualization. Manually sliced sections (ca. 2 mm thickness) were produced from one large specimen. Specimens and sections were examined using an Olympus SZX9 stereoscopic microscope and a Reichert-Jung Polyvar light microscope, equipped with a digital camera.

Examined specimens of *A.* cf. *triradiatus* (with standard length): clearing and staining: 4 (male: 101.9, 95 mm; female: 76.6, 69.6 mm); dissection: 4 (male: 86, 94 mm; female: 71, 70 mm); manual sectioning: 1 (male: 108 mm); 5 μm serial sections: 1 (gender unknown: 33.5 mm). Some specimens of other loricariids were studied for comparison: *Ancistrus ranunculus* (58 mm), *Ancistrus dolichopterus* (93 mm), *Pterygoplichthys lituratus* (63, 150 mm); *Farlowella acus* (124, 109 mm), *Sturisoma aureum* (83, 85 mm), *Rineloricaria parva* (75 mm) and *Otocinclus vestitus* (23, 24 mm).

Results

The following description is based on mature males, where the cheek-spine apparatus is best developed, and the associated structural implications for the neurocranium are most pronounced (see figure captions for length of specimens).

Bones of the cheek-spine apparatus

The cheek-spine apparatus consists of several bones in the lateral cheek region of the head (Fig. 1). The key element in the functioning of the cheek-spine apparatus is the opercle (Figs. 2(a)–(c)). Its articulation with the hyomandibular bone is reinforced by an anterior serration (two small ‘processes’), and a more weakly serrated, ligamentous connection between both bones posteriorly (Figs. 2(b) and 3(c)–(d)). The result is one long, strong and more or less horizontally oriented articulatory hinge around which the opercle pivots outwardly and inwardly (Figs. 3(a)–(d)). On the dorsal side insertion facets are present for the dilatator and levator operculi muscles, while the lateralmost hyohyoidei adductores bundle and the adductor operculi insert at the medioventral side (Figs. 2(b) and (c)). A very prominent anteroventral process articulates with the caudalmost ossicles carrying odontodes (Figs. 2(c) and 3(b)).

There are about 14 of these thick bony ossicles, most of which carry only one large odontode (Fig. 2(d)). To ease interpretation, and to avoid confusion with the larger cheek plates more anteriorly, we will refer to these structures as cheek spines throughout the text. The odontodes are immobile relative to the ossicles to which they are anchored.

There are four small and two larger cheek plates anterior to the cheek spines that, like other dermal bones in loricariids, carry only minute odontodes (not shown in the figures). The largest of these plates bears the distal portion of the preopercular canal (Fig. 2(e)). Its anterior edge articulates with the quadrate. All cheek plates and cheek spines are embedded in thick connective tissue, facilitating a chain of articulations (see below).

Opercular musculature

The dilatator operculi is the largest opercular muscle, and, in adult males, even the largest of all cranial