Extensive Jaw Mobility in Suckermouth Armored Catfishes (Loricariidae): A Morphological and Kinematic Analysis of Substrate Scraping Mode of Feeding*

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ABSTRACT

Loricariidae, or suckermouth armored catfishes, possess upper and lower jaws that are ventrally oriented and that bear teeth that touch the substrate from which algae and other food items are scraped. The ventral orientation and the highly specialized morphology of the jaws, characterized by protrusible upper jaws and left-right decoupled lower jaws, are observed in *Pterygoplichthys disjunctivus*, the species investigated here. Kinematic data of the scraping feeding movements, obtained by external high-speed and x-ray recordings, are used to quantify jaw movement, especially to test for upper jaw mobility and versatility during substrate scraping. Our results show that the mobility of the jaws is indeed high compared with what is standard for catfishes. The upper jaw's ability to perform a substantial degree of rostrocaudal movement is quite unique for catfishes. The ventromedially oriented lower jaws, with the teeth and the coronoid process at opposite sides, display an extensive mobility: they rotate around the suspensorial articulation and around their longitudinal axis, resulting in an extended scraping movement and thereby covering a large surface area. The lower jaws also show a left-right asymmetry in their movements during scraping. Thus, our results suggest that the

extreme morphological specializations of the jaws in loricariid catfishes are linked to an increased mobility and functional versatility, allowing these animals to efficiently scrape algae from substrates with irregular surfaces.

Introduction

Catfishes in general show a jaw morphology that is more constrained, both structurally and functionally, compared with many teleost lineages such as percomorphs. The catfish upper jaw generally comprises tooth-bearing premaxillary plates that are firmly connected to the neurocranial ethmoid and hardly exhibiting any mobility (Adriaens 2003). The mandible generally comprises two jaw halves that are rather firmly connected by a symphysis and that bear multiple rows of teeth of various shapes. Variation does occur along this general pattern, and some of the most extreme deviations from this pattern are definitely found in catfishes exhibiting a suckermouth, which allows them to strongly adhere to the substrate. This system evolved independently in some African mochokid catfishes (*Chiloglanis*, *Euchilichthys*, and *Atopochilus* species) and some Neotropical loricarioid catfishes (Astroblepidae and Loricariidae; Schaefer and Lauder 1986). Especially in the latter group of suckermouth catfishes, structural modifications of the feeding apparatus are prominent in relation to substrate scraping: enlarged and mobile upper jaw tooth plates and ventrally rotated mandible halves also bearing enlarged tooth plates (Schaefer 1987; Geerinckx et al. 2007a, 2008). Although many loricariids are known to feed on algae (Angelescu and Gneri 1949; Angermeier and Karr 1983; Power 1984; Buck and Sazima 1995; Aranha et al. 1998), ecological data concerning their diet are surprisingly scarce. It is known, however, that they can feed not only on algae but also on detritus and other small food items or even wood (Saul 1975; Schaefer and Stewart 1993; Fugi et al. 1996; Grosman et al. 1996; Nelson et al. 1999; Delariva and Agostinho 2001; Nelson 2002; Armbruster 2004).

Detailed studies about the morphology of the feeding apparatus in loricarioids are relatively rare and fragmentary compared with the commonly known trophic diversity (but see Howes 1983; Schaefer and Lauder 1986, 1996; Schaefer 1987, 1988, 1997; Geerinckx and Adriaens 2007a, 2008; Geerinckx et al. 2008). However, Schaefer and Lauder (1986), relying on a comparative anatomical study, suggested a series of evolutionary transformations of the jaw apparatus and associated musculature in the loricarioid clade, from a basal to a more spe-
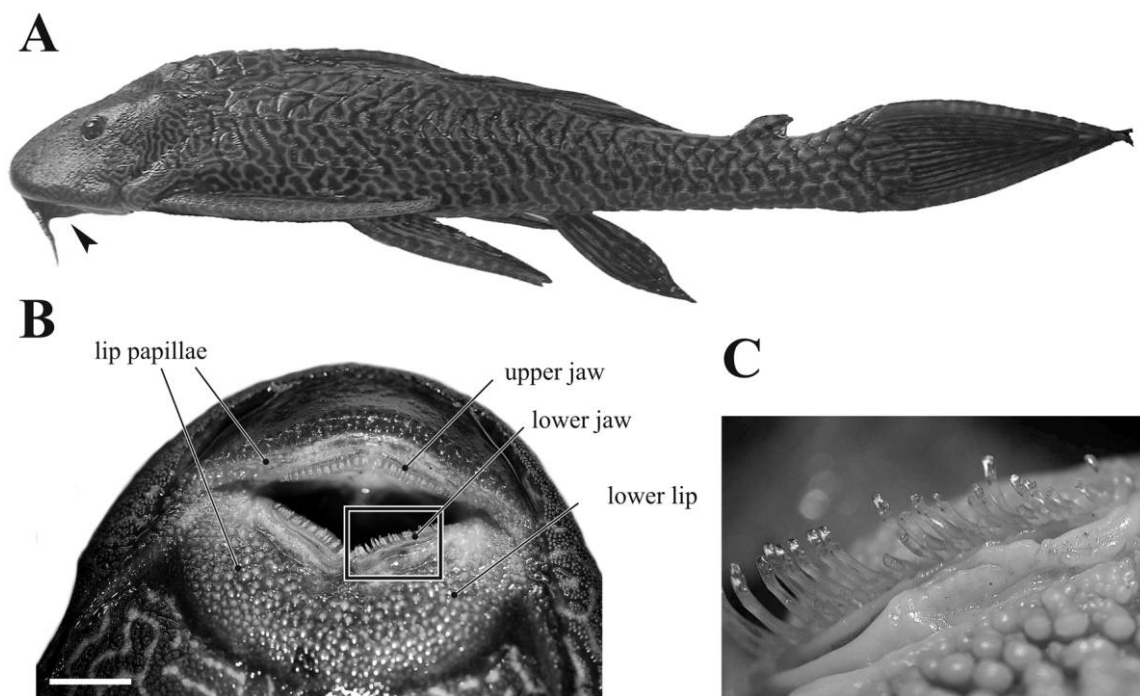
Figure 1. Habitus and external mouth morphology of *Pterygoplichthys disjunctivus*: *A*, Habitus (334-mm standard length specimen; arrow indicating the position of the mouth). *B*, Mouth in ventral view showing the single row of functional teeth per jaw half (as well as dermal papillae covering the lip tissue; scale bar = 10 mm). *C*, Detail of teeth in a 235-mm standard length specimen (indicated by box in *B*).

cialized configuration that could allow these animals to exploit the scraping niche. Of these morphological transformations, the authors emphasized those that resulted in an increased morphological complexity leading to greater mobility of the jaw elements (see table 1 of Schaefer and Lauder 1986). Moreover, Schaefer and Lauder (1986) considered the evolution of the loricariid jaw system as a case supporting the decoupling hypothesis suggested by Vermeij (1973) and Lauder (1985), wherein decoupling of primitively constrained elements leads to an increase in the number of functional linkages and ultimately to an increase in functional versatility. In a later article, Schaefer and Lauder (1996) tested the predicted association between decoupling events and an increased morphological diversity, but a specific test for increased kinematic versatility in the jaw apparatus resulting from this decoupling is lacking so far. However, to date, empirical data to support this hypothesis remain untested, even though Schaefer and Lauder (1986) emphasized the need for kinematic and electromyographic studies to verify their predictions.

Properly testing an increased and functional versatility as a result of evolutionary decoupling events would require an extensive comparative kinematic analysis based on a phylogenetic framework. As a potential onset to such an extensive study, here we provide the first kinematic data on jaw mobility in loricariids as the most derived (and hence considered to be the most extensively decoupled) loricarioids. As such, this study will not fully allow the testing of the functional implications of the decoupling hypothesis, but it will provide empirical data on jaw mobility and functional versatility in the most derived

lineage. This study allows testing of specific hypotheses related to jaw mobility, such as the presence of upper jaw mobility (which is considered to be absent in basal loricarioids and other catfishes). We present the results of a study on the morphology and movements of the jaw system in the hypostomine loricariid *Pterygoplichthys disjunctivus* during substrate scraping. In this study, we used both external high-speed and x-ray video recordings to quantify jaw movements and to gain insights into the function of the complex feeding apparatus of loricariids.

Material and Methods

Pterygoplichthys disjunctivus is a relatively large suckermouth armored catfish (Fig. 1*A*) from the upper Madeira tributaries in the southwestern Amazon basin (Weber 1992). In this study, we used two live individuals of 158 and 240 mm standard length. One additional 150-mm specimen was cleared and stained following the method of Taylor and Van Dyke (1985). A fourth 235-mm specimen was used for investigation of some soft tissues (ligament and muscle attachments to jaw bones). Examination of the specimens was performed using an Olympus SZX9 stereoscopic microscope equipped with a camera lucida for drawing. All specimens were obtained through the commercial aquarium trade.

During the high-speed video recordings, the two individuals fed on algae on the aquarium wall. Because of the difficulty in getting the individuals to feed on the preferred spot in front of the camera, x-ray video sequences were recorded of *P. disjunctivus* feeding on a thin slice of zucchini attached to the

horizontal floor of the aquarium. The external video recordings were made in ventral view using a Redlake Imaging Motion Pro 500 digital high-speed video camera set at 100 frames s^{-1}. For the external high-speed video recordings, illumination was provided by four arrays of eight ultra-bright-red LEDs. Anatomical points of interest were the rostro- and caudomedial ends of the upper and lower jaws and three reference points on the ventral aspect of the head. For the x-ray recordings, small radio-opaque metal markers were inserted subcutaneously, touching the jaws: one on the left premaxilla (Fig. 2*a*), one on the dento-mentomeckelium of each lower jaw half (Fig. 2*f*, 2*g*), and two in the skull roof as reference points (mesethmoid and parieto-supraoccipital; Fig. 2*i*, 2*j*, respectively), using hypodermic needles (some additional markers were placed at the rostral tip of the autopalatine [Fig. 2*b*, 2*c*], the distal tip of the maxillaries [Fig. 2*d*, 2*e*], and at the left hyoid [Fig. 2*h*]). Potential sliding of the markers inserted in the soft tissue (next to the jaws) proved to be very low to absent, as could be derived from the low amplitude in the movements in a lateromedial direction. Before implantation of these radio-opaque markers, the animals were anesthetized with MS 222 (Sigma Chemical). High-speed x-ray videos were recorded using a Philips Optimus x-ray generator (Royal Philips Electronics NV, Eindhoven, the Netherlands) coupled to a 14-inch image intensifier (10-inch zoom function) and a Redlake Motion Pro 2000 camera (1,248 to 1,024 pixels; Redlake, San Diego, CA) set at 100 frames s^{-1}. All experiments were approved by the Animal Care and Use Committee at the University of Antwerp.

The anatomical points as represented by radio-opaque markers (during x-ray recordings) were digitized frame by frame from the high-speed videos using Didge (Version 2.2.0, Alistair Cullum, Creighton University, Omaha, NE). The coordinates of all landmarks were recalculated to a frame of reference moving with the neurocranium (as determined by markers in the anterior and posterior part of the skull roof; Fig. 2*i*, 2*j*). After data filtering (fourth-order Butterworth zero phase-shift low-pass filter, cut-off frequency of 9 Hz [for x-ray data] and 10 Hz [for external kinematic data]), timing and distances of jaw movements were analyzed. Fourteen scraping-feeding cycles were digitized from the x-ray recordings (10 of the 158-mm specimen, 4 of the 240-mm specimen); four cycles were digitized from external video recordings (158-mm specimen).

The 158-mm specimen was scanned at the modular micro-CT setup at Ghent University (Masschaele et al. 2007; http://www.ugct.ugent.be; Fig. 3). The setup is a dual-head x-ray tube with a transmission-type head, with a focal spot size of 900 nm below 40-kV tube voltage for high-resolution applications and a directional high-power head (up to 160 kV, up to 150 W) for scanning of larger samples. The specimen was scanned using the directional tube head, at 80-kV tube voltage. The detector was an aSi flat panel (Varian Paxscan 2520) with a CsI scintillator. One thousand projections of 748 × 940 pixels were recorded, covering 360°, with an exposure time of 1 s per projection. The isometric voxel size in the sample was 115 μm. The raw data were processed and reconstructed using the in-
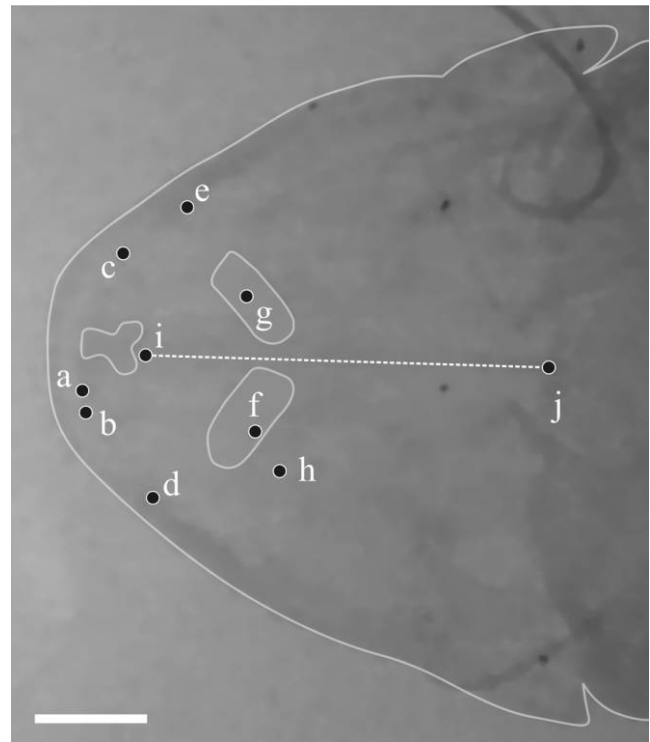

Figure 2. Ventral x-ray view of a 240-mm *Pterygoplichthys disjunctivus* specimen with indication of radio-opaque markers. *a*, Base of left premaxillary tooth row. *b*, *c*, Rostral tip of left and right autopalatine. *d*, *e*, Distal tip of left and right maxillae. *f*, *g*, Left and right lower jaw tooth plates. *h*, Middle of the left hyoid bar reference point on mesethmoid bone. *i*, *j*, Reference points on mesethmoid and parieto-supraoccipital bones, respectively. Scale bar = 10 mm.

house-developed CT software Octopus (Vlassenbroeck et al. 2007) and rendered using Amira 4.1 (Mercury Systems).

One smaller specimen (63 mm standard length), although fully ossified and thus representing the adult morphology, was used for serial histological sectioning. The head was processed by decalcifying (using Decalc) and embedding in Technovit 7100 (Kulzer Heraus), and was sectioned using a Leica Polycut microtome equipped with tungsten carbide-coated metal knives. The 5-μm sections were stained with toluidine and digitally photographed using a Colorview8 CCD camera mounted on a Polyvar light microscope.

Differences in mean displacement distances between lower and upper jaws were tested using a factorial ANOVA (specimen and jaw type—lower vs. upper—were used as two independent factors and jaw displacement distance was the dependent variable), using Statistica 6.0 (Statsoft).

Results

Morphological Analysis

The completely ventrally directed mouth, when open, is surrounded by upper and lower tooth plates in a diamond-shaped pattern (Figs. 1*B*, 3*A*). The jaws form an intricate complex of
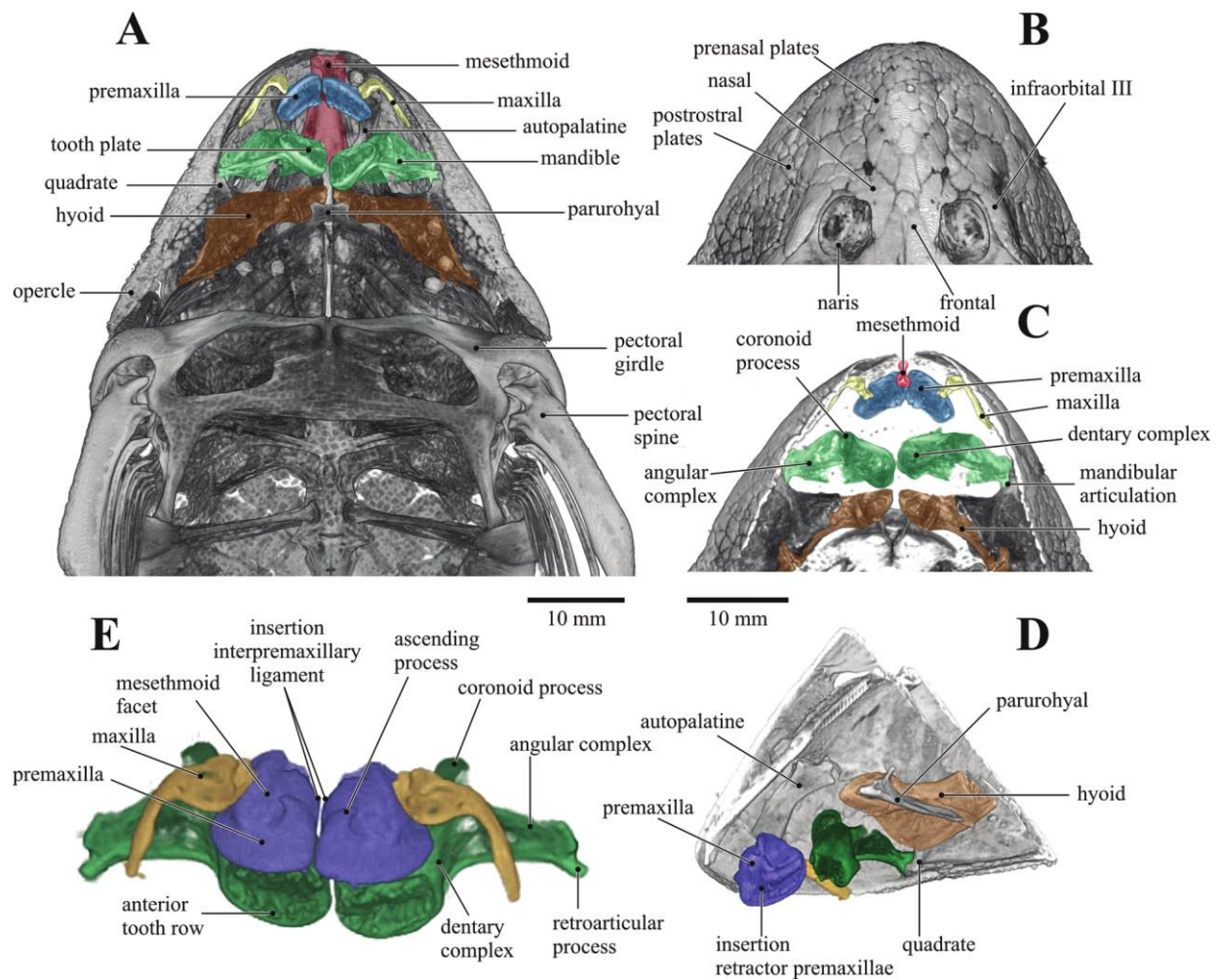
Figure 3. Head skeleton of *Pterygoplichthys disjunctivus* reconstructed using micro CT-scanning. *A*, Ventral view of the skull. *B*, Detail of rostral region in dorsal view. *C*, Same as *B* but with the neurocranial roof removed, showing the jaws in dorsal view. *D*, Medial view of the skull with jaws and hyoid (mediosagitally transected). *E*, Detail of the jaws and maxillae, in a dorsorostral view (color code: *red*, mesethmoid; *yellow*, maxillae; *blue*, premaxillae; *green*, mandible; *orange*, hyoid).

interconnected elements, in which the autopalatine and maxillary bones are involved as well.

Upper jaws in loricariids comprise two large, toothed bones, loosely connected medially to the mesethmoid. The upper jaw comprises the premaxillae (Fig. 3), dorsally articulating with a ventrally directed bony rim on the mesethmoid and supporting a battery of teeth ventrally, with only one row of about 24 curved and functional teeth (Fig. 1*B*). The upper jaw bears rectangular tooth plates lying in the same plane as those of the lower jaw, and is connected to the premaxilla by a nondistinct strip of connective tissue (no true ligament could be observed in the serial sections).

The oval-to-rectangular tooth pads are like upside-down baskets, with their ventral concave surface housing a set of tooth rows that have not erupted and thus are not yet functional (Geerinckx et al. 2007*b*). The articulation with the mesethmoid is indirect, because a distinct cartilaginous element lies between them as a kind of articular meniscus (Fig. 4). On the dorsal

side, the premaxillae bear a rostral ascending process (Figs. 3*E*, 4*B*, *arrow*) that articulates with a rostrolateral facet of this articular meniscus. Caudally, this cartilage has a paired process with which a posteromedial rim of the premaxillae is articulating (Fig. 4*C*, *arrow*). Both premaxillae are strongly interconnected by an interpremaxillary ligament. The articular meniscus also encloses the ventral rim of the medioventral mesethmoid process (Fig. 4*C*). As well, two pairs of mesethmoid-premaxillary ligaments are present (Fig. 4*B*), as is a paired ligament connecting the articular meniscus to the mesethmoid more posteriorly. Only one muscle, the retractor premaxillae that originates on the hyomandibula, inserts onto each premaxilla directly.

The mandible consists of two jaw halves not interconnected by a symphysis, with each half comprising the angulo-articular (further referred to as "angular complex") and the dento-mentomeckelium complexes (further referred to as "dentary complex"; Fig. 3). Both halves are separated by a cartilaginous plug
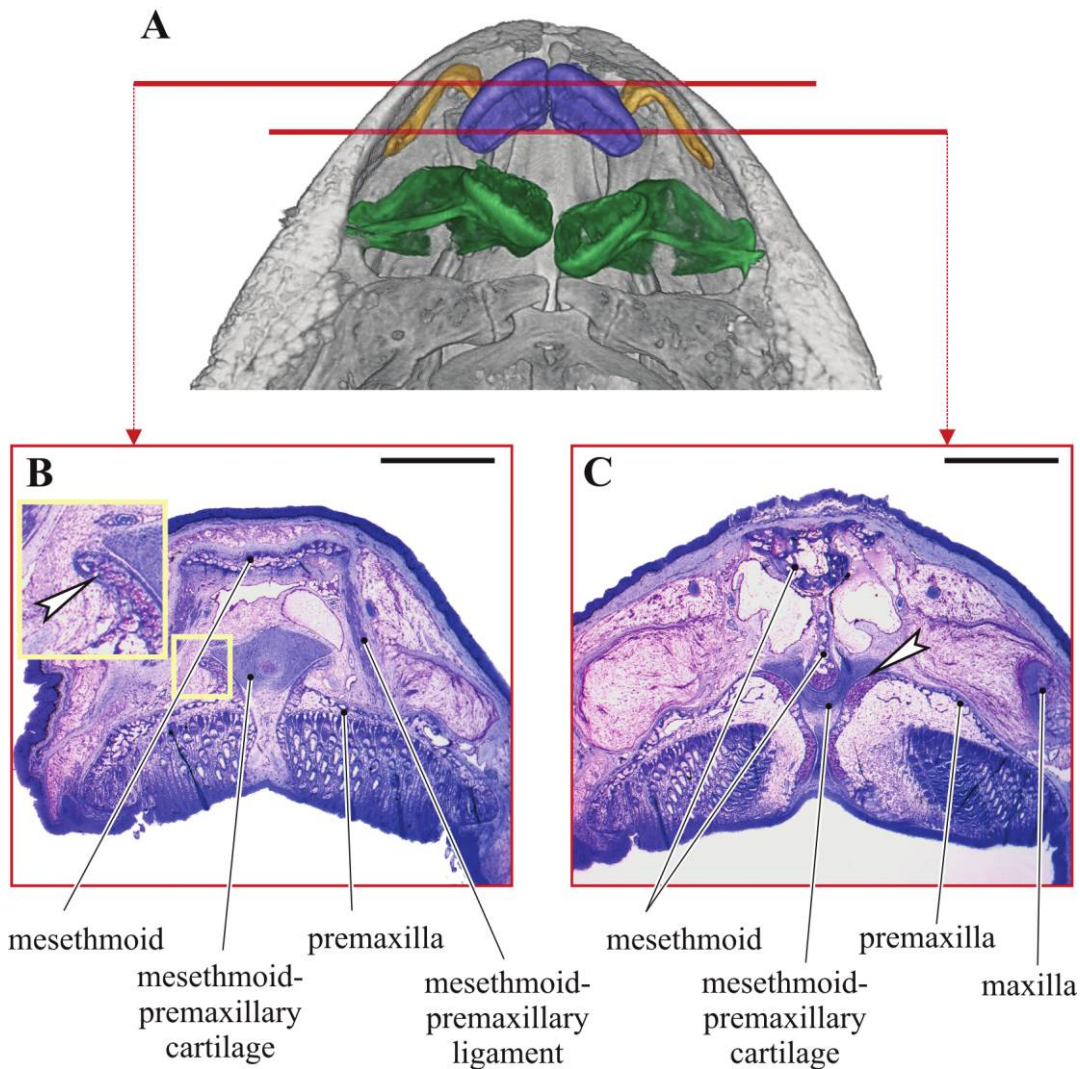
Figure 4. Transverse section through the articular meniscus in a 63-mm *Pterygoplichthys disjunctivus*. *A*, Ventral view of a reconstructed snout region indicating the position of the sections shown in *B* and *C*. *B*, Section showing the rostral articulation between the ascending process of the premaxilla (*inset with arrow*) and the articular meniscus. *C*, Section at the level of the posterior articulation between premaxillae and the articular meniscus (arrow indicates the articulation facet). Developing replacement teeth are visible in the basketlike premaxillae. Scale bars = 1 mm.

connecting the jaws to the hyoids (see Geerinckx et al. 2007*a*; Fig. 5*D*). The dentary complex caudoventrally carries one row of about 24 functional teeth (Fig. 1*B*, 1*C*; Fig. 3*E*). As with the upper jaw, the lower jaw tooth plates also bear a concave surface housing multiple rows of nonerupted teeth (Fig. 3*A*, 3*E*). The shape of the tooth-bearing dentary complex is very similar to that of the premaxillae, albeit somewhat rounder. It also carries a long and narrow rostrodorsally directed coronoid process (Fig. 3*E*). Contact between the dentary complex and the angular complex is through a suture (ventrally) and a remnant of Meckel's cartilage (dorsally). At the level of the angular complex, the lower jaw articulates with the quadrate of the suspensorium (Fig. 3*A*, 3*C*, 3*D*). Another prominent feature of the lower jaw is the orientation of the mandibular rami. From the articulation point with the suspensorium, they almost lie

within the same transverse plane (and do not run rostrally as in most teleosts) when at rest, as well as in the same coronal plane (Fig. 3*A*, 3*C*). From a functional point of view, this orientation may suggest a restricted ventral excursion of the mandibular tip during scraping, unless they are coupled to a suspensorial adduction (hence decreasing the dorsal angle between left and right mandibular rami). Still, it can be expected that the lower jaws are potentially more mobile than the upper jaws, as more muscles attach to them and they are not interconnected nor are they ligamentously connected to the hyoid medially. A thin mandibulo-hyoid ligament reaches from the lateralmost edge of the angular complex to the posterior ceratohyal. There is no interoperculo-mandibular ligament (nor an interopercular bone), as is observed in many loricariids (Armbruster 2004). The internal and external adductor mandibulae bundles (ter-
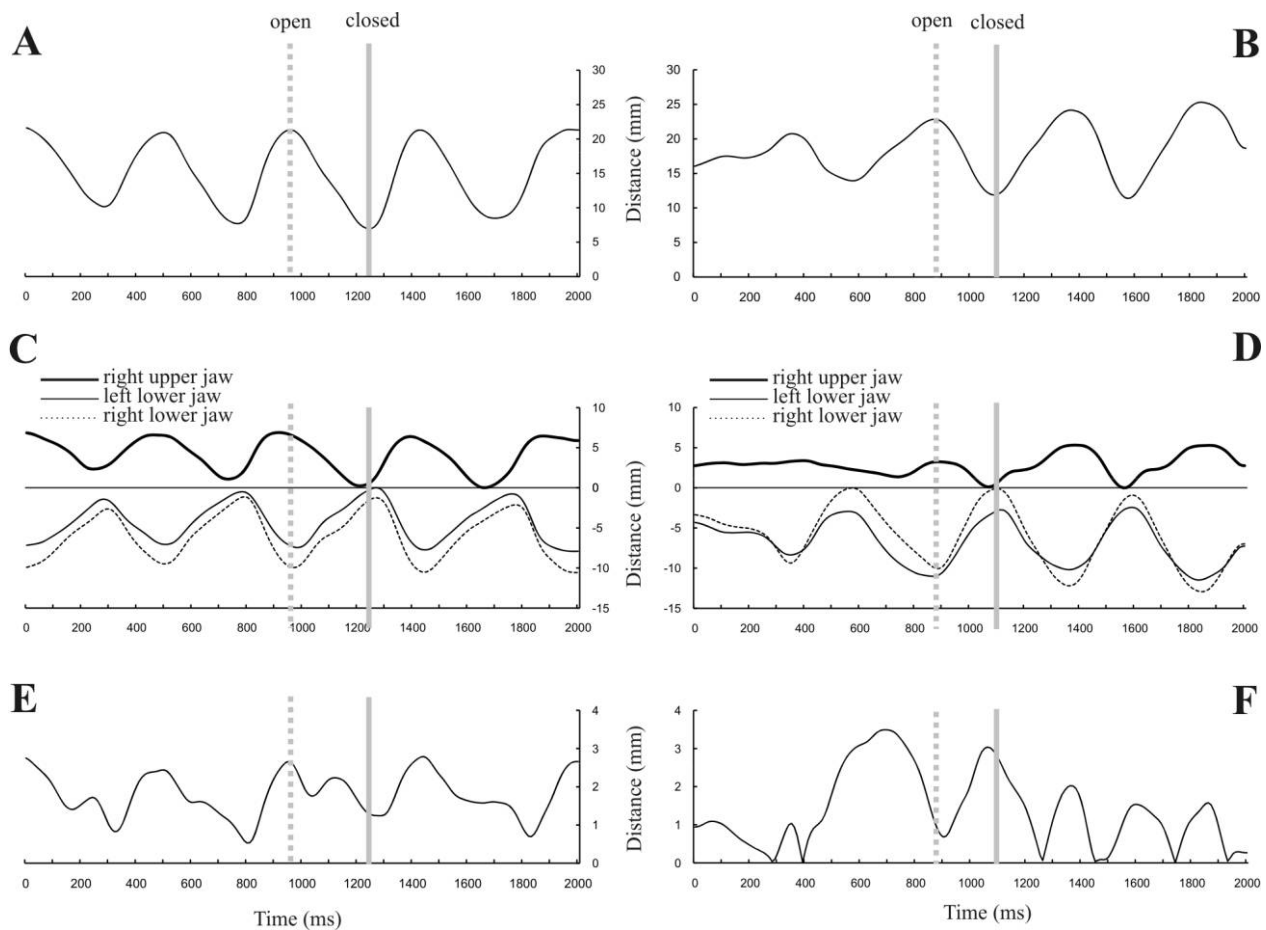
Figure 5. Graphs showing movement of jaws of (A, C, E) the 158-mm and (B, D, F) the 240-mm *Pterygoplichthys disjunctivus* specimens during a 2-s interval. *A, B,* Distance between radio-opaque markers at base of right upper and lower jaw tooth rows. *C, D,* Protraction and retraction movements of right upper and both lower jaws (zero line refers to maximal upper jaw retraction and maximal lower jaw protraction). *E, F,* Left-right asymmetry of lower jaw movements (represented by left-right interdistance on anteroposterior axis).

minology according to Geerinckx et al. [forthcoming]) attach broadly to the dorsal side of both lower jaw halves, including to the coronoid process. The lateral face of the basketlike dentary serves as an insertion site for the dentary parts of the anterior and posterior intermandibularis muscles (terminology according to Geerinckx and Adriaens [2007]). Although both lower jaws are connected to the hyoid through this cartilage, they are only very loosely connected to this plug by connective tissue, which explains the observed substantial degree of freedom.

Although the maxillae and autopalatines are closely connected and are presumably interacting with upper jaw movement, they may not be involved in the mechanism used for scraping off food. As in other catfishes, the maxillae bear a head that articulates with the rostral tip of the autopalatine, with the articulation lying immediately dorsal to the premaxillae (Figs. 3, 4C).

Kinematic Analysis

To specifically address the decoupled and highly mobile upper and lower jaws, our kinematic analysis focuses on (1) jaw move-

ments involved in mouth opening and closing, (2) the relative contribution of upper and lower jaw to mouth opening and closing, (3) aspects of jaw rotation during mouth opening and closing, and (4) asymmetrical movements in the jaws. To describe jaw kinematics, the terminology used considers the atypical orientation (and thus, the movements) of the jaws with respect to movements in generalized teleosts. Because the lower jaw tooth plates are directed more ventrally (lying in the same coronal plane as the ventral body wall), their movements mainly involve a protraction during the scraping phase followed by a retraction during the recovery phase. To emphasize this distinct movement of the lower jaw in loricariids compared with the generalized teleostean condition, "pro-" and "retraction" are used instead of "elevation" and "depression," respectively. The same terminology ("pro-" and "retraction") is used for the upper jaw movements; however, here "protraction" would be analogous to upper jaw protrusion.

From 23 scraping cycles (12 from the 158-mm specimen, 11 from the 240-mm specimen), the calculated average duration of a full jaw opening-closing cycle is 449 ms (SD 140 ms), with the jaw opening phase usually shorter (207 ms ± 41 SD) than
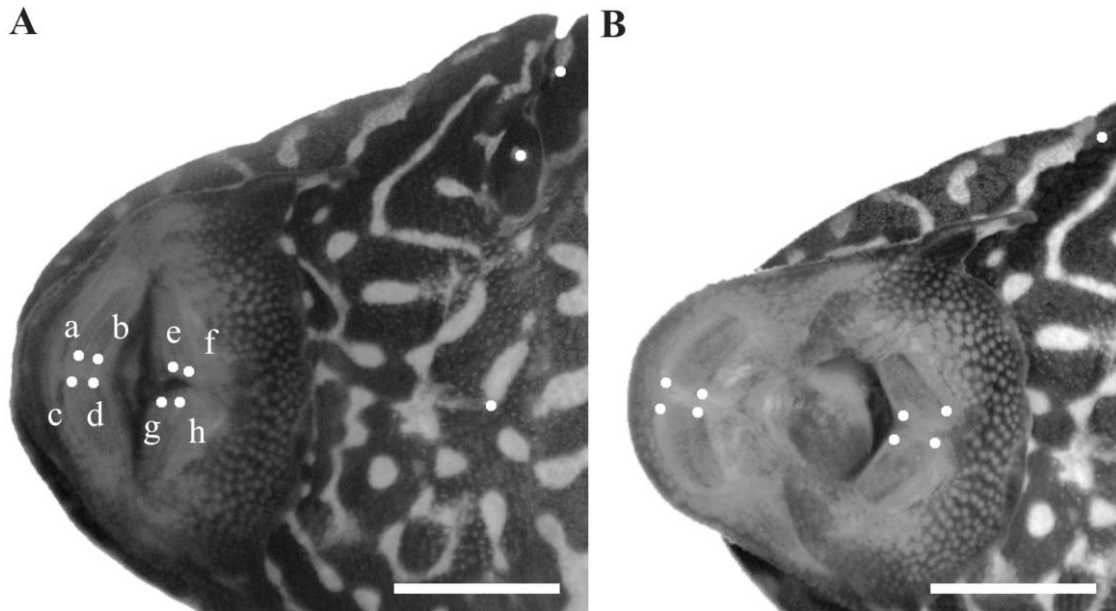
Figure 6. Ventral views of head region of the 158-mm *Pterygoplichthys disjunctivus* specimen with (*A*) closed and (*B*) almost maximally opened mouth. The distance between the rostromedial point *a* and the caudomedial point *b* represents the horizontal projection of the width of the externally visible part of the left upper jaw. The changes in this distance reflect the rotation or tilting of the left upper jaw (compare *A* and *B*). Points *c–h* are rostro- and caudomedial points on the visible parts of the right upper and both lower jaws. See Figure 7 for a kinematic analysis of these distances. Left-right asymmetry is visible in the movements of the lower jaws (*B*). Nonlabeled points are reference points on the ventral skin. Scale bars = 10 mm.

the closing phase (239 ms ± 46 SD). There is substantial variation in these durations in individual scraping cycles.

At the end of the scraping cycle, the lower jaws are fully protracted, leading to an almost completely closed mouth, whereas at the onset of the cycle, the retracted jaws result in a widely opened mouth (Fig. 5*A*–5*D*). In rest, the position of the lower jaws is intermediate. During the scraping phase, the row of rakelike teeth touch and scrape the substrate. Similarly, the scraping cycle of the upper jaws contains a retraction phase (scraping, closing the mouth) and a protraction phase (nonscraping, opening the mouth; Fig. 5*A*–5*D*). A subtle difference was observed in the onset and maximum extent of upper jaw retraction and lower jaw protraction, with the upper jaw retraction slightly preceding the lower jaw protraction.

The distance covered by the upper and lower jaws during scraping is variable, with consistently larger average scraping distances for the lower jaw, but exceptions to this pattern were observed. In the smaller specimen (158 mm SL), from which more data were collected, the average lower jaw scraping distance is 15% of the head length (min, 12%; max, 20%; $n = 16$), while the average upper jaw scraping distance is 13% of the head length (min, 9%; max, 16%; $n = 8$). In the larger specimen, the lower jaw did not move during scraping in some cases. However, each time both upper and lower jaws were moving, the lower jaw scraping distance was consistently higher, with a larger difference in the larger specimen than in the smaller specimen: 13% of the head length for lower jaw (min., 8%; max., 17%; $n = 6$) and 5% of the head length for the upper jaw (min., 1%; max., 8%; $n = 4$). This difference proved

to be significant in the scaled displacements (scaled to head length; ANOVA, $P < 0.001$ for both specimens); this difference was significantly larger in the larger specimen (ANOVA, level of interaction, $P = 0.005$). Thus, substantial differences exist in the degree in which the upper and lower jaws participate in scraping (see also Fig. 5*C*, 5*D*).

The orientation of the upper and lower tooth plates with respect to the horizontal plane (thus, the level of tilting of the plates) was determined by the distances between points *a* and *b* and *c* and *d* (for the upper jaw) and points *e* and *f* and *g* and *h* (for the lower jaw; Fig. 6). The kinematic profile of the tooth plates shows a pattern that, to some degree, deviates from what is to be expected from a lower jaw rotating around its axis (passing through both mandibular articulations) and from an upper jaw rotating around a fixed point at the mesethmoid (Fig. 7). Especially during the phase of maximal mouth opening, the upper jaw tooth plates show a plateau in the amount of tilting (where a sinusoidal pattern would be expected).

With respect to left-right asymmetry, and hence, the decoupled movements of the jaw halves, a comparison of left versus right jaw movements showed a certain degree of left-right asymmetrical movement in the lower jaw (Fig. 5*E*, 5*F*, graph representing subtraction of anteroposterior excursion of one ramus from the others), but not in the upper jaw.

Discussion

Specialized Jaw Morphology in Loricariid Catfishes

Both upper and lower jaws of *Pterygoplichthys disjunctivus* (and other loricariids) differ substantially from those in most non-
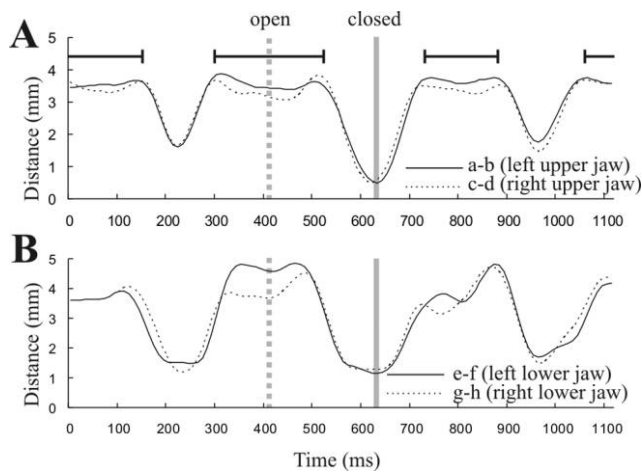
Figure 7. Graph representing tilting, with respect to the horizontal plane, of (*A*) upper and (*B*) lower jaws of the 158-mm *Pterygoplichthys disjunctivus* specimen. Horizontal bars indicate the plateaus with limited changes in tilting. See Figure 6 for references of points *a–h*.

loricariid catfishes, at different levels: (1) dentition, (2) jaw shape and position in the head, and (3) structural modifications linked to mobility (Schaefer and Lauder 1986; Adriaens and Verraes 1998; Arratia 2003; Huysentruyt and Adriaens 2005).

First, there is the aspect of a single row of functional teeth followed by multiple rows of newly formed, nonfunctional teeth (Geerinckx et al. 2007*b*). This pattern of teeth renewal, with posterior nonfunctional teeth developing and shifting anteriorly along the jaw surface, is considered to be typical of elasmobranchs but is also found in some other substrate-scraping teleosts (Norris and Prescott 1959; Roberts 1967). The major difference in loricariids, however, is that teeth develop in a basketlike cavity in the jaws (whereas in elasmobranchs, they follow the outer surface of the jaw cartilage). In batoids it has been shown that, even with homodont dentition, multiple functions may be exerted by teeth within a single ontogenetic series, depending on their position in the jaws (i.e., occlusal vs. external teeth; Dean et al. 2008). Having new teeth develop under mechanically unloaded conditions (because only the first row is functional) provides a dynamic system for tooth development, yielding scraping tools with a very distinct shape (Z-like teeth; Geerinckx et al. 2007*b*; Fig. 2).

Second, the shape and mechanical interaction with surrounding structures is different from the situation found in basal loricarioid catfishes (and most other catfishes). The latter have premaxillae that are strongly connected to the mesethmoid, without any potential to move back and forth (Fig. 8). These catfishes also lack an ascending process, a character typical of teleost fishes that perform premaxillary protrusion (Westneat 2004). Such a process, although small, is present on the premaxillae in *P. disjunctivus* (Figs. 3*E*, 4*B*) and has originated independently from that of other teleosts (basal diplomystid and nematogenyid catfishes lack it; Arratia 1987; Diogo et al. 2006). These morphological differences can be related to the scraping-feeding mode of the family. Geerinckx et al. (2008)

discuss the anteroventral extension of the upper snout region during ontogeny, with a shifting of the upper jaws anteroventrally. This is reflected in the ontogenetic shift from a larval subterminal mouth to a juvenile ventral mouth. The ventrally directed mesethmoid, and especially its medioventral disk, provide a suspension point for the premaxillae that lies even more ventral, thereby more ventrally positioning the upper jaws.

Third, there is the presence of an articular cartilage intermediating the connection between the premaxillae and the medial and ventrally directed disk of the ethmoid (Fig. 4). In most siluriforms, the premaxillae are firmly attached to lateral cornua of the mesethmoid, with a total inability to perform protrusion of any kind (Adriaens 2003). In the loricarioid lineage, there is a varying degree of premaxillary mobility, as demonstrated here for loricariids and as suggested for their sister group (astroblepids; Howes 1983; Schaefer and Lauder 1986; Schaefer 1990; Diogo 2005; Fig. 8). The presence and morphology of the cartilaginous structure found in *P. disjunctivus*, functioning as an articular meniscus, suggest that this forms the structural basis for an improved upper jaw mobility. A similar cartilaginous structure is considered to be absent in astroblepids and thus may be a novelty in loricariids (Armbruster 2004, character 72). Serial sections confirm the presence of this cartilage in *P. disjunctivus*, as well as in other loricariid genera (such as *Ancistrus* and *Otocinclus*; T. Geerinckx, personal observation). On the basis of this morphology, as observed in *P. disjunctivus*, it is suggested that the upper jaws can rotate and potentially even slide anteriorly and posteriorly around their cartilaginous suspension on the mesethmoid disk.

Even more atypical for a siluriform jaw apparatus are the medially directed lower jaw rami in loricariids, with the teeth-bearing basketlike dentary structure additionally being displaced ventrally. Most other catfishes have a more elongate jaw that is more rostrally directed. As well, the shape of the lower jaw in loricariids is remarkably different from that of nonloricariid catfishes and other teleosts: the tooth row and coronoid process are situated on almost opposite sides of the jaw (caudoventrally and almost rostrodorsally, respectively; Fig. 3*C*, 3*E*), whereas in most fishes, they are both found on the dorsal aspect of the jaw. Unlike the upper jaw in *P. disjunctivus*, the halves of which are tightly interconnected by the short interpremaxillary ligament, the lower jaw rami can be moved more or less independently, within certain boundaries (indirect connection through lip tissue, etc.). No medial connection (symphysis) between the rami of the lower jaw is present (Fig. 3*C*), nor is there any medial ligamentous connection to the hyoid arch. A cartilage plug, found in *P. disjunctivus* and other loricariids, attaches to the hyoid arch at the midline and protrudes into the region behind and between the lower jaws (Geerinckx et al. 2007*a*; Fig. 5*D*). It has been hypothesized that this is a supporting device for the dento-mentomeckelian bones, preventing them from merely being pulled caudally (Geerinckx et al. 2007*a*): the plug may partly restrict their caudal motion, and the contraction of the adductor mandibulae, inserting on the dorsocaudal aspects of the jaws and the dorsally ascending
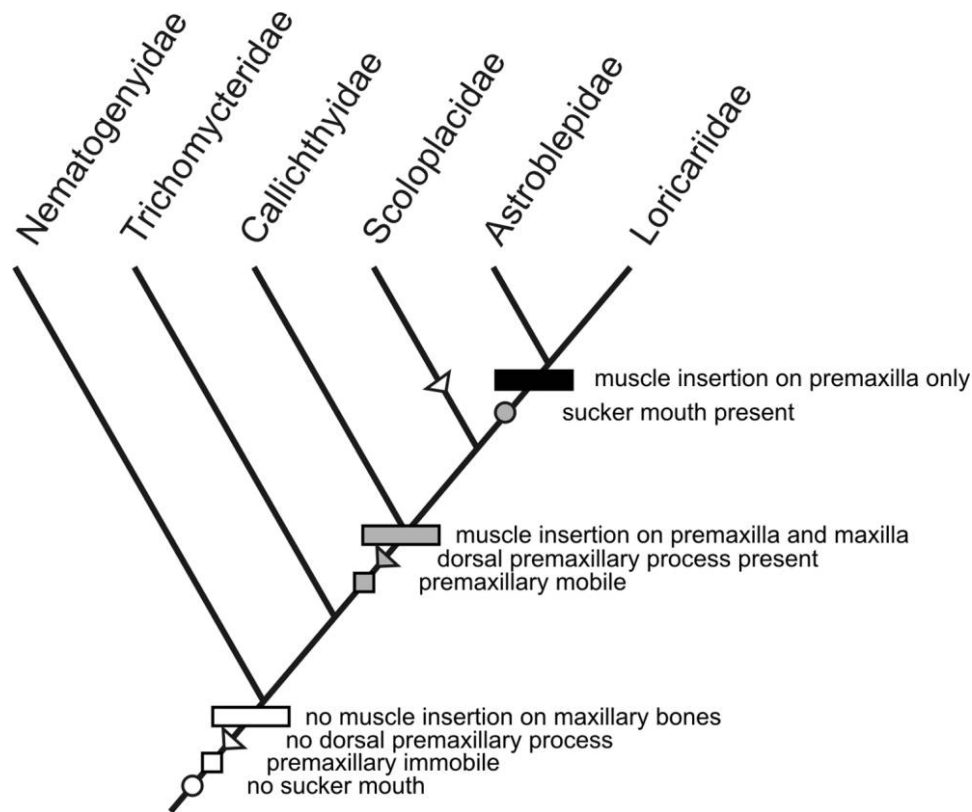
Figure 8. Cladogram of Loricarioidea (based on Sullivan et al. 2006) showing the most important evolutionary changes toward the scraping apparatus of loricariids (white markers refer to the plesiomorphic condition, gray and black filled markers refer to different derived conditions; marker shape reflects different characters).

coronoid process, is then hypothesized to partly cause a rotation around the longitudinal axis of the jaws themselves.

Jaw Mobility and Substrate Scraping

The kinematic results presented here for the first time quantitatively confirm upper jaw mobility, a condition quite unique for catfishes, in a loricariid representative. These results also demonstrate the wide extent of jaw protraction and retraction. It does seem, however, that protraction of the upper jaw in loricariids does not correspond to the movements generally considered to be "protrusion" (sensu Motta 1984). Motta considered protrusion to be a sliding motion of the premaxillae along their ascending process on the rostrum that is facilitated by a cartilaginous strut. Both morphological and kinematic data presented here suggest that premaxillary movements in loricariids mainly involve a rotation, but this rotation seems to be combined with some level of sliding. The displacement of the upper jaw (Fig. 5C–5D) indicates that the observed plateau in the level of tooth plate tilting (Fig. 7A) cannot be explained by a stop in premaxillary movement (hence its tilting). Even taking into consideration a potential error as a result of parallax issues, this discrete plateau suggests a translation of the upper jaw; however, further study is needed to test this.

Loricariids do differ in the driving mechanism behind pre-maxillary protrusion, because (1) the lower jaw is never ultimately located anterior to the upper jaw (and thus cannot pull it along by way of a primordial ligament) and (2) the maxillae are small and are involved in supporting a small maxillary barbel (hence, they cannot push the premaxillae forward). Thus, the actual premaxillary protrusion should be caused by another mechanism. One plausible mechanism may involve the autopalatine, the rostral head of which is connected to the maxilla lying immediately above the premaxilla (Fig. 4C). A ventral displacement of this head and maxilla may thus push the premaxilla forward during the recovery stroke. Additionally, the involvement of an anterior derivative of the adductor arcus palatini muscle has recently been suggested (Geerinckx et al., forthcoming). All of these movements could have originated as a part of a modified siluriform maxillary mechanism (Gosline 1975).

Premaxillary retraction, the power stroke during scraping, is provided by the retractor premaxilla, a muscle unique to Loricariidae and Astroblepidae. A comparative and ontogenetic survey of the jaw adductor muscle complex has shown that this retractor is derived from this complex (Geerinckx et al., forthcoming).

The kinematic profiles of the lower jaw shown in this study clearly indicate a certain left-right independence of jaw rami in *P. disjunctivus* (Fig. 5E), as well as a complex rotational

movement wherein rotations along the long axes of the rami may be involved. A comparison of the data presented in Figures 5A and 7B seems to confirm this rotation around the longitudinal axes as they are rotating forward and backward around the quadrate joint. This longitudinal jaw rotation may have the advantage of keeping tooth plates at optimal angles against the substrate for longer periods along a larger surface (i.e., optimal for efficient scraping). This lower jaw movement has not been described in any other teleost so far, and it represents a major biomechanical innovation in the loricarioid lineage. Whether this mechanism exists in other loricarioids, however, is not known. The loricariid feeding system could clearly benefit from this additional degree of freedom of the lower jaw, because the tooth row of each lower jaw can be kept in an extended phase of contact with the substrate, thus enabling the collection of more food per feeding cycle. Still, this study only partly resolves the complex lower jaw mobility. More kinematic data, especially a more thorough x-ray video study coupled with electromyography, are needed to elucidate the interaction of the different bony and muscular elements in the lower jaw region.

Liem (1980) recorded irregular and often noncyclical jaw movements in algae-feeding cichlids, which are apparently adjusted to irregularities of the substrate. This study demonstrates that this is also the case in loricariids. Increased mobility, including left-right flexibility, supports the idea of jaws as (to some degree) a passively adaptable system able to cope with irregularities in the substrate surface (but electromyography data would be required to rule out asymmetric muscle contraction). Especially for the more mobile lower jaws, bilateral asymmetry of muscle activity would even allow a finer regulation of the scraping of irregular substrates. Such an asymmetry has been found in cichlids (Liem 1979). Although certain cichlids and many loricariids feed on encrusted algae, their feeding apparatuses are different: cichlids lack a suckermouth and a medially directed lower jaw, and they bite pieces of the algae off the substrate (Yamaoka 1983), whereas loricariids more thoroughly rake encrusted matter off the substrate and are in closer contact with the often irregular feeding substrates.

Whether the decoupling of the upper jaw from the neurocranium in loricarioids (both structurally and functionally) has indeed led to the extensive diversity of species and morphotypes in loricariids still needs to be addressed with a suited experimental design. Other specializations, such as body armor, may also have been crucial causative factors. This study does show, however, that (1) jaw mobility is high in loricariids compared with catfishes in general (although comparative kinematic data on jaw movements in other catfishes are still lacking, comparative morphological evidence supports this), (2) the observed kinematic flexibility seems to provide some benefits for scraping on irregular surfaces, and (3) it is evident that, considering the high species diversity (716 species according to Ferraris [2007]), jaw mobility definitely did not restrain speciation (compared with, e.g., other loricarioid catfishes).

In summary, our data show that the jaw system of loricariids is capable of a high level of mobility and functional versatility in this lineage (compared with other catfishes), allowing an efficient scraping system. Some aspects of this increased mobility (upper jaw translation and lower jaw rotation along the long axis), as well as asymmetrical mobility in the lower jaw, may well be beneficial for efficient algae scraping. Clearly, further functional studies combining x-ray videography and electromyography are needed to investigate whether the extreme jaw morphology in scraping catfish goes hand in hand with the evolution of novel motor patterns, as suggested by Schaefer and Lauder (1986).

Literature Cited

Adriaens D. 2003. Feeding mechanisms. Pp. 221–248 in G. Arratia, A.S. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes. Vol. 1. Science, Enfield, NH.

Adriaens D. and W. Verraes. 1998. Ontogeny of the osteocranium in the African catfish, *Clarias gariepinus* (1822) (Siluriformes: Clariidae): ossification sequence as a response to functional demands. J Morphol 235:183–237.

Angelescu V. and F.S. Gneri. 1949. Adaptaciones del aparato digestivo al régimen alimenticio en algunos peces del Río Uruguay y del Río de la Plata. Tipo omnívoro e ilófago en representantes de las familias "Loricariidae" y "Anostomidae." Rev Inst Nac Investig Cienc Nat Mus Argent Cienc Nat Bernardino Rivadavia (Zool) 1:161–272.

Angermeier P.L. and J.R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Environ Biol Fishes 9:117–135.

Aranha J.M.R., D.F. Takeuti, and T.M. Yoshimura. 1998. Habitat use and food partitioning of the fishes in a coastal stream of Atlantic Forest, Brazil. Rev Biol Trop 46:951–959.

Armbruster J.W. 2004. Phylogenetic relationships of the suckermouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. Zool J Linn Soc 141:1–80.

Arratia G. 1987. Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy, and phylogenetic implications. Bonn Zool Monogr 24:1–120.

———. 2003. Catfish head skeleton: an overview. Pp. 3–46 in G. Arratia, A.S. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes. Vol. 1. Science, Enfield, NH.

Buck S. and I. Sazima. 1995. An assemblage of mailed catfishes

(Loricariidae) in southeastern Brazil: distribution, activity, and feeding. Ichthyol Explor Freshw 6:325–332.

Dean M.N., J.B. Ramsay, and J.T. Schaefer. 2008. Tooth re-orientation affects tooth function during prey processing and tooth ontogeny in the lesser electric ray, *Narcine brasiliensis*. Zoology 111:123–134.

Delariva R.L. and A.A. Agostinho. 2001. Relationship between morphology and diets of six Neotropical loricariids. J Fish Biol 58:832–847.

Diogo R. 2005. Morphological Evolution, Aptations, Homoplasies, Constraints, and Evolutionary Trends: Catfishes as a Case Study on General Phylogeny and Macroevolution. Science, Enfield, NH.

Diogo R., M. Chardon, and P. Vandewalle. 2006. On the osteology and myology of the cephalic region and pectoral girdle of *Nematogenys inermis* (Ghichenot, 1848), with comments on the autapomorphies and phylogenetic relationships of the Nematogenyidae (Teleostei: Siluriformes). Belg J Zool 136:15–24.

Ferraris C.J. 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. Zootaxa 1418:1–628.

Fugi R., N.S. Hahn, and A.A. Agostinho. 1996. Feeding styles of five species of bottom-feeding fishes of the high Paraná River. Environ Biol Fishes 46:297–307.

Geerinckx T. and D. Adriaens. 2007. Ontogeny of the intermandibular and hyoid musculature in the suckermouth armoured catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes). Anim Biol 57:339–357.

———. 2008. Ontogeny of the suspensorial and opercular musculature in the suckermouth armoured catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes). Zoomorphology 127:83–95.

Geerinckx T., M. Brunain, A. Herrel, P. Aerts, and D. Adriaens. 2007*a*. A head with a suckermouth: a functional-morphological study of the head of the suckermouth armoured catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes). Belg J Zool 137:47–66.

Geerinckx T., J. De Poorter, and D. Adriaens. 2007*b*. Morphology and development of teeth and epidermal brushes in loricariid catfishes. J Morphol 268:805–814.

Geerinckx T., F. Huysentruyt, and D. Adriaens. Ontogeny of the jaw and maxillary barbel musculature in the armoured catfish families Loricariidae and Callichthyidae (Loricarioidea, Siluriformes), with a discussion on muscle homologies. Zool J Linnean Soc (forthcoming).

Geerinckx T., Y. Verhaegen, and D. Adriaens. 2008. Ontogenetic allometries and shape changes in the suckermouth armoured catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes), related to suckermouth attachment and yolk sac size. J Fish Biol 72:803–814.

Gosline W.A. 1975. The palatine-maxillary mechanism in catfishes, with comment on the evolution and zoogeography of modern siluroids. Occas Pap Calif Acad Sci 120:1–31.

Grosman M.F., J.R. González Castelain, and E.J. Usunoff. 1996. Trophic niches in an Argentine pond as a way to assess functional relationships between fishes and other communities. Water SA 22:345–350.

Howes G.J. 1983. The cranial muscles of loricarioid catfishes, their homologies and value as taxonomic characters. Bull Br Mus Nat Hist (Zool) 45:309–345.

Huysentruyt F. and D. Adriaens. 2005. Descriptive osteology of *Corydoras aeneus* (Gill, 1858) (Siluriformes: Callichthyidae). Cybium 29:261–273.

Lauder G.V. 1985. Aquatic feeding in lower vertebrates. Pp. 210–229 in M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, eds. Functional Vertebrate Morphology. Harvard University Press, Cambridge, MA.

Liem K.F. 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. J Zool (Lond) 189:93–125.

———. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Am Zool 20:295–314.

Masschaele B.C., V. Cnudde, M. Dierick, P. Jacobs, L. Van Hoorebeke, and J. Vlassenbroeck. 2007. UGCT: new x-ray radiography and tomography facility. Nucl Inst Meth Phys Res A 580:266–269.

Motta P.J. 1984. Mechanics and functions of jaw protrusion in teleost fishes: a review. Copeia 1984:1–18.

Nelson J.A. 2002. Metabolism of three species of herbivorous loricariid catfishes: influence of size and diet. J Fish Biol 61:1586–1599.

Nelson J.A., D.A. Wubah, M.E. Whitmer, E.A. Johnson, and D.J. Stewart. 1999. Wood-eating catfishes of the genus *Panaque*: gut microflora and cellulolytic enzyme activities. J Fish Biol 54:1069–1082.

Norris K.S. and J.H. Prescott. 1959. Jaw structure and tooth replacement in the opaleye, *Girella nigricans* (Ayres) with notes on other species. Copeia 4:275–283.

Power M.E. 1984. Grazing response of tropical freshwater fishes to different scales of variation in their food. Pp. 25–37 in T.M. Zaret, ed. Evolutionary Ecology of Neotropical Freshwater Fishes. Dr. W. Junk, The Hague.

Roberts T.R. 1967. Tooth formation and replacement in characoid fishes. Stanford Ichthyolog Bull 8:231–247.

Saul W.G. 1975. An ecological study of fishes at a site in Upper Amazonian Ecuador. Proc Acad Nat Sci Phila 127:93–134.

Schaefer S.A. 1987. Osteology of *Hypostomus plecostomus* (Linnaeus) with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). Contrib Sci 394:1–31.

———. 1988. Homology and evolution of the opercular series in the loricarioid catfishes (Pisces: Siluroidei). J Zool (Lond) 214:81–93.

———. 1990. Anatomy and relationships of the scoloplacid catfishes. Proc Acad Nat Sci Phila 142:167–210.

———. 1997. The Neotropical cascudinhos: systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). Proc Acad Nat Sci Phila 148:1–120.

Schaefer S.A. and G.V. Lauder. 1986. Historical transformation of functional design: evolutionary morphology of feeding mechanisms in loricarioid catfishes. Syst Zool 35:489–508.

———. 1996. Testing historical hypotheses of morphological change: biomechanical decoupling in loricarioid catfishes. Evolution 50:1661–1675.

Schaefer S.A. and D.J. Stewart. 1993. Systematics of the *Panaque dentex* species group (Siluriformes: Loricariidae), wood-eating armored catfishes from tropical South America. Ichthyol Explor Freshw 4:309–342.

Sullivan J.P., J.G. Lundberg, and M. Hardman. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using rag1 and rag2 nuclear gene sequences. Mol Phylogenet Evol 41:636–662.

Taylor W.R. and G.C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.

Vermeij G.J. 1973. Adaptation, versatility, and evolution. Syst Zool 22:466–477.

Vlassenbroeck J., M. Dierick, B. Masschaele, V. Cnudde, L. Van Hoorebeke, and P. Jacobs. 2007. Software tools for quantification of x-ray microtomography at the UGCT. Nucl Inst Meth Phys Res A 580:442–445.

Weber C. 1992. Révision du genre *Pterygoplichthys* sensu lato (Pisces, Siluriformes, Loricariidae). Rev Fr Aquariol 19:1–36.

Westneat M.W. 2004. Evolution of levers and linkages in the feeding mechanisms of fishes. Integr Comp Biol 44:378–389.

Yamaoka K. 1983. Feeding behaviour and dental morphology of algae scraping cichlids (Pisces: Teleostei) in Lake Tanganyika. Afr Stud Monogr 4:77–89.