

# Morphology and Development of Teeth and Epidermal Brushes in Loricariid Catfishes

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**ABSTRACT** Loricariidae or suckermouth armored catfishes are one of several aquatic taxa feeding on epilithic and epiphytic algae. Their upper and lower jaws bear exquisitely curved teeth, which usually are asymmetrically bicuspid. The enlarged lower lip carries papillae with keratinous unicellular epidermal brushes or uncili. Teeth, and probably uncili too, assist in scraping food off substrates. Their morphology, growth, and replacement is examined and compared among several loricariid species, using cleared and stained specimens, serial sections, and SEM. Apart from the general tooth form and crown shape, the anterior layer of soft tissue on the lower shaft region, present in several species, appears to be a specialization for enhancing the mobility of individual teeth when scraping on uneven surfaces. During early ontogeny, a transition from simple conical to mature tooth occurs. The first uncili appear together with the first teeth carrying a bicuspid crown, 2 days after the first exogenous feeding, but synchronous with the complete resorption of the yolk sac. *J. Morphol.* 268:805–814, 2007. © 2007 Wiley-Liss, Inc.

**KEY WORDS:** dentition; Loricariidae; ontogeny; suckermouth armored catfishes; uncili

Brush- and gouge-like devices are ideal for scraping food off substrates, and are most often found in aquatic organisms, particularly aquatic insect larvae (Arens, 1994), amphibian larvae (Orton, 1953; Wassersug and Yamahita, 2001), and fishes. In all these cases the diet primarily consists of adherent algae. Examples in teleosts are the rake-like denticles of the osmeriform ayu (Howes and Sanford, 1987; Uehara and Miyoshi, 1993), the tooth-like keratinous hooks of Gyrinocheilidae (Ono, 1980; Benjamin, 1986), spatulate teeth of certain Cichlidae (Vandervennet et al., 2006) and Mochokidae, and the scraping teeth of species of the Loricariidae or suckermouth armored catfishes. The latter family exhibits the most exquisite and diverse teeth forms (e.g., Muller and Weber, 1992; Schaefer and Stewart, 1993; Delariva and Agostinho, 2001): the S- or Z-shaped recurved teeth are generally asymmetrically bicuspid, but, in some taxa, have one cusp only. Teeth of the related loricarioid, scoloplacid, and astroblepid families are usually symmetrically bifid (Schaefer, 1990), although shape variation exists (e.g., Cardona and Guerao, 1994). Teeth are absent in adults of the more basal callichthyids, while simple conical teeth have been found in small

juveniles (Huysseune and Sire, 1997a). While many genera of the basal loricarioid trichomycterids have rather conical teeth, *Henonemus* has (unicuspid) recurved teeth, reminiscent of loricariid teeth (DoNascimento and Provenzano, 2006).

Loricariidae are able to attach onto surfaces using a not well understood process allowing respiration during attachment, and scrape off algae and other food with their ventrally oriented upper and lower jaws. Ono (1980) and Roberts (1982) described unicellular keratinous lip projections or “uncili” on the surface of the expanded lower lip of loricariids. These epidermal projections might serve as abrasive brushes or protective structures for the associated taste buds. Ono (1980) studied the internal microstructure of the loricariid uncili. Unicellular and multicellular keratinous structures are found in several teleostean orders, with functions often related to reproduction, protection, abrasion, adhesion, and hydrodynamics (Branson, 1962; Wiley and Collette, 1970; Roberts, 1973, 1982; Arratia, 1987; Arratia and Huaquín, 1995; Chen and Arratia, 1996).

In this article we describe the morphology of loricariid teeth and uncili, their growth, and their shape during early ontogeny. Results are then discussed in view of the possible role of both structures in feeding.

## MATERIALS AND METHODS

Teeth and lips of several loricariid species were examined, using the clearing and staining method of Taylor and Van Dyke (1985), and SEM (Table 1): *Ancistrus* cf. *triradiatus*, *Pterygoplichthys lituratus*, *Panaque nigrolineatus*, *Otocinclus vestitus*, *Rineloricaria parva*, *Farlowella acus*, and *Sturisoma aureum*. All species were obtained commercially. After sedation in MS 222

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TABLE 1. Specimens used in the present study

Species	SL (mm)	Age (dPF)	Method
<i>Ancistrus cf. triradiatus</i>	6.1	4	SS (2 $\mu$ m)
<i>Ancistrus cf. triradiatus</i>	6.7	4	SEM
<i>Ancistrus cf. triradiatus</i>	8.0	7	SS (2 $\mu$ m)
<i>Ancistrus cf. triradiatus</i>	8.2	6	SEM
<i>Ancistrus cf. triradiatus</i>	9.8	8	SEM
<i>Ancistrus cf. triradiatus</i>	10.2	10	SEM
<i>Ancistrus cf. triradiatus</i>	10.2	14	SS (2 $\mu$ m)
<i>Ancistrus cf. triradiatus</i>	10.7	14	SEM
<i>Ancistrus cf. triradiatus</i>	33.5	160	SS (5 $\mu$ m)
<i>Ancistrus cf. triradiatus</i>	69.6	? (adult)	C+S
<i>Ancistrus cf. triradiatus</i>	75.0	? (adult)	C+S
<i>Ancistrus cf. triradiatus</i>	76.6	? (adult)	C+S
<i>Ancistrus cf. triradiatus</i>	85.4	? (adult)	C+S
<i>Ancistrus cf. triradiatus</i>	94.0	? (adult)	C+S
<i>Ancistrus cf. triradiatus</i>	101.9	? (adult)	C+S
<i>Ancistrus cf. triradiatus</i>	114.6	? (adult)	C+S
<i>Pterygoplichthys lituratus</i>	63	? (subadult)	SS (5 $\mu$ m)
<i>Pterygoplichthys lituratus</i>	94	? (subadult)	SEM
<i>Pterygoplichthys lituratus</i>	150	? (subadult)	C+S
<i>Panaque nigrolineatus</i>	71	? (subadult)	C+S
<i>Panaque nigrolineatus</i>	76	? (subadult)	SEM
<i>Otocinclus vestitus</i>	22	? (adult)	SS (5 $\mu$ m)
<i>Otocinclus vestitus</i>	24	? (adult)	C+S
<i>Otocinclus vestitus</i>	28	? (adult)	SEM
<i>Farlowella acus</i>	124	? (adult)	C+S
<i>Farlowella acus</i>	125	? (adult)	SEM
<i>Farlowella acus</i>	125	? (adult)	SS (5 $\mu$ m)
<i>Rineloricaria parva</i>	75	? (adult)	C+S
<i>Rineloricaria parva</i>	76	? (adult)	SEM
<i>Sturisoma aureum</i>	85	? (adult)	C+S
<i>Sturisoma aureum</i>	86	? (adult)	SEM

C+S, clearing and staining; dPF, days post-fertilization; SEM, scanning electron microscopy; SL, standard length; SS, serial sectioning.

the specimens were fixed in a 4% buffered formalin solution (at neutral pH).

*Ancistrus cf. triradiatus* was selected for the ontogenetic study. It is a medium-sized, mostly herbivorous and easily reared loriciid. Its teeth are extremely curved. Eggs were obtained from adults kept in a 24–26°C aquarium (30–130 cm). At different time intervals eggs and free-living embryos were sedated and fixed in a paraformaldehyde–glutaraldehyde solution. One subadult and three free-living embryonic specimens of this species were selected for serial sectioning (section thickness 2 or 5  $\mu$ m), using Technovit 7100 as plastic embedding medium, a Reichert-Jung Polycut microtome, and toluidin blue stain for visualization. One specimen of *Pterygoplichthys lituratus*, *Otocinclus vestitus*, and *Farlowella acus* was serially sectioned as well (Table 1).

Scanning electron micrographs were taken of teeth and lip tissues of all examined species and of five ontogenetic stages of *Ancistrus cf. triradiatus*. After isolation of the tissue samples from the in toto fixed specimens (see earlier), the material was dehydrated and critically point-dried with CO<sub>2</sub> using a Balzers CPD 020, and gold coated using a Balzers SCD 040. The material was then examined using a Jeol JSM-840 scanning electron microscope (15 kV; magnification up to 15,000 $\times$ ).

## RESULTS

### Morphology and Growth of Teeth

Upper and lower jaws of loriciids are oriented so that the teeth point ventrally, touching the substrate to which the fish is attaching (Fig. 1). Adult

*Ancistrus cf. triradiatus* specimens carry one row of 40–67 emergent teeth per premaxilla ( $n = 7$ , mean = 55), and 58–79 teeth per dentary ( $n = 7$ , mean = 69). No distinct differences were noted in tooth shape for each jaw, except for those on the lateral side being somewhat smaller. Teeth are Z-shaped, and are composed of a thick, curved base (which is covered by the jaw epithelium), a thin lower shaft, a thicker upper shaft, and a curved bicuspid crown (Fig. 2C). The base is movably connected to the jaw bone. The base and the shaft form an angle of about 90°, as do the shaft and the crown. The small lateral cusp has an angle of 110°–150° to the main cusp, and is about half as long. The anterior region of the lower shaft is not calcified, but is composed of soft material. A distal protuberance of this soft layer, seen only in *A. cf. triradiatus*, is stained blue with alcian blue and purple (metachromatic) with toluidin blue (Fig. 2C,I). Manipulating individual teeth of freshly killed *A. cf. triradiatus* specimens reveals that the lower shaft can actually bend up to 90° with respect to the tooth base (Fig. 3). Such considerable bending as shown in this figure (here caused by manipulation with tweezers) probably seldom occurs in natural circumstances, as the lip tissue, situated behind the teeth, hinders such excessive movement (e.g., Fig. 5A). Manipulated bending in the opposite, anterior direction, invariably causes breaking after bending only about 10°–20°.

One row of teeth emerges from the jaw epithelium (Figs. 1 and 2H). The jaws are essentially basket-shaped; the lower jaw also has a lateral “handle” articulating with the quadrate and consisting of the angulo-articular and part of the dento-mentomeckelium (Geerinckx et al., 2007). Tooth germs are

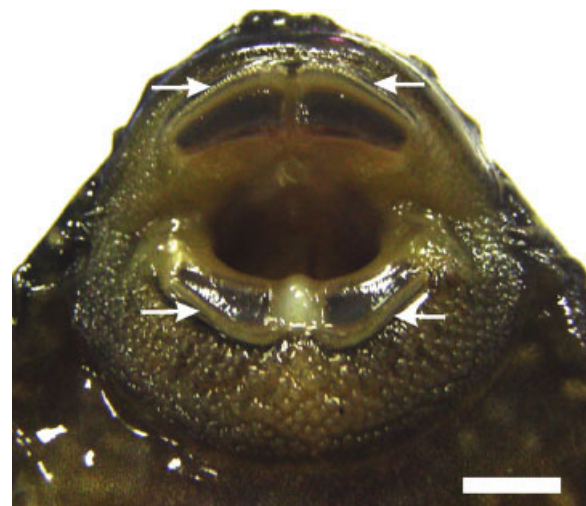


Fig. 1. Ventral view of head of adult *Ancistrus cf. triradiatus* showing the upper and lower jaws with tooth rows (arrows). Dark zones on jaws are the epithelium covering the replacement tooth rows. Scale bar is 5 mm.

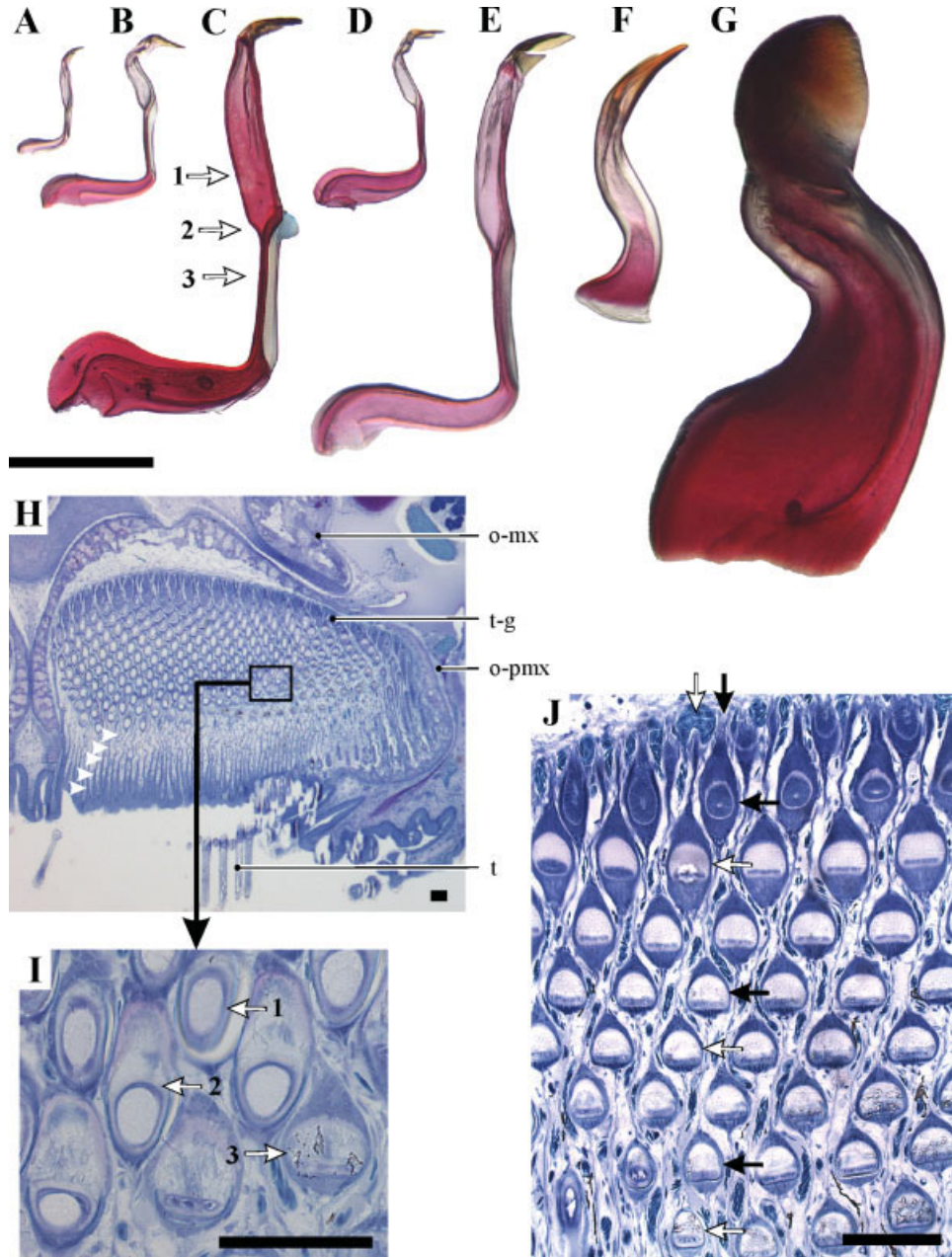


Fig. 2. Representative teeth of lower jaw. **A:** *Otocinclus vestitus*. **B:** *Sturisoma aureum*. **C:** *Ancistrus cf. triradiatus*. **D:** *Farlowella acus*. **E:** *Pterygoplichthys lituratus*. **F:** *Rineloricaria parva*. **G:** *Panaque nigrolineatus*. Scale bar for A–G is 500  $\mu$ m. **H:** Section through left premaxilla of a 33.5 mm *A. cf. triradiatus*, showing emergent teeth (below) and replacement teeth (above) and replacement tooth rows. Arrowheads point at scars left by emerging tooth. **I:** Detail of H, showing sections of the upper shaft (1), transition zone between upper and lower shaft, with distal protuberance (2), and lower shaft (3). **J:** Detail of premaxillary replacement teeth with indication of two series of successive replacement teeth (indicated by white and black horizontal arrows, respectively). The vertical arrows indicate the loci where each series originates. Scale bars for H–J are 50  $\mu$ m. o-mx, os maxillare; o-pmx, os praemaxillare; t-g, tooth germs; t, (erected) teeth.

found deep inside the basket; growing teeth migrate within the basket. The individual tooth germs are not found in bony crypts; serial sections show that the bases of emergent teeth are connected to the bone via soft tissue, most probably containing a large amount of collagen. Thus the development is completely extraosseous, as in other siluriforms and many other teleosts (Trapani, 2001). In the premaxilla, there is a progression of less- to more-developed teeth from posterior to anterior (vice versa for dentary). An anteroposterior cross-section through the jaws (Fig. 4) clearly shows this progression, but at the same time gives the false impres-

sion of the presence of numerous replacement tooth rows (up to 20). Serial sections, however, reveal the presence of only about four successive teeth in one tooth family: the arrows on Figure 2J show the replacement teeth originating from two distinct loci; an epithelial “track” connects the subsequent replacement teeth. A tooth becomes erected after it has been fully formed (Fig. 4): it penetrates the jaw epithelium, thereby rotating  $40^{\circ}$ – $80^{\circ}$  (large arrowheads on Fig. 5A indicate emerging teeth). This possibly rather sudden tooth movement leaves trail-like scars in the weak jaw epithelium (small arrowheads on Figs. 2H and 5A). Once in use, the crown

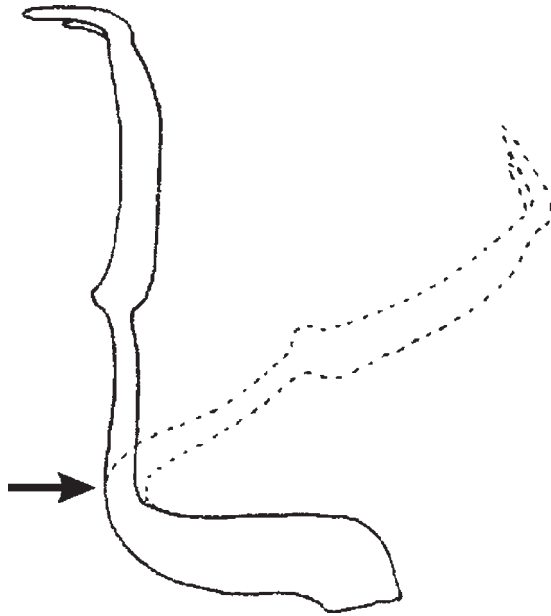


Fig. 3. Tooth of *Ancistrus* cf. *triradiatus* with indication of bendable lower shaft portion. The stippled line represents the nearly maximum extent of bending. See text for details.

is worn and consequently shortened; Figure 5B shows obvious signs of wear caused by scraping on substrates.

Previous authors have described the diversity in number and shape of teeth in various loricariids (Muller and Weber, 1992; Delariva and Agostinho, 2001). We limit our description to the most remarkable shape observations. The teeth of *Pterygoplichthys lituratus* and *Otocinclus vestitus* resemble those of *Ancistrus* cf. *triradiatus*, but the soft layer in the lower shaft region is thinner, lacking the distal protuberance (Figs. 2A,E and 5C,D). Long spatulate crowns with almost similarly sized cusps characterize *Sturisoma aureum* and *Farlowella acus* (Figs. 2B,D and 5E,F). *Panaque nigrolineatus* has sturdy, unicuspid, spoon-shaped teeth (Figs. 2G

and 5G). Both unequally sized cusps of the teeth of *Rineloricaria parva* are pointed (Figs. 2F and 5H). Teeth in the latter two species are least curved and lack the soft layer. They appear to be rigid, while teeth of all other species can bend to a certain degree between the lower shaft and the base. While 15–25 apparent replacement tooth rows are seen at first sight in adult specimens of all specimens (Fig. 4), only about four are present (as observed on serial sections of *P. lituratus* and *Farlowella acus*), as in *A. cf. triradiatus*. Analogous to this, the 7–8 apparent replacement rows seen in *O. vestitus* actually represent only two rows. One to two rows are probably present in *P. nigrolineatus* (5 apparent rows), and *R. parva* (4 apparent rows).

### Tooth Shape During Early Ontogeny

*Ancistrus* cf. *triradiatus* hatches 5–6 days after fertilization. The yolk sac is depleted after an additional 4–5 days. Ingested food particles are found in the intestine from 3 to 4 days after hatching. The first teeth appear on the premaxilla and erupt before hatching, at 4 days after fertilization. The (5–9) premaxillary teeth are conical, bearing no resemblance at all to the adult tooth shape (Fig. 6A). Analogous to the appearance of the skin odontodes, these first teeth are observed before the supporting bone materializes (Geerinckx et al., 2007).

Six days after fertilization, half a day after hatching, similar teeth are still present on the premaxilla, and identical teeth have appeared on the dentary as well. One replacement tooth row is present (7 days PF; arrows on Fig. 7A). Serial sections show that, as in adults, these teeth are connected to the bone via soft (collagenous) tissue. At 8 days new teeth possess a flattened, unicuspid tip (arrowheads on Fig. 6B); the curvature between the base and the shaft has now developed. Consequently, these new teeth are recurved backward (Fig. 6B), instead of slightly forward (conical teeth on Fig. 6A). A rudi-

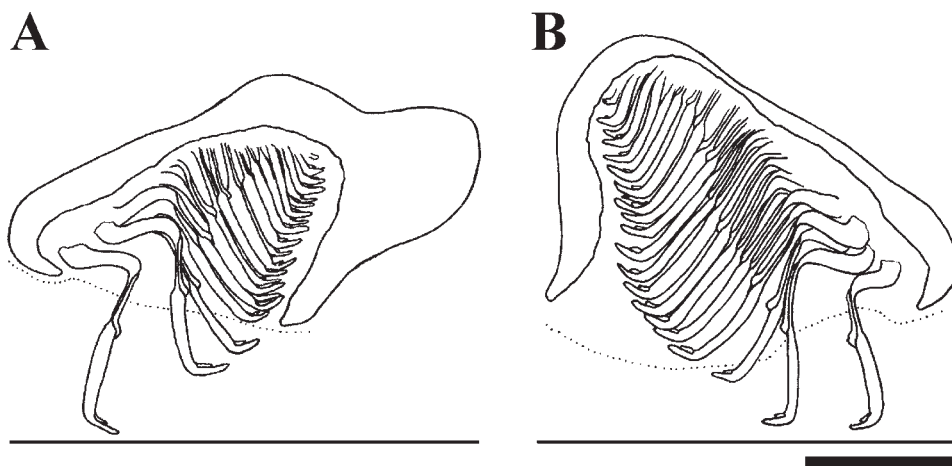


Fig. 4. Medial view on an anteroposterior cross-section through the right (A) upper and (B) lower jaw of a 75 mm SL *Ancistrus* cf. *triradiatus*, indicating emergent tooth and the apparent multiple series of replacement tooth. Notice that there are actually only about four replacement teeth per emergent tooth. The stippled lines indicate the approximate position of the jaw epithelium. Position of the substrate is indicated by a horizontal line. Scale bar is 1 mm.

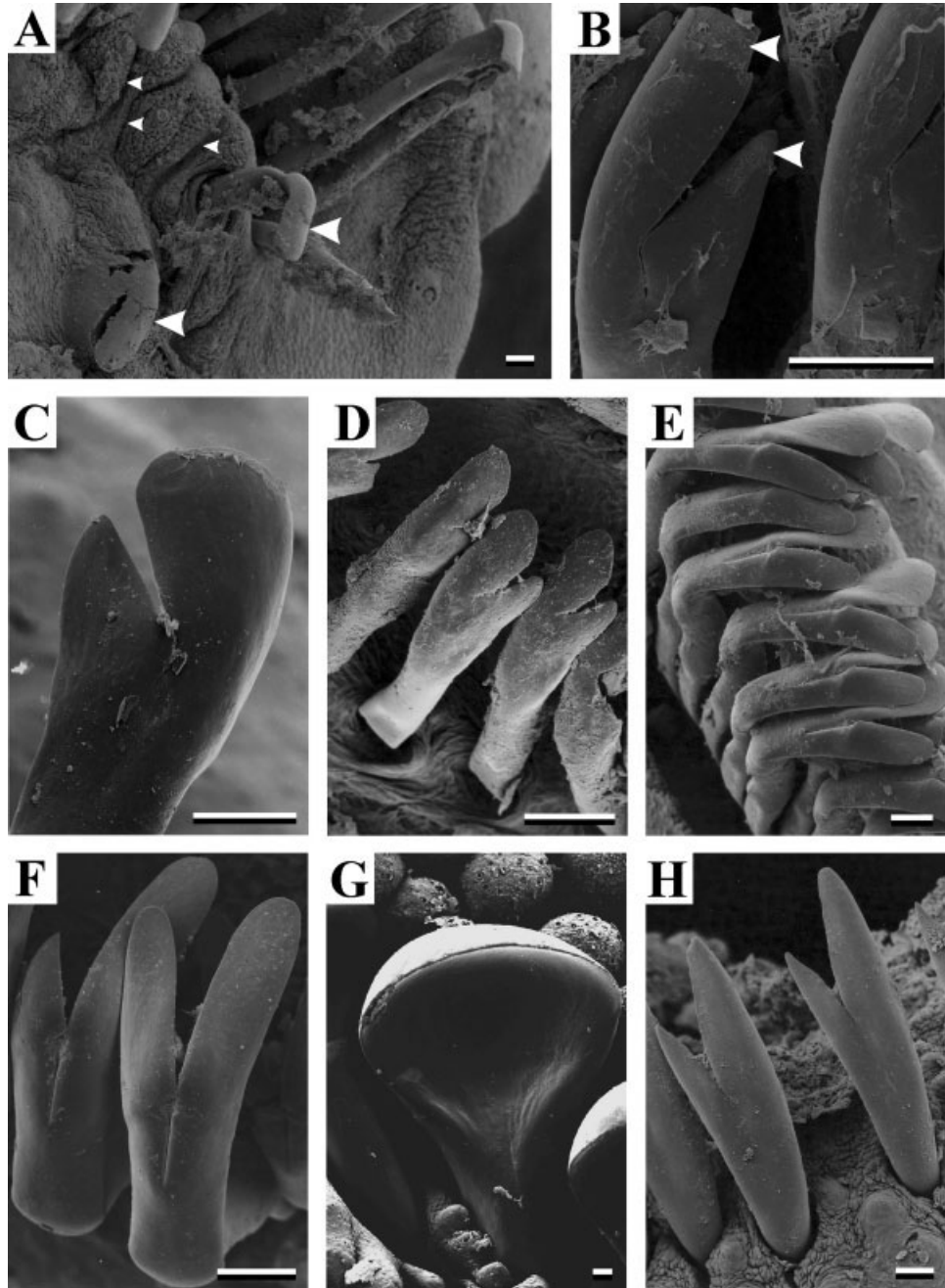


Fig. 5. Loricariid tooth crowns. SEM. **A:** Anterior view of dentary teeth of *Ancistrus* cf. *triradiatus* (large arrowheads indicate emerging teeth; small arrowheads indicate scars left by emerging teeth). **B:** Ventral close-up of heavily worn dentary tooth crown of same species (arrowheads indicate wear zone). **C:** Ventral close-up of dentary tooth crown of *Pterygoplichthys lituratus*. **D:** Ventral view of dentary tooth crowns of *Otocinclus vestitus*. **E:** Ventral view of dentary tooth crowns of *Sturisoma aureum*. **F:** Ventral view of dentary tooth crowns of *Farlowella acus*. **G:** Anterior view of dentary tooth crown of *Panaque nigrolineatus*. **H:** Ventral view of dentary tooth crowns of *Rineloricaria parva*. Scale bars are 50  $\mu$ m.

mentary bicuspid crown is present on some teeth at 10 days (both cusps are indicated by arrowheads on Fig. 6C). The curvature between the shaft and the crown, added to the one between the base and the shaft, results in the first Z-like teeth. Only 14 days after fertilization bicuspid crowns are present (Fig. 6D); cartilage resorption has made place for already 3–4 replacement rows (arrows on Fig. 7B). This is already the maximum of tooth rows observed in *Ancistrus* cf. *triradiatus*. The number of teeth has risen to 13–17 teeth for each of the four jaw bones. Already some of the teeth appear to

have a damaged crown. As opposed to the number of replacement rows, the number of teeth progressively increases during further ontogeny.

Pharyngeal teeth are present in all examined species [as opposed to Alexander's (1965) statement that they are absent]; they are cone-shaped. Their number more or less correlates with body size, without any further substantial difference between species. In *Ancistrus* cf. *triradiatus*, the first pharyngeal teeth appear at 3 days after hatching (Geerinckx et al., 2007), and about 30 teeth are present per single jaw quadrant.

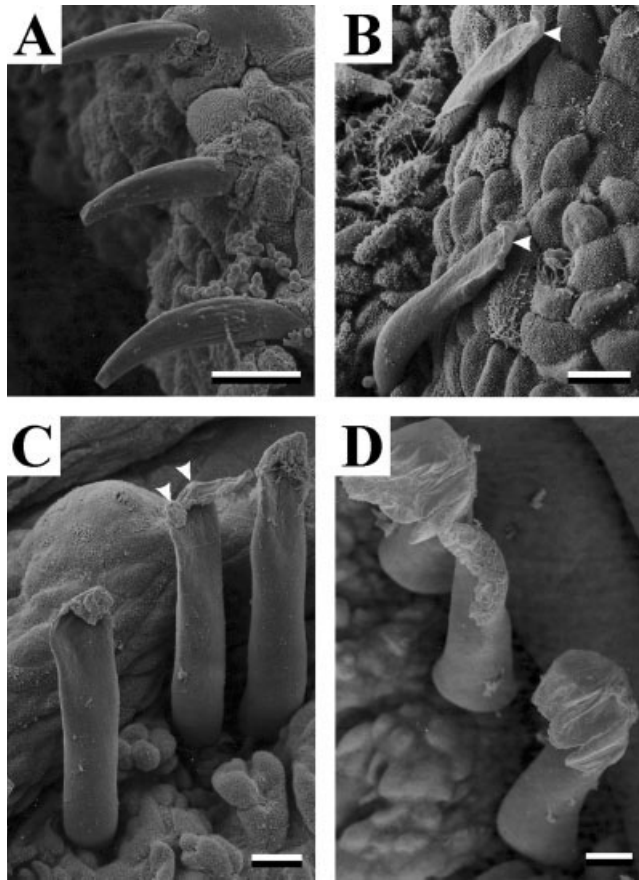


Fig. 6. Teeth of early stages of *Ancistrus* cf. *triradiatus* SEM. **A**: 4 days PF (6.7 mm SL; upper jaw). **B**: 8 days PF (9.8 mm SL; lower jaw). **C**: 10 days PF (10.2 mm SL; lower jaw). **D**: Fourteen days PF (10.7 mm SL; upper jaw). Scale bars are 10  $\mu$ m.

### Morphology and Growth of Unculi

Unicellular epidermal brushes or unculti are found in a field on the top of labial papillae of the lower lip. In some species with unculti not all papillae bear unculti; unculti are rare on the upper lip. In those cases where taste buds are present on the papillae as well, the unculti are found rostrally to these. Counts of unculti on five randomly chosen papillae, and height measurements of 10 randomly chosen unculti at the scanning electron microscope yielded the following ranges: *Ancistrus* cf. *triradiatus*: 40–80 unculti per papilla, sometimes covering the whole top of the papilla, height 7–15  $\mu$ m, unculti slender with the tip curved rostrally (Fig. 8A); *Pterygoplichthys lituratus*: 25–50 unculti per papilla, height 12–16  $\mu$ m, straight with a slightly flattened tip (Fig. 8B); *Panaque nigrolineatus*: several hundreds of unculti per papilla, also covering the sides of the papilla, height 5–10  $\mu$ m, broad with a flattened tip (Fig. 8C); *Sturisoma aureum*: 20–35 unculti per papilla, height 8–12  $\mu$ m, tip flattened; *Farlowella acus*: 40–70 unculti per papilla, height

12–17  $\mu$ m, sometimes covering whole top of papilla, unculti slender, tip straight (not flattened) (Fig. 8D); *Rineloricaria parva*: no unculti present on papillae; and *Otocinclus vestitus*: 40–70 unculti per papilla, height 2–4  $\mu$ m, unculti broad, and tip extremely flattened (Fig. 8E).

Epidermal cell diameter is  $\sim$ 8–12  $\mu$ m in all species. Taste buds are numerous on the papillae in *R. parva*, rare in *F. acus*, *O. vestitus*, and *P. nigrolineatus* (arrowheads on Fig. 8C,E), and absent on many (but not all) papillae in the other species. Unculti appear to be replaced when parts of the upper epidermal layer of the lip are shed, as seen in *A. cf. triradiatus* (Fig. 8F). Figure 8F, as well as Figure 9, suggest that the shedding occurs more or less per papilla. In the specimen in Figure 9, only three of the total amount of papillae was in an obvious process of shedding.

### Shape of Unculi During Early Ontogeny

Embryonic specimens of *Ancistrus* cf. *triradiatus* have rudimentary papillae 1 day after hatching (Fig. 10A). First sloughing of epidermis occurs at 3

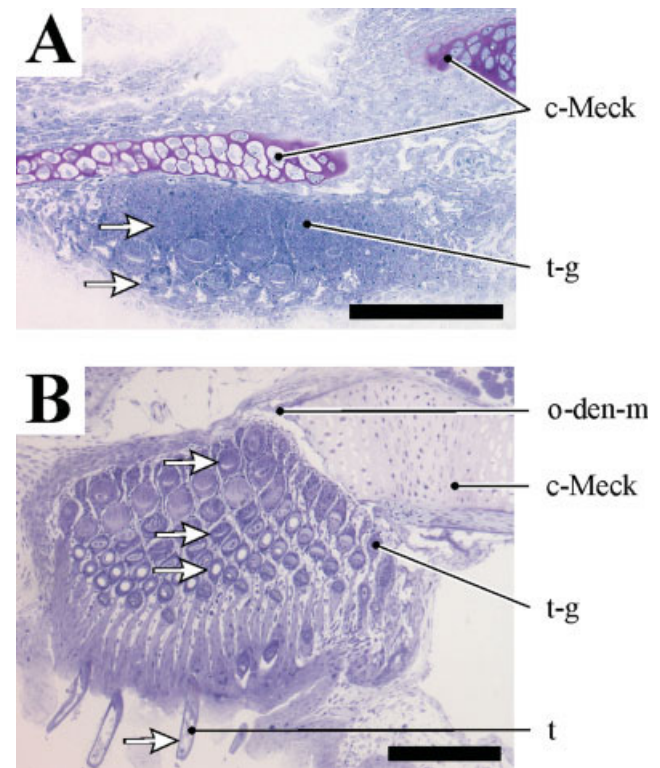


Fig. 7. Serial sections through the left lower jaw of. **(A)** 7 days PF old (8.0 mm SL) and **(B)** 14 days PF old (10.2 mm SL) *Ancistrus* cf. *triradiatus*. Cartilage resorption of the medial part of the Meckel's cartilage has occurred between both stages. Arrows point to one tooth series (emergent tooth and replacement teeth originating from the same locus). Scale bars are 100  $\mu$ m. c-Meck, cartilago Meckeli; o-den-m, os dento-mento-meckelium; t-g, tooth germ; t, (erected) tooth.

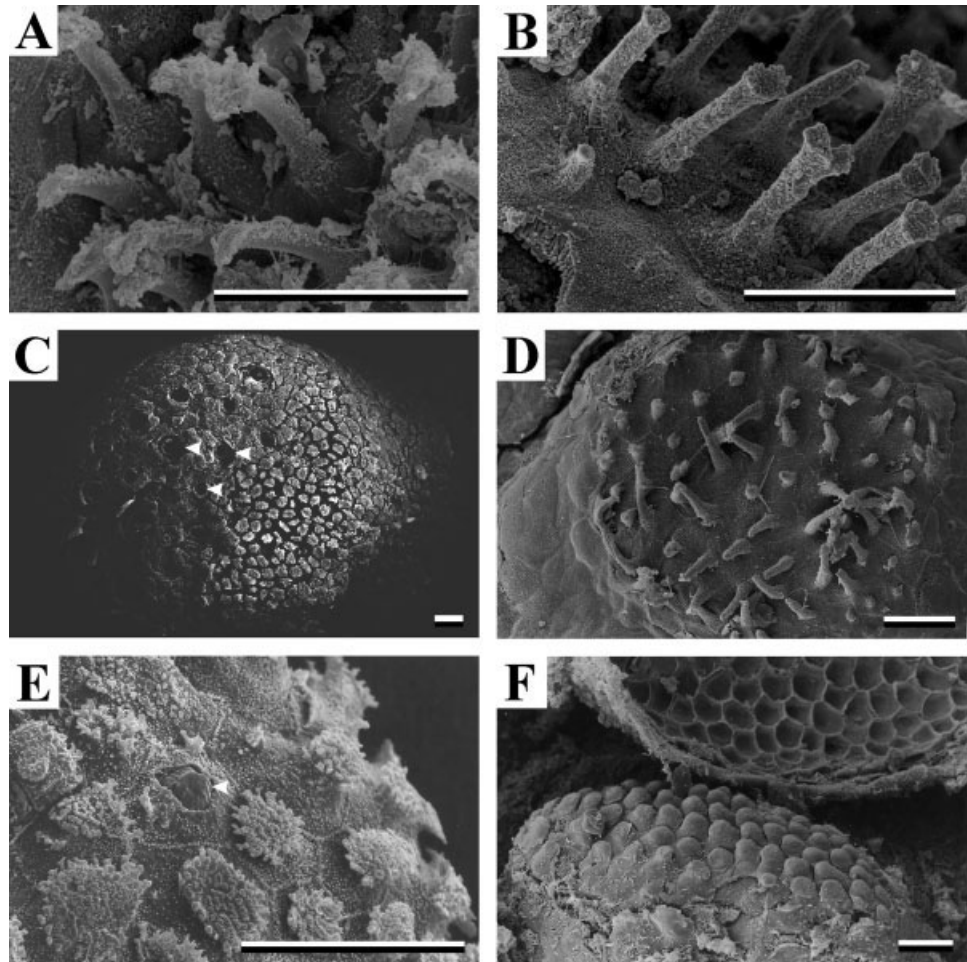


Fig. 8. Loricariid lower lip papillae and uncini. SEM. **A:** Rostrally inclined uncini of *Ancistrus* cf. *triradiatus* (anterior toward bottom). **B:** Straight uncini of *Pterygoplichthys lituratus*. **C:** Papilla of *Panaque nigrolineatus* bearing short and sturdy uncini. **D:** Papilla of *Farlowella acus* bearing long and slender uncini. **E:** Short and flat uncini of *Otocinclus vestitus*. **F:** Shedding of epidermis of papilla of *A.* cf. *triradiatus* revealing new cell layer with partly developed uncini. Arrowheads on C and E indicate taste buds. Scale bars are 20  $\mu\text{m}$ .

days after hatching (Fig. 10B). The first uncini appear together with the first well developed tooth cusps, at 5 days after hatching (Fig. 10C,D). This is the moment of complete resorption of the yolk sac.

## DISCUSSION

As in several (but not all) other *Ancistrus* species, the number of dentary teeth in *Ancistrus* cf. *triradiatus* is equal to (or slightly higher than) the number of premaxillary teeth (Muller and Weber, 1992; Miquilarena et al., 1994; Fisch-Muller et al., 2001). No significant intraspecific differences between both jaws were noted in the other examined species. The morphology of teeth of *A.* cf. *triradiatus* appears to be the most interesting of all loricariids examined by us and other authors thus far (e.g., Schaefer, 1987; Muller and Weber, 1992; Schaefer and Stewart, 1993; Delariva and Agostinho, 2001; Armbruster, 2004). The teeth are characterized by a strong Z-shaped curvature, the differentiation of the shaft in a thin lower and a thick upper portion, and the presence of an anterior layer of soft tissue along the lower shaft. This layer has been found in all examined species except *Panaque nigrolineatus*

and *Rineloricaria parva*. The thicker distal protuberance was found in *A.* cf. *triradiatus* only. The histological nature of the soft layer is unclear, but might well have a strain-resistant function: if the crown jolts along a rough substrate during

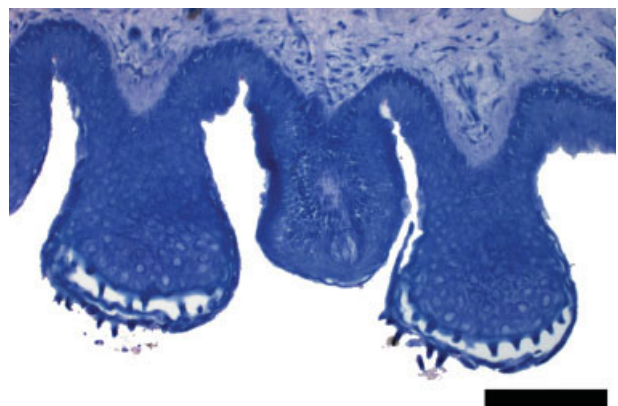


Fig. 9. Serial section through some lower lip papillae of *Ancistrus* cf. *triradiatus* (33.5 mm SL). On two papillae a "replacement" epidermal layer with uncini is present, while the top layer of the epidermis appears as if soon to be shed. Scale bar is 100  $\mu\text{m}$ .

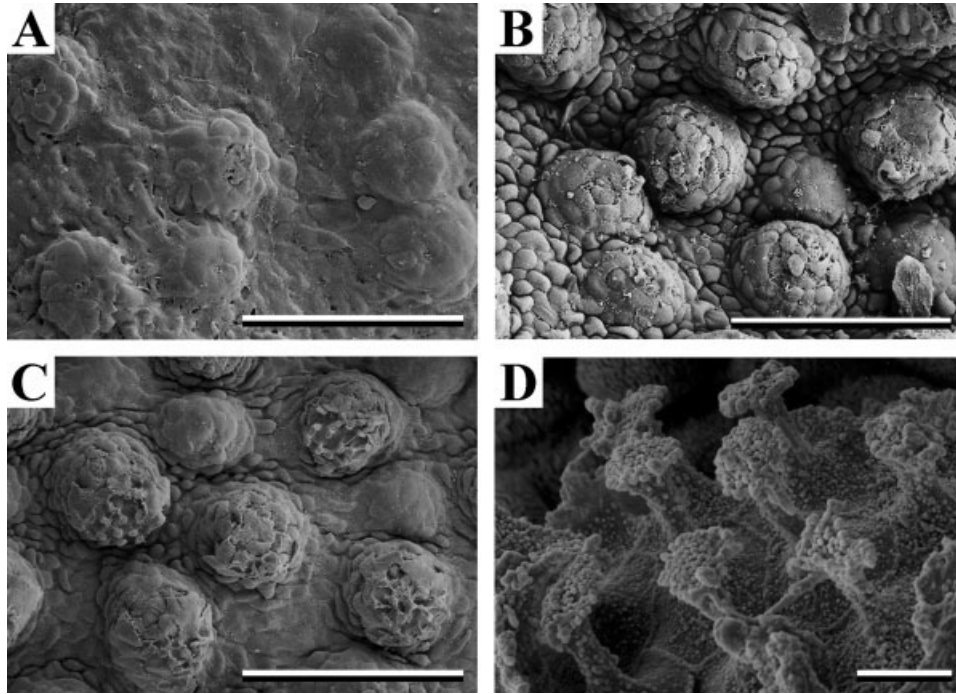


Fig. 10. Lower lip surface of early stages of *Ancistrus* cf. *triradiatus* SEM. **A:** 6 days PF (8.2 mm SL). **B:** 8 days PF (9.8 mm SL). **C:** 10 days PF (10.2 mm SL). **D:** Detail of first true uncini (10 days old specimen). Scale bars for A–C are 100  $\mu$ m, for D, 5  $\mu$ m.

scraping, the anterior region of the tooth is prone to strain, especially near the base of the lower shaft, where the bending occurs. A completely calcified tooth might easily break. Figure 2I suggests that the posterior lower shaft region (near the base) is far from completely calcified: it is almost not stained by the toluidin blue stain (compare tooth section “3” to “1” and “2” on Fig. 2I). This might represent an elaborate adaptation to the fact that the shaft of loricariid teeth encounters sideward (anterior) forces instead of axial forces during feeding. The unmineralized (collagenous) attachment of the tooth base, present in most ostarioclupeomorph teleosts (Fink, 1981), further increases the mobility of the individual tooth (with respect to the jaw bone).

The link between tooth shape and diet has been inferred from several studies, with the general conclusion that slender teeth are appropriate for scraping smaller particles from surfaces, while larger, stronger, and spatulate teeth are better for scraping coarser food items off hard surfaces (Delariva and Agostinho, 2001). This is best illustrated by the two extreme conditions. Robust teeth are present in taxa like *Panaque* and the *Hypostomus cochliodon* group (Schaefer and Stewart, 1993; Armbruster, 2004; this article), of which at least *Panaque* has been proven to be able to eat and digest wood (Nelson et al., 1999). On the other hand, sometimes complete absence of teeth is observed in some loricariines, a subfamily containing many detritus-feeders living on soft substrates (Salazar et al., 1982; Rapp Py-Daniel, 2000). The lack of the soft tissue layer and the lesser mobility of the tooth base of *Panaque nigrolineatus* relative to the bone

might reflect the need for more robust, better anchored and rigid (thus completely mineralized) teeth for scraping wood. The diet of the loricariine *Rineloricaria parva* is less known; aquarium specimens were commonly observed on sand and gravel, when compared to the other species (stones, wood pieces, and plants were provided as well). Some *Loricaria* species are known to feed more on small animals and detritus on soft bottoms (as opposed to hard substrates) (Saul, 1975; Aranha et al., 1998; Reis and Pereira, 2000). More ecological data confirming this for *R. parva* are needed to substantiate the hypothesis that this species scrapes less on hard substrates than the other loricariids examined in this study. The lack of a soft layer in both *P. nigrolineatus* and *R. parva* also coincides with a low number of replacement tooth rows.

The mineralized tooth portion of advanced actinopterygians does not contain enamel (a purely epithelial product), but enameloid (to which ectomesenchymal tissue contributes) (Huysseune and Sire, 1998). However, a soft tooth portion, as found in the lower shaft of several loricariid species, has neither been reported before, nor in any other teleost group. It is possible that the thin, “hard” part of the lower shaft near the base is not as intensely mineralized as the remainder of the tooth. It is hard to find alternative explanations for the fact that this zone can bend without immediately breaking. A possible hypo-mineralization might be tested using micro-radiography.

No clear correlation, but a scale of different combinations is found between tooth and uncus shape in the examined species. Of the loricariines, *Farlo-*



*wella acus* has slender teeth and unculti, and *Sturiosoma aureum* has similar teeth but sturdier unculti. Unculi are absent in *Rineloricaria parva*, which has pointed tooth cusps and no soft anterior layer. Among the hypostomines, slender unculti co-occur with relatively slender teeth in *Pterygoplichthys lituratus*; unculti are somewhat thicker and rostrally inclined, and teeth are somewhat narrower in *Ancistrus* cf. *triradiatus*. *Panaque nigrolineatus* is characterized not only by the spoon-shaped teeth without anterior soft layer, but also by numerous short and flattened unculti. Unculi are even shorter and equally flattened, but less numerous in the hypoptopomatine *Otocinclus vestitus*, which has few and rather slender teeth. Unculi were not found in *Otocinclus* sp. by Ono (1980).

The interspecific shape diversity, and the rostral inclination of the unculti on the lower lip in *Ancistrus* cf. *triradiatus*, corroborate the hypothesis that unculti in loricariids may serve as abrasive structures (Ono, 1980). Ono (1980) mentioned the presence of unculti on the upper lip of certain hypostomines; the upper lip is moved far less during scraping, and papillae are less numerous. She did not elaborate on the relative position of unculti and taste buds on the upper lip papillae. Keratinization, though rare in teleosts, has been found in several taxa; we refer to Das and Nag (2006) for an overview of such reports in teleosts and a histological examination in keratinized spines (~ unculti) in the cyprinid *Garra gotyla gotyla*. In the latter species, direction of the spines on the lower lip is opposite to the unculus direction in *A.* cf. *triradiatus*. This, and the distribution of the spines along the outer edge of the lip, surrounding a central callus part, suggests a function in adhesion rather than in feeding. In most loricariids, the unculti might well serve both functions.

It might be that the shedding of lip epidermis contributes to a “renewal” of unculti. The shedding of the epidermis of single papillae on Figures 8F and 9 proves that such shedding does occur in *Ancistrus* cf. *triradiatus*, although similar processes in teleosts are not well treated in the literature. One could hypothesize that the abrasive function of the unculiferous papillae causes them to wear, a scenario in which shedding would be beneficial.

Unculus structure might be an underestimated aspect of the adaptive radiation present in the loricariid family, next to shape, size, and number of the teeth, morphology and orientation of the jaws, and the presence of labial filaments or fimbriae (Rapp Py-Daniel, 2000; Delariva and Agostinho, 2001; Armbruster, 2004), and deserves a closer look in ecological studies where several loricariid species are often found to live syntopically (Power, 1984; Buck and Sazima, 1995; Aranha et al., 1998; Delariva and Agostinho, 2001). As pointed out by Zaret and Smith (1984), explanations for the small differences (and similarities) between ecologically important

structures like teeth and unculti of similar or related species, are not easy and will have to rely on a significant amount of ecological information including present and past syntopy of the various species.

Generally the first tooth generations in teleosts consist of simple, conical teeth, irrespective of the adult tooth shape (Huysseune and Sire, 1997b; Sire et al., 2002; Vandervennet et al., 2006). Even loricariids are no exception, as observed in *Ancistrus* cf. *triradiatus*. During further growth in the juvenile and adult phases, only a weak allometry in shaft and crown length has been observed in several *Ancistrus* and *Hypostomus* species (Muller and Weber, 1992). Schaefer and Stewart (1993) noted more pronounced shape transitions (from standard bicuspid to unicuspid and spoon-shaped) in juveniles of the *Panaque dentex* group.

In the lower jaw, we did not observe cartilage resorption at the level of formation of individual tooth germs of the first generations, as observed in some cichlids by Huysseune (1990). This might be related to the relatively large distance between the tooth germs (and the dentary bone anlage) and Meckel's cartilage in the 8.0 mm *Ancistrus* specimen. In the 10.2 mm specimen Meckel's cartilage is completely resorbed at the level of the teeth, but we cannot infer a direct relation with the tooth germs that now develop at the former location of the cartilage (Fig. 7B).

In conclusion, we consider the teeth and less known unculti of Loricariidae to be highly diverse tools, which most certainly are the result of an adaptive radiation. The unculti most probably have the same function as the teeth, i.e., scraping food off substrates, and as such, a comparable selective pressure can be expected. The morphology and diversity of teeth and unculti surely adds to the adaptations to the broad ecological niche occupied by this successful neotropical catfish family.

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