

Functional and evolutionary anatomy of the African suckermouth catfishes (Siluriformes: Mochokidae): convergent evolution in Afrotropical and Neotropical faunas

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Abstract

Of those fishes scraping food off substrates and using head parts in substrate attachment for station-holding, the catfish families Loricariidae, Astroblepidae and Mochokidae display the most dramatically adapted morphologies. Loricariidae and Astroblepidae, living in the Neotropical freshwaters, exclusively contain suckermouth catfish species, and their anatomy and head kinematics have already been studied into detail. Among Mochokidae, living in the tropical freshwaters of Africa, only the chiloglanidine subfamily has a sucker mouth, and occupies similar niches in Africa as both Neotropical families do in South America. Having derived from relatively unrelated catfish ancestors, their anatomy is poorly known, and the nature of their scraping and station-holding capabilities is not known at all. This paper provides details on the chiloglanidine head anatomy and function (relating their anatomy to that of the non-suckermouth Mochokidae), and compares this Afrotropical suckermouth taxon with both Neotropical suckermouth families. It identifies both convergences and differing anatomical and kinematic solutions to the same key needs of food-scraping and station-holding suckermouth fishes. Chiloglanidine mochokids differ from both Neotropical families in having less mobile jaws, with an upper jaw assisting more in station-holding than in feeding. They share the highly mobile lower lip with both Neotropical taxa, although the configuration of the intermandibular/protractor hyoidei muscle system, changing the volume of the sucker-disc cavity, differs in all three taxa. Chiloglanidines have a single, posterior inflow opening into this cavity, whereas Loricariidae have two lateral openings, and Astroblepidae have none, using an opercular incurrent opening instead. The chiloglanidine buccal valve system consists of two passive valves, as in Astroblepidae. Although less diverse in number of genera and species, this Afrotropical suckermouth taxon possesses the anatomical and kinematic key elements allowing a successful occupation of a niche similar to the one found in the Loricariidae + Astroblepidae clade.

Key words: Astroblepidae; Chiloglanidinae; kinematics; Loricariidae; station-holding.

Introduction

Freshwater fishes living in fast-flowing rivers face challenges regarding the availability of both spatial and trophic resources. The habitat consists of a fast-flowing medium, and it contains little seston, or planktonic organisms and floating detritus. Food is concentrated on and in the bottom, mainly in the form of well attached algae and sessile,

burrowing or crawling invertebrates. Fish species living in this type of habitat face two major challenges. First, mere suction feeding or even biting might not suffice to extract the food. For well attached food items, a ventral mouth and scraping devices are needed. Secondly, life in fast-flowing waters requires either a strong and continuous swimming capacity, or a body that can be stationary appressed to the substrate.

In fishes, as in many invertebrate and some amphibian lineages, various specialized taxa have entered this niche (Hora, 1930; Arens, 1994). Among the Neotropical fish assemblages, astroblepid and loricariid catfishes have evolved the most intense adaptations: a ventral sucker-like mouth and ventrally directed jaws, acted upon by specifically evolved jaw and hyoid muscles (Geerinckx et al. 2007, 2011; Adriaens et al. 2009; De Crop et al. 2013). Among the

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Accepted for publication 4 April 2014
Article published online 20 May 2014

Paleotropical fish assemblages, the chiloglanidine catfishes of the African mochokid family appear as one of the most adapted taxa, found in rapids and cascades. They too evolved a well developed sucker mouth and ventrally directed jaws. Although both these Neotropical and Afrotropical groups are catfishes, they are far from closely related (Sullivan et al. 2006). Anatomical data on Mochokidae are not abundant. Vigliotta (2008) provided an excellent morphological-phylogenetic study of mochokid taxa, using mainly osteology to identify the subfamily of Chiloglanidinae as a monophyletic taxon within Mochokidae, in a polytomy with *Synodontis* and *Microsynodontis*. Four chiloglanidine genera exist, with *Atopochilus*, *Atopodontus* and *Euchilichthys* forming the tribe Atopochilini, and *Chiloglanis* being in urgent need of revision (Vigliotta, 2008). Myological data do exist for *Synodontis* (Taverne & Aloulou-Triki, 1974), although several muscles have been erroneously named or described in this paper (adductor and levator arcus palatini, levator and dilatator operculi). Chiloglanidines are still quite unknown in terms of their musculo-skeletal apparatus and kinematics, and so the first aim of the current paper is to provide an account on the head morphology and kinematics of chiloglanidine representatives, comparing these with the morphology of related non-suckermouth mochokid relatives (*Synodontis*). As such, key elements or evolutionary transitions can be better understood.

Both groups (sister groups Astroblepidae + Loricariidae, and Mochokidae: Chiloglanidinae) derived from less specialized ancestors (Sullivan et al. 2006; Vigliotta, 2008), and both have close relatives that are generalist feeders not found in the most torrential waters (e.g. Van Wassenbergh et al. 2009). Evolutionary convergence thus led to a highly similar morphology and niche occupation. The second aim of this paper is a comparative analysis of the transitions in both the Neotropical and the Afrotropical lineages, assuming both parallel and convergent paths in their morphological evolution. Given the morphologies of the suckermouth taxa and their non-specialized close relatives, it is possible to deduce what minimal requirements exist to become a successful torrential suckermouth feeder, and how these requirements can be met.

Materials and methods

For the study of anatomy, nine mochokid species were used. *Synodontis ocellifer* Boulenger, *Synodontis annectens* Boulenger, *Synodontis ansorgii* Boulenger and *Synodontis schall* (Bloch & Schneider) represent the non-suckermouth mochokids. *Atopodontus adriaensi* Friel & Vigliotta, *Atopochilus savorgnani* Sauvage, *Chiloglanis lukugae* Poll and *Euchilichthys royauxi* Boulenger represent the suckermouth Chiloglanidinae. The non-suckermouth *Mochokus niloticus* Joannis and *Microsynodontis batesii* Boulenger were examined externally only. Table 1 lists the details of the specimens used.

Cleared and stained specimens were processed according to the method of Taylor & Van Dyke (1985). Dissections were performed

Table 1 Mochokid specimens used for the anatomical study.

Species	Catalog no.	SL (mm)	Procedure
<i>Mochokus niloticus</i>	MRAC 92-P52-P-374	28	Dissection
<i>Microsynodontis batesii</i>	MRAC 95-89-P-1531	43	Dissection
<i>Synodontis annectens</i>	MRAC 92-59-P-1852-1871	102	Dissection
<i>Synodontis ansorgii</i>	MRAC 92-59-P-1918-1925	162	Dissection
<i>Synodontis ocellifer</i>	MRAC 73-15-P-1327-1329	135	Dissection
	(Commercially obtained)	79	Dissection
	(Commercially obtained)	71	Clearing and staining
	(Commercially obtained)	56	Serial sectioning
<i>Synodontis schall</i>	MRAC 81-3-P-473-477	69	Clearing and staining
	MRAC 81-3-P-473-477	70	Clearing and staining
	MRAC 81-3-P-473-477	70	Clearing and staining
	MRAC 81-3-P-473-477	71	Clearing and staining
<i>Chiloglanis lukugae</i>	MRAC 93-150-P-94-125	64	Dissection
<i>Atopodontus adriaensi</i>	MRAC B1-27-P-37-43	77	Dissection
	MRAC B1-27-P-37-43	69	Clearing and staining
	MRAC 98-29-P-3348	43	Serial sectioning
<i>Atopochilus savorgnani</i>	MRAC B1-27-P-25-36	94	Dissection
	MRAC B1-27-P-25-36	95	Dissection
	MRAC 99-90-P-1974-1978	93	Clearing and staining
	MRAC 99-90-P-1974-1978	100	Clearing and staining
<i>Euchilichthys royauxi</i>	MRAC 78-6-P-1027-1045	78	Dissection

using an Olympus SZX9 stereoscopic microscope equipped with a camera lucida for drawing. One specimen of *S. ocellifer* and *A. adriaensi* each was selected for serial histological sectioning. Each head was processed by decalcifying (using Decalc) and embedding in Technovit 7100 (Kulzer Heraeus), and was sectioned using a Leica Polycut microtome equipped with a tungsten carbide-coated metal knife. The 5-µm sections were stained with toluidine and digitally photographed using a Colorview8 CCD camera mounted on a Polyvar light microscope.

For the study of respiratory and station-holding kinematics, specimens of *A. savorgnani* and *A. adriaensi* were collected using a cast net in the rapids of the Ivindo River at Loa Loa near Makokou, Gabon (0°31'17.5908"N, 12°49'30.4242"E, ca. 300 m altitude). High-speed recordings (at 120 frames per second) were performed using an aquarium setup imitating natural flow conditions, and a Casio Exilim EX-FH100 high-speed camera, in Makokou, Gabon, thus

minimizing specimen transport. Three individuals of the following species were recorded from angles showing ventral and/or lateral body parts: *A. savorgnani* (94, 98 and 114 mm standard length, or SL) and *A. adriaensi* (72, 75 and 87 mm SL). Recording mostly occurred during respiration with suckermouth attachment, in still or flowing water. Respiration without any attachment could be observed only rarely and briefly, as this usually happened only during brief bursts of swimming. Water in- and outflow was visualized by the motion of minute suspended particles in the water. A water flow of a measured ca. 250 mm s^{-1} was generated by a standard aquarium pump. As flow speeds in the Ivindo rapids vary quite strongly (with calm parts and estimated local peak flows of more than 2 m s^{-1}), this test speed was deemed a natural, non-extreme condition for both species.

The anatomical points of interest were a medioventral point on the hyoid, a lateral point on the suspensorium, the edge of the opercular flap, the pectoral girdle near the pectoral fin insertion, points on the tooth-bearing face of the upper and lower jaw, points on the upper lip and on the left and right half of the lower lip, two additional reference points on the head and, when visible, the buccal valve in the mouth roof, and particles in the incurrent and excurrent water. As it was not possible to follow the exact same point on a particular anatomical element in different recordings (due to recording angle, shade or specimen coloration), absolute measurements of excursion amplitudes of these structures most often could not be compared. The points were digitized using a marker tracking and direct linear transformation program (Hedrick, 2008) in MATLAB R2011b (The Mathworks, USA). Data were filtered using a fourth order zero-phase shift Butterworth low-pass data noise filter with a cut-off frequency of 3–7 Hz (add-in for EXCEL written by Sam Van Wassenbergh; procedure in Erer, 2007).

Results

Head morphology

The *Synodontis* species (Table 1) have a subventral mouth, with thick lips, two pairs of mandibular barbels and one pair of long maxillary barbels (Fig. 1). In contrast, the mouth in all chiloglanidines is equipped with a sucker-disc formed by the much enlarged lips (Fig. 2A–C). The maxillary barbel is small, and the two mandibular barbels are embedded in the posterior lower lip tissue of the sucker. The sucker is reinforced by thick, dense fibrous tissue layers. Whereas the sucker coincides with a relatively broader snout in chiloglanidines (vs. a more pointed snout in *Synodontis*), the whole head is also found to have a lower depth/width ratio, when compared with *Synodontis* (Fig. 1,

Table 2). *Synodontis* and chiloglanidines possess a dorsal oral valve large enough to close the buccal cavity without closing the mouth. When attached to a substrate, the chiloglanidines possess a substantial suckermouth cavity (or 'pre-buccal' cavity) bordered by the lips, jaws, valves and (ventrally) the substrate.

Osteology

For general osteology of the skull of mochokid species, we refer to the detailed and well illustrated account by Vigliotta (2008). Here we focus on those elements most important in the lip, jaw and buccal mobility systems.

Compared with *Synodontis* and other non-suckermouth mochokids, the preorbital region of the chiloglanidines is somewhat elongated. This elongation involves both bones (frontal, mesethmoid, lateral ethmoid, parasphenoid and orbitosphenoid) and muscles (adductor arcus palatini and extensor tentaculi), and brings the upper jaw further anterior to the lower jaw. The chiloglanidine autopalatine, however, has not elongated, but has become broader, especially so in *A. adriaensi*, *A. savorgnani* and *E. royauxi*. The mesethmoid of these three species (but not of *Chiloglanis lukugae*) bears a ventromedial process anteriorly, protruding between both upper jaws. Along with the autopalatine, the maxillary of the chiloglanidines is substantially more robust than the one in *S. ocellifer* and congeners.

The suspensorium of *S. ocellifer*, consisting of hyomandibular, quadrate, metapterygoid and preopercular, has a length/width ratio of 1.86 ($n = 1$). This is similar to what has been found in *S. schall* (1.76–1.88, $n = 4$). The chiloglanidine suspensorium is much shorter, with a ratio of 1.09–1.13 in *A. adriaensi* ($n = 2$), 1.17 in *E. royauxi* ($n = 1$) and 1.14–1.24 in *A. savorgnani* ($n = 6$): its anterior end is thus positioned somewhat more caudally. Consequently, the suspensorium-jaw articulation is more caudal, too.

The upper jaw bones, or premaxillae, of *S. ocellifer*, are rigidly ligamentously interconnected, even intimately touching. A medial meniscus-like cushion connects each of them to the ventral surface of the mesethmoid, as do two articulation facets and one medial and two lateral pairs of ligaments. The premaxillae of *A. adriaensi* are more loosely interconnected by a posterior medial articulation; more anteriorly, the meniscus-like cushion connecting to the



Fig. 1 (A) Habitus of *Synodontis ocellifer* (84 mm SL) in lateral view. (B) Ventral view of the mouth region. Apart from the long, lateral, maxillary barbels, two pairs of mandibular barbels are present, projecting caudally from the lower lip base (arrow). Scale bars: 1 cm.

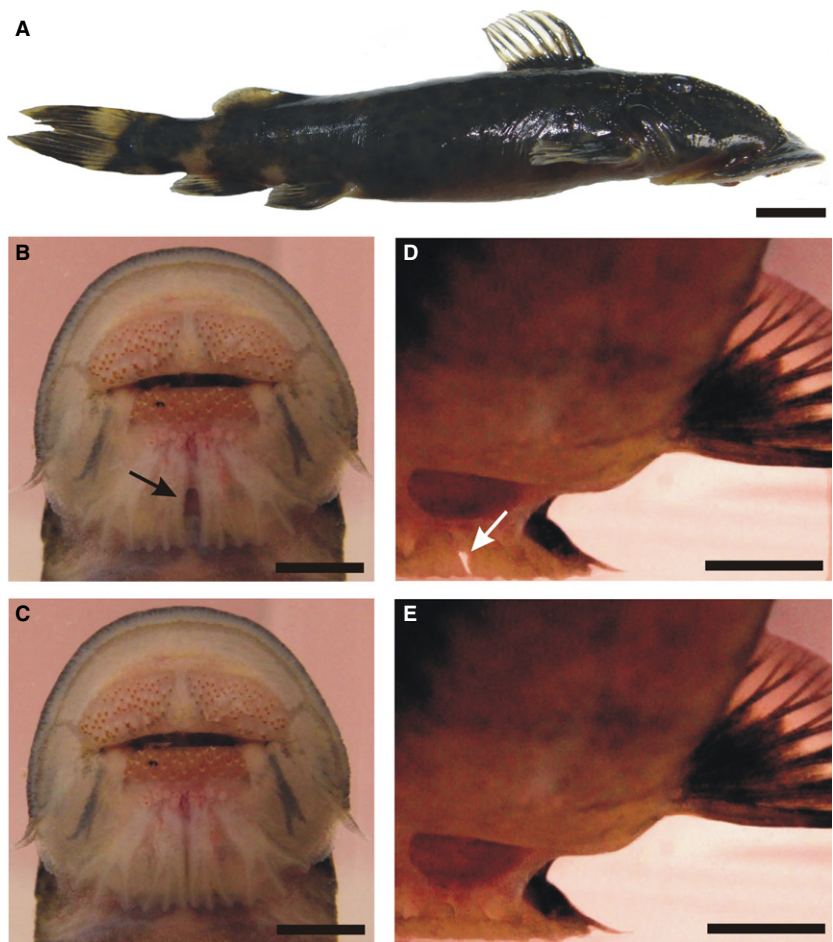


Fig. 2 (A) Habitus of *Atopodontus adriaensi* (75 mm SL) in lateral view. (B,C) Ventral views of the sucker mouth. (D,E) Posterior views of the lower lip disc portion. During inspiration (B,D) the lower lip elevates and the medioventral slit is open (arrows). During expiration (C,E) the lip depresses and the slit is closed. Scale bars: 1 cm.

Table 2 Ratio of width of lip disc vs. head width (LDW/HW) and vs. head width at orbit (LDW/OHW), ratio of head depth vs. head width (HD/HW), and ratio of head depth at orbit vs. head width at orbit (OHD/OHW). Chiloglanidines have broader lip discs and less deep heads than the related *Synodontis* species. Ratios are in percentage; *n* = number of measured specimens.

Species	<i>n</i>	LDW/HW	LDW/OHW	HD/HW	OHD/OHW
<i>Mochokus niloticus</i>	1	50.36	61.78	68.85	59.69
<i>Microsynodontis batesii</i>	1	58.19	67.25	84.65	70.62
<i>Synodontis annectens</i>	5	62.89–69.55	60.65–80.34	98.29–114.65	71.7–94.83
<i>Synodontis ansorgii</i>	5	46.07–67.79	54.51–74.82	104.49–111.80	81.13–87.46
<i>Synodontis ocellifer</i>	5	40.76–42.01	47.13–52.07	79.68–100.05	69.46–77.64
<i>Synodontis schall</i>	5	39.03–68.17	53.13–74.03	78.86–96.54	64.21–83.48
<i>Chiloglanis lukugae</i>	5	79.84–84.35	88.55–95.14	69.44–77.63	53.27–63.79
<i>Atopodontus adriaensi</i>	5	88.40–97.08	92.87–99.61	67.09–69.31	59.86–64.87
<i>Atopochilus savorgnani</i>	5	88.39–93.07	92.15–97.14	75.52–86.02	60.99–67.32
<i>Euchilichthys royauxi</i>	5	97.68–105.85	100.56–109.39	54.56–63.33	50.64–60.56

mesethmoid separates both upper jaws. The two articulation facets for the mesethmoid are more developed. Three mesethmoid–premaxillary ligaments are present, as in *S. ocellifer*. In both species, one long ligament connects each premaxilla to its adjoining maxilla, but the two bones are not in close contact. In *S. ocellifer* and congeners, the premaxillae bear ventrally directed teeth anteriorly, and

caudally directed teeth posteriorly, in a vast, continuous field. In *A. adriaensi* and the other chiloglanidines, the posterior, conical teeth are separated from the more anterior, larger and curved teeth.

Among *Synodontis* species, the dentaries of *S. schall* possess both dorsorostrally directed conical, so-called primary teeth, and ventrorostrally directed curved, so-called

auxiliary teeth (terminology according to Vigliotta, 2008), situated in a basket-like cavity. The dentaries of *S. ocellifer* and the chiloglanidines bear auxiliary teeth only. In *S. annectens* and *S. ansorgii*, primary teeth were not found but may be small and inconspicuous. The dentaries of the lower jaw itself are immovably joined by a symphysis in all these species. A true coronoid process is absent. A short angulo-articular articulates with the suspensorial quadrate.

Myology

For myology, focal species are *S. ocellifer* and the chiloglanidine *A. adriaensi*, with reference to other species when relevantly differing. In *S. ocellifer* and *A. adriaensi*, the adductor mandibulae is a large muscle, pierced anteriorly by the mandibular branch of the trigeminal nerve. The muscle is undivided in *S. ocellifer* (Fig. 3A), but in *A. adriaensi* it is larger, and a bulky lateral subdivision can be discerned from a less compact, more medial bundle (not visible on Fig. 4A). Insertion is invariably on the angulo-articular and the dentary of the lower jaw. The retractor tentaculi muscle of the maxillary barbel is simple in *S. ocellifer*, but in *A. adriaensi* and the other chiloglanidines it possesses two bundles, with the lateral one inserting on the maxillary, and the medial one bifurcating into a portion contacting the maxillary and a portion reaching tendinously toward the premaxillary.

The extensor tentaculi inserts on the posterodorsal side of the autopalatine, posterior of the articulation with the lateral ethmoid. It originates broadly on the lateral ethmoid in *S. ocellifer*, but much more extensively on the (longer) lateral ethmoid and even the frontal, next to the orbit, in *A. adriaensi*. As such it is much more massive; it joins the skull in the elongation of the ethmoid region in all sucker-mouth mochokids. At least in *A. adriaensi* a sesamoid bone is seen in the anterior part of the tendon; it was not observed in the examined *S. ocellifer* specimens, although it was found in *Synodontis* and termed anterior pterygoid element by Vigliotta (2008: p. 95).

The ventral musculature strongly differs between *S. ocellifer* and the chiloglanidines (Figs 3B, 4B and 5). On the ventral side of the head of *S. ocellifer*, the protractor hyoidei connects the hyoid to the lower jaw and, to a lesser degree, to the tissue supporting the lower lip (Fig. 3B). A broad transverse band of intermandibularis muscle, continuous with the protractor hyoidei, connects left and right hyoid with the lower lip and mandibular barbel cartilages. Some muscle bundles inserting on the cartilages (here termed muscles of mandibular barbels) run strictly rostrocaudally, while all other portions run transversely (termed labial part of intermandibularis muscle). A separate and more dorsal, dentary part of the intermandibularis connects both dentaries. Among chiloglanidines, changes and variations are remarkable. In *C. lukugae*, the labial part of the intermandibularis, through a raphe-like contact with the protractor hyoidei, still connects both ends of the hyoid with the lower

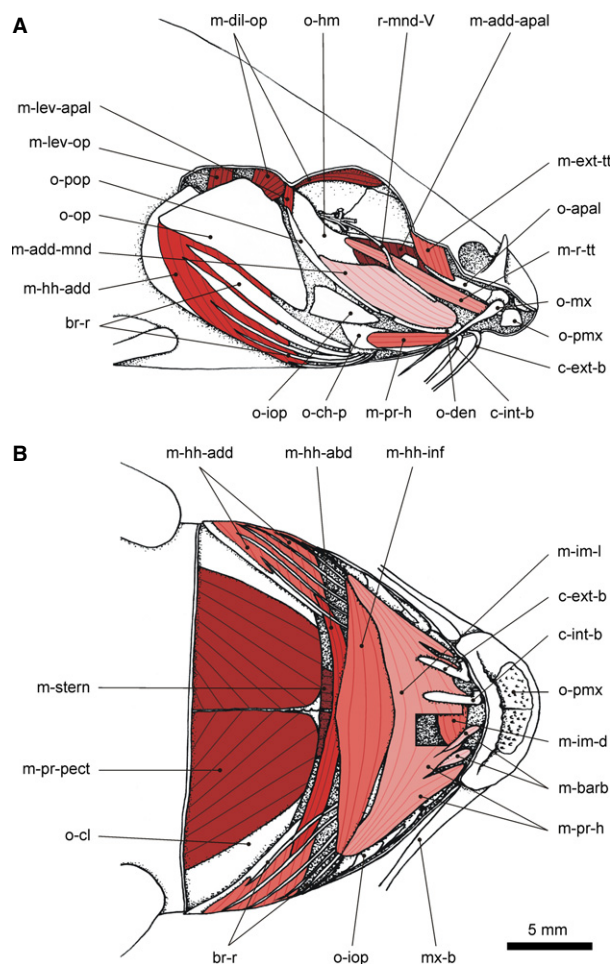


Fig. 3 Cranial musculature of *Synodontis ocellifer* (79 mm SL).

(A) Lateral view. (B) Ventral view, with cartilages of left mandibular barbels removed to visualize the attaching muscles, and the deeper mandibular part of the intermandibular muscle shown by a cut in the labial part of the muscle. br-r, branchiostegal rays; c-ext-b, cartilage of external mandibular barbel; c-int-b, cartilage of internal mandibular barbel; m-add-apal, musculus adductor arcus palatini; m-add-mnd, musculus adductor mandibulae; m-barb, muscles of mandibular barbels; m-dil-op, musculus dilatator operculi; m-ext-tt, musculus extensor tentaculi; m-hh-abd, musculus hyohyoideus abductor; m-hh-add, musculus hyohyoidei adductores; m-hh-inf, musculus hyohyoideus inferior; m-im-d, dentary part of musculus intermandibularis; m-im-l, labial part of musculus intermandibularis; m-lev-apal, musculus levator arcus palatini; m-lev-op, musculus levator operculi; m-pr-h, musculus protractor hyoidei; m-pr-pect, musculus protractor pectoralis; m-r-tt, musculus retractor tentaculi; m-stern, musculus sternohyoideus; o-apal, os autopalatium; o-ch-p, os ceratohyale posterior; o-cl, os cleithrum; o-den, os dentale; o-hm, os hyomandibulare; o-iop, os interoperculare; o-mx, os maxillare; o-op, os operculare; o-pmx, os praemaxillare; o-pop, os praeoperculare; r-mnd-V, ramus mandibularis of trigeminal nerve.

lip (Fig. 5C). In *A. adriaensi*, *A. savognani* and *E. royauxi*, this part is reduced to a short medial slip of muscle connecting left and right half of the lower lip (Figs 4B and 5A,B). In all chiloglanidines the longitudinal muscle bundles of the mandibular barbels have become completely separate entities (Fig. 4B), without the connections with the protractor

hyoidei muscle parts that exist in *S. ocellifer* (Fig. 3B). The dentary part of the intermandibularis is strongly reduced (most so in *A. adriaensi* and *A. savorgnani*), still connecting both lower jaws. The protractor hyoidei consists of one bundle reaching the lower jaw, and a varying number of discrete bundles serving the lower lip tissue. Exact homology of these bundles among chiloglanidines is not obvious, as illustrated by a comparison of Fig. 5A–C.

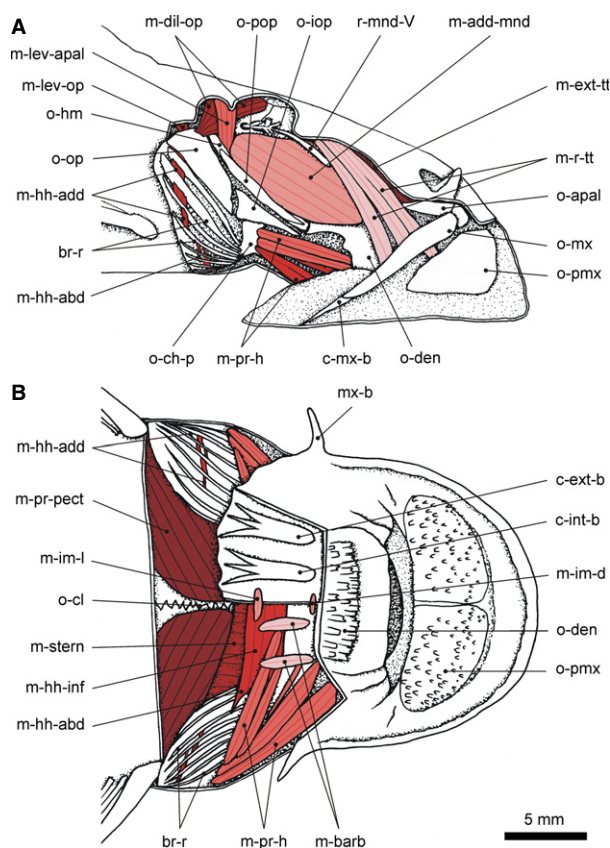


Fig. 4 Cranial musculature of *Atopodontus adriaensi* (77 mm SL). (A) Lateral view. (B) Ventral view, with skin of right half of lower lip removed to show barbel cartilages, and complete left lower lip tissue and cartilages of left mandibular barbels removed to visualize the attaching intermandibular and barbel muscles. br-r, branchiostegal rays; c-ext-b, cartilage of external mandibular barbel; c-int-b, cartilage of internal mandibular barbel; c-mx-b, cartilage of maxillary barbel; m-add-mnd, musculus adductor mandibulae; m-barb, muscles of mandibular barbels; m-dil-op, musculus dilatator operculi; m-ext-tt, musculus extensor tentaculi; m-hh-abd, musculus hyohyoideus abductor; m-hh-add, musculus hyohyoidei adductores; m-hh-inf, musculus hyohyoideus inferior; m-im-d, dentary part of musculus intermandibularis; m-im-l, labial part of musculus intermandibularis; m-lev-apal, musculus levator arcus palatini; m-lev-op, musculus levator operculi; m-pr-h, musculus protractor hyoidei; m-pr-pect, musculus protractor pectoralis; m-r-tt, musculus retractor tentaculi; m-stern, musculus sternohyoideus; mx-b, maxillary barbel; o-apal, os autopalatini; o-ch-p, os ceratohyale posterior; o-cl, os cleithrum; o-den, os dentale; o-hm, os hyomandibulare; o-iop, os interoperculare; o-mx, os maxillare; o-op, os operculare; o-pmx, os praemaxillare; o-pop, os preoperculare; r-mnd-V, ramus mandibularis of trigeminal nerve.

The hyohyoideus inferior and hyohyoideus abductor of all examined mochokids are well developed, with the hyohyoideus abductor connecting the posteromedial fascia of the hyohyoideus inferior with the medialmost two or three branchiostegal rays. The hyohyoidei adductores extensively connect the branchiostegal rays in *S. ocellifer*, but are reduced to a few posterior muscle slips in the chiloglanidines.

In the suspensorial region of the head, the adductor arcus palatini of *S. ocellifer* is a broad muscle plate connecting the metapterygoid and hyomandibular with the parasphenoid (Fig. 3A). In *A. adriaensi*, it is similarly located, but remarkably bulkier. It also has a substantial insertion on the orbitosphenoid. The antagonistic levator arcus palatini is a relatively small muscle connecting the hyomandibular with the sphenotic. In the opercular region, the dilatator operculi and levator operculi insert on the dorsolateral and dorsal edge of the opercular, respectively, with a much larger volume and origin surface for the dilatator, including parts of the hyomandibular and even frontal. The antagonistic adductor operculi, connecting the medial face of the opercular to the prootic, has an intermediate volume. There is no substantial difference in these opercular muscles between *S. ocellifer* and *A. adriaensi*.

Kinematics

Atopodontus adriaensi and *A. savorgnani* have been examined for respiratory suckermouth kinematics. For kinematics of *Synodontis* we refer to the comparative study by Van Wassenbergh et al. (2009). When not swimming, the observed specimens of *A. adriaensi* almost continuously contacted a substrate with the sucker mouth. Even during swimming, brief bursts of propulsion were followed by stationary moments with mouth attachment. Specimens of *A. savorgnani*, although behaving similarly, could sometimes be observed resting on the bottom without full contact of the sucker mouth. Between this attached and unattached respiration, proportions of inspiration and expiration did not differ markedly (Table 3). For both species, no biologically meaningful difference in these timings was observed between respiration when residing in still water, and respiration when residing in a current (head-on flow of approximately 250 mm s^{-1}). Apart from breathing more rapidly in flowing water, species or individuals differed very variably between both modes (Table 3). The overall data also indicate that a rather high variability in timings exists, both among and within individuals; statistical analysis of the data would be hampered by this variability and not add to these results. Yielding no tendency that could easily be statistically tested, the data do suggest a versatility in motor pattern timing. When individuals interacted or a reaction of stronger suckermouth attachment was otherwise provoked (visual disturbance), no consistent changes in timings were observed.

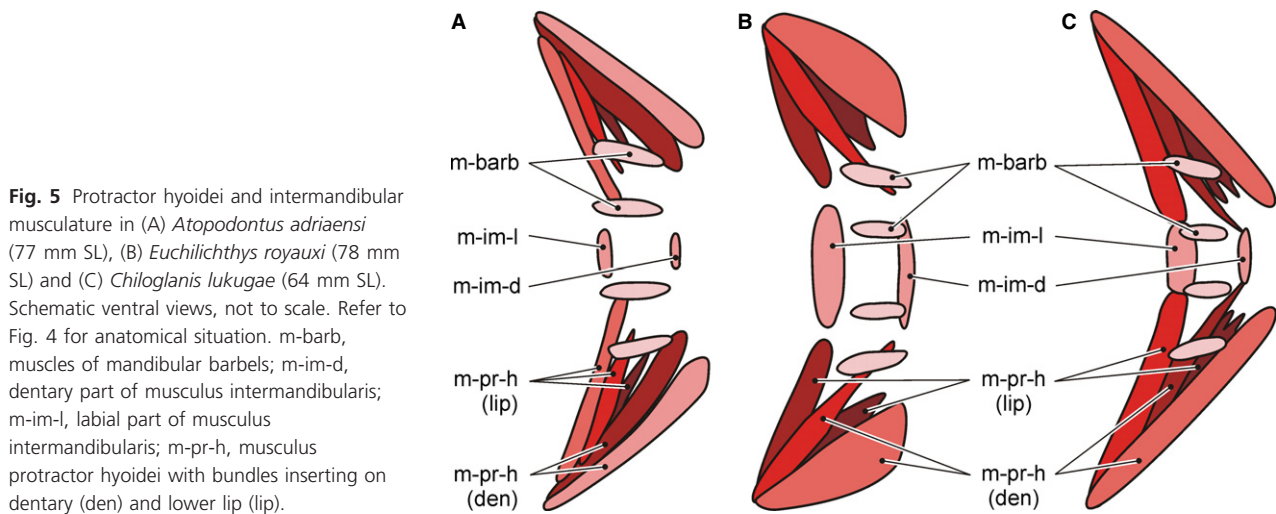


Fig. 5 Protractor hyoidei and intermandibular musculature in (A) *Atopodontus adriaensi* (77 mm SL), (B) *Euchilichthys royauxi* (78 mm SL) and (C) *Chiloglanis lukugae* (64 mm SL). Schematic ventral views, not to scale. Refer to Fig. 4 for anatomical situation. m-barb, muscles of mandibular barbels; m-im-d, dentary part of musculus intermandibularis; m-im-l, labial part of musculus intermandibularis; m-pr-h, musculus protractor hyoidei with bundles inserting on dentary (den) and lower lip (lip).

Table 3 Total cycle times, and relative durations of inspiration and expiration phases in three individuals of *Atopodontus adriaensi* (Aa1–3) and *Atopochilus savorgnani* (As1–3) each (average \pm SD). Compared modes include: individual attached using sucker mouth (or not), individual attached in still water, or facing current, individual (provoked) strongly attached. Numbers of measured cycles are given in parentheses.

	Total cycle time (ms)	Inspiration time (%)	Expiration time (%)
<i>Atopodontus adriaensi</i>			
Aa1 (87 mm SL) attached	298.58 \pm 17.67 (29)	56.84 \pm 2.67 (29)	43.16 \pm 2.67 (29)
Aa2 (72 mm) attached	336.33 \pm 27.92 (38)	56.10 \pm 3.64 (38)	43.90 \pm 3.64 (38)
Aa3 (72 mm) attached	283.42 \pm 28.50 (38)	58.98 \pm 2.86 (38)	41.02 \pm 2.86 (38)
Aa3 (75 mm) attached, no current	308.42 \pm 9.00 (19)	57.87 \pm 1.93 (19)	42.13 \pm 1.93 (19)
Aa3 (75 mm) attached, in current	258.42 \pm 16.42 (19)	60.08 \pm 3.25 (19)	39.92 \pm 3.25 (19)
Aa3 (75 mm) strongly attached	275.42 \pm 25.83 (11)	56.40 \pm 3.55 (11)	43.60 \pm 3.55 (11)
<i>Atopochilus savorgnani</i>			
As1 (98 mm) attached	616.67 \pm 157.00 (30)	50.91 \pm 8.72 (31)	49.90 \pm 9.12 (33)
As1 (98 mm) attached, no current	786.17 \pm 33.83 (13)	56.21 \pm 9.90 (14)	45.43 \pm 11.27 (15)
As1 (98 mm) attached, in current	487.08 \pm 51.17 (17)	46.62 \pm 4.42 (17)	53.63 \pm 4.42 (18)
As1 (98 mm) not attached	272.00 \pm 19.92 (30)	46.69 \pm 2.69 (29)	53.31 \pm 2.69 (29)
As2 (94 mm) attached	309.33 \pm 30.25 (29)	54.09 \pm 4.38 (29)	45.87 \pm 4.45 (29)
As2 (94 mm) not attached	219.25 \pm 12.58 (13)	50.14 \pm 3.40 (13)	49.71 \pm 3.31 (13)
As3 (114 mm) attached	496.25 \pm 83.00 (51)	52.14 \pm 9.91 (53)	48.09 \pm 9.80 (52)
As3 (114 mm) attached, no current	510.67 \pm 55.75 (29)	55.36 \pm 6.22 (31)	45.22 \pm 5.81 (29)
As3 (114 mm) attached, in current	477.25 \pm 107.75 (22)	47.60 \pm 12.30 (22)	51.71 \pm 12.46 (23)
As3 (114 mm) strongly attached	430.00 \pm 8.17 (7)	53.77 \pm 0.80 (8)	46.19 \pm 0.85 (7)

Expansion and constriction of the buccal cavity are caused by movements of the lateral walls supported by the suspensoria, and the ventral floor supported by the lower jaws, hyoid and pectoral girdle. For both species, relative timings indicate that all elements move in almost perfect synchrony (Table 4); there is no anteroposterior sequence of elevation/depression movements of the buccal floor parts. Although exact numeric measurements of element excursions were not possible, it was unambiguously visible in the recordings that the larger buccal floor movements are of greater importance for volume changes of the buccal cavity than the suspensorial movements. The participation of the pectoral girdle is substantial. The lower jaw, too,

mediates the volume of the buccal cavity, but it also influences the volume of the sucker-disc cavity, and the connection between the cavities, as elevation narrows it. A dorsal oral valve, situated on the roof of the mouth, anterodorsal to the lower jaw position, moves in synchrony with the lower jaw and other elements of the buccal floor: it is moved (rosto)dorsally at the onset of buccal floor depression and (caudo)ventrally (stretched) at the onset of buccal floor elevation. Given the absence of muscles or ligaments connecting the valve to other (simultaneously moving) structures, and given the average minute delay with respect to the hyoid motions (Table 4), it is assumed to move passively, dependent on water pressure and flow direction.

Table 4 Relative timing averages \pm SD (in ms) of some important movements during attached respiration in *Atopodontus adriaensi* (Aa1–3) and *Atopochilus savorgnani* (As1–3). Standard lengths and measurement sample sizes are shown in parentheses.

Specimen	Aa1 (87 mm)	Aa2 (72 mm)	Aa3 (75 mm)	As1 (98 mm)	As2 (94 mm)	As3 (114 mm)
Pectoral girdle depression max.	4 \pm 12 (13)	6 \pm 10 (15)	3 \pm 11 (21)	0 \pm 21 (19)	10 \pm 7 (15)	14 \pm 18 (17)
after hyoid depression max.						
Pectoral girdle elevation max.	6 \pm 9 (13)	–1 \pm 9 (15)	0 \pm 8 (21)	16 \pm 12 (19)	9 \pm 12 (15)	17 \pm 17 (16)
after hyoid elevation max.						
Suspensorium abduction max.	10 \pm 8 (13)	16 \pm 7 (15)	10 \pm 11 (22)	7 \pm 14 (18)	–3 \pm 12 (15)	10 \pm 31 (16)
after hyoid depression max.						
Suspensorium adduction max.	8 \pm 9 (12)	14 \pm 7 (15)	10 \pm 7 (22)	1 \pm 11 (18)	–2 \pm 12 (11)	12 \pm 26 (16)
after hyoid elevation max.						
Lower jaw depression max.	–	16 \pm 7 (8)	18 \pm 24 (15)	6 \pm 11 (9)	–	–
after hyoid depression max.						
Lower jaw elevation max.	–	11 \pm 8 (8)	16 \pm 19 (15)	4 \pm 12 (10)	–	–
after hyoid elevation max.						
Lower lip max. down after hyoid elevation max.	–	–51 \pm 14 (8)	–50 \pm 10 (7)	–	–	–40 \pm 8 (12)
Lower lip max. up after hyoid depression max.	–	–88 \pm 12 (7)	–63 \pm 11 (7)	–	–	–92 \pm 14 (12)
Lower lip slit opened after hyoid elevation max.	2 \pm 9 (10)	–2 \pm 13 (7)	–4 \pm 20 (15)	–26 \pm 10 (19)	–29 \pm 14 (4)	–31 \pm 10 (6)
Lower lip slit closed after hyoid depression max.	–2 \pm 13 (10)	4 \pm 16 (7)	28 \pm 15 (16)	–8 \pm 11 (19)	13 \pm 11 (4)	19 \pm 20 (7)
Oral valve opened after hyoid elevation max.	–	–	–5 \pm 11 (9)	–	–	4 \pm 5 (4)
Oral valve closed after hyoid depression max.	–	–	8 \pm 10 (10)	–	–	15 \pm 13 (4)
Opercular slit opened after hyoid depression max.	27 \pm 9 (13)	26 \pm 8 (15)	33 \pm 14 (21)	32 \pm 16 (19)	19 \pm 11 (12)	33 \pm 26 (19)
Opercular slit closed after hyoid elevation max.	–6 \pm 17 (13)	–3 \pm 12 (15)	2 \pm 11 (21)	11 \pm 15 (19)	3 \pm 17 (13)	14 \pm 26 (19)

Max., maximum.

A ventral oral valve rests on top of the lower jaws; its movements could not be observed during the recordings. Size and positions of both valves clearly enable a full closure of the buccal cavity from the pre-buccal, sucker-disc cavity (see above). Tracking of particles in the water corroborates this full closure: no backflow is observed during expiration.

The mobile posterior part of the sucker-disc, formed by the lower lip, has an intricate motion pattern (Fig. 6, Table 4). Its general movement is dorsoventral: it elevates (dorsally), increasing the sucker-disc volume, well before the onset of buccal cavity increase. Equally, it decreases the sucker-disc volume by depressing (ventrally) well before the onset of buccal cavity decrease. Apart from this main dorsoventral motion, its medial slit is open while positioned dorsally, and closed while positioned ventrally (Fig. 2B–E). It is interesting to note that these both main lower lip movements are not always perfectly synchronous. As a result of this motion pattern, water inflow is guaranteed but well controlled, while the sucker-disc rim never disconnects from the substrate. In both species, but mainly in *A. savorgnani*, the degree of opening and closing of the slit, and degree of motion of the lower lip, has been seen to be modulated substantially by the individual.

The opercular movements appear to be largely passive, given the fact that the opercle opens soon after maximal depression and closes immediately after maximal elevation in both species. Although the opercle starts to bulge outward, its rim stays appressed to the body for a short time span, suggesting some brief active restraint.

Finally, the movable rostrum merits attention. It includes the upper jaw and the upper lip, which forms the anterior half of the sucker-disc. While the head and body may move as a result of respiration acts or slight motion of the whole body due to muscle activity or surrounding water flow, the rostrum stays closely attached to the substrate, movably 'articulating' with the remaining, moving part of the head. No significant upper jaw movement is noted during normal respiration acts.

Discussion

Within the mochokid lineage, the examined chiloglanidines clearly exhibit the anatomical traits that characterize them as suckermouth-station-holding fishes. In a similar study on Neotropical loricariid catfishes (Geerinckx et al. 2011), the following essential key traits were stressed for successful

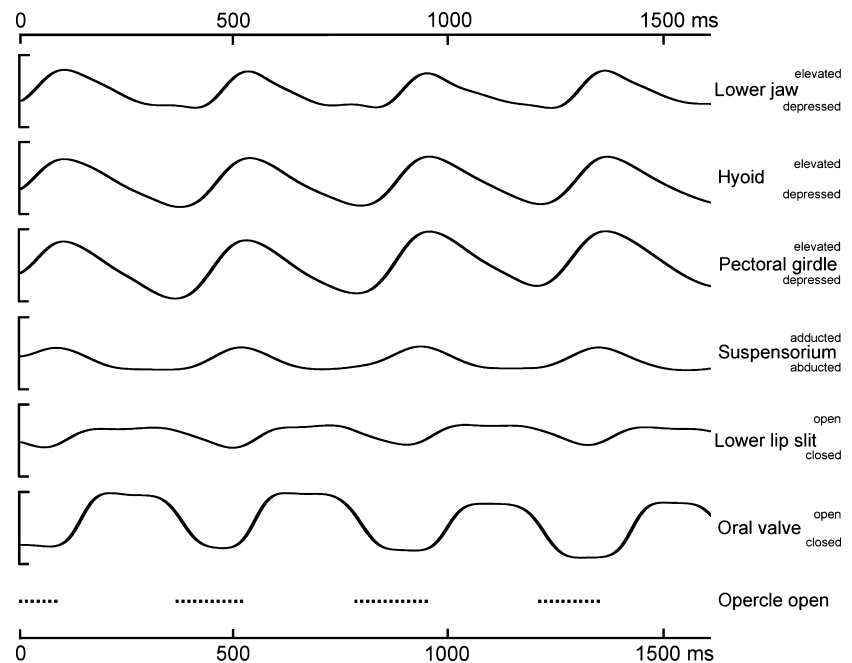


Fig. 6 Graph showing movements of anatomical points of interest measured in a 1600-ms recording of *Atopochilus savognani* (As3, 114 mm SL) in lateroventral view during attached respiration. Opening of the opercular slit is indicated by stippled bars.

suckermouth behaviour: (i) a two-chambered mouth with a robust valve system; (ii) an extensive lip disc surrounding the first chamber; and (iii) a well regulated water inlet. Chiloglanidines possess two oral valves, large enough to overlap and passively prevent backflow during expiration. As such, the buccal cavity and the pre-buccal, sucker-disc cavity can be given different internal pressures through actively mediated volume changes. The chiloglanidine valve system actually strongly resembles the two-valved situation in Astroblepidae (De Crop et al. 2013), sistergroup to Loricariidae. Loricariidae possess only a dorsal, but muscular, oral valve.

The fact that the buccal floor of the examined Chiloglanidinae, like the one in Astroblepidae and Loricariidae, contributes very substantially to the buccal cavity volume changes, falsifies the hypothesis of Van Wassenbergh et al. (2009) that an important contribution of the buccal floor would be disadvantageous in scraping, station-holding catfishes, as the anterior buccal floor, at the level of the lower jaws, is positioned quite close to that substrate. As the anterior buccal floor in all three groups is also beneficial in mediating the volume and thus pressure in the sucker-disc cavity, selection for a decreasing role of the buccal floor may never have existed in the lineage towards station-holding, scraping catfishes.

The second trait, a sucker-disc that creates a sucker-disc cavity isolated from the environment, is obvious and quite extensive in all chiloglanidines, also providing the strikingly similar habitus of this Afrotropical group and the Neotropical Loricariidae and Astroblepidae. Myological investigation revealed a chiloglanidine muscle arrangement closely resembling the loricariid situation, with a diversified

protractor hyoidei (or intermandibularis posterior) muscle, and transverse labial and dentary parts of the intermandibularis anterior muscle (Geerinckx et al. 2007). The position of the protractor hyoidei bundles inserting on the lower lip tissue indicates that these bundles enlarge the sucker-disc cavity, ensuring low pressure during inspiration. In Astroblepidae, the intermandibularis posterior muscle is less divided, and the left-right connection between the intermandibularis anterior is almost non-existent (De Crop et al. 2013). Unique among these groups, the upper-lip portion of the chiloglanidine sucker-disc, together with the rostrum of the head, is somewhat passively movable, immobilizing the sucker-disc (and fixing it to the substrate) while the body may be moving because of water current or body motion, so further preventing leakage. As such, the upper jaw assists in station-holding by providing a toothed anti-slip pad.

Interestingly, the third trait, having a controllable water inlet, strongly differs in the three catfish groups. Chiloglanidines only allow respiratory inflow through the medioposterior slit in the sucker-disc (Fig. 2B,D), and open and close this slit using the mandibular barbel system which they inherited from their assumedly barbel-probing ancestors (cf. Fig. 1B). All non-chiloglanidine Mochokidae possess two pairs of mandibular barbels, often branched (Vigliotta, 2008). The combination of our anatomical and kinematic results strongly suggests that the muscles acting on the barbel-supporting cartilages, found similarly in *Synodontis*, acquired a new function in chiloglanidines: opening the water inlet (protractor hyoidei) or closing it (intermandibularis anterior, especially the labial part). Thus, the barbel cartilages not only strengthen the lip disc but have become crucial for inspiration. In the Neotropical loricarioid lineage,

the one pair of mandibular barbel cartilages found in the more basal loricarioid families Nematogenyiidae, Trichomycteridae (some species only), Callichthyidae and Scoloplacidae (own observations; Schaefer, 1990; Evers & Seidel, 2005) apparently has been lost in the suckermouth taxa Loricariidae and Astroblepidae. Loricariidae use the single pair of maxillary barbels as movable support for a pair of lateral furrows for inspiration (Geerinckx et al. 2007, 2011), functioning analogously to the single posterior slit of chiloglanidines. Astroblepidae, though intimately related to Loricariidae, completely skip their well developed sucker-disc cavity for inspiration, inhaling through a dorsal, accessory gill opening at the back of the head, bringing water directly into the central buccal cavity (De Crop et al. 2013); oral inspiration, however, remains important for food uptake. Still, kinematic analyses of Geerinckx et al. (2011), De Crop et al. (2013) and the current paper indicate that all three families use their ventral musculature (intermandibularis or protractor hyoidei) to mediate the volume of the sucker-disc cavity by elevating or depressing the lower lip.

With regard to feeding, chiloglanidines may well already have inherited a subventral mouth with ventrally facing teeth and well developed lips, as present in most *Synodontis* and *Microsynodontis* (own observations; Ng, 2004) (chiloglanidines form a polytomy with both these genera; Vigliotta, 2008). Many *Synodontis* species use their rough lips to attach loosely to substrates and are exceptionally contact-oriented, often positioning themselves vertically or upside-down, hiding between logs or stones (own observations; Seegers, 2008). The more caudal position of the lower jaw, due to the shortened suspensorium, provides space for the upper jaw to come into a ventral position rostral to the lower jaw, closely contacting the substrate below. A shortened suspensorium, with more caudal lower jaw, is not seen in loricarioids, but the upper jaw is brought much more rostrally here during ontogeny, as shown in the loricariid *Ancistrus* (Geerinckx et al. 2008). The upper jaw, mostly immobile in *Synodontis* and chiloglanidines, and supporting a field of backward-pointing teeth, acts as a rough anti-slip pad. Convergent to both Neotropical families (Geerinckx et al. 2007; De Crop et al. 2013), the premaxillas of many chiloglanidines are connected to the neurocranial mesethmoid via a medioventral protuberance of the latter bone; this protuberance is present in the genera *Atopochilus*, *Atopodontus* and *Euchilichthys*, but not in *Chiloglanis* (this paper; Vigliotta, 2008). Lacking direct or indirect musculature, the chiloglanidine upper jaw is not mobile. The direct muscular attachment of the retractor premaxillae on the upper jaw in Astroblepidae and Loricariidae increases the importance of the upper jaw in scraping, especially in the Loricariidae, where the upper jaw can move along an extensive surface to feed (Adriaens et al. 2009).

The lower jaw of chiloglanidines and sister genera *Synodontis* and *Microsynodontis* has a symphyseal angle between 135° and 180° (Vigliotta, 2008), atypically large for

catfishes, but clearly facilitating the evolution towards a transversely positioned lower jaw, rotating around its own axis, and so well able to scrape the substrate. The angle is comparably large in both Neotropical families. As both lower jaw halves are in very close contact in chiloglanidines (e.g. almost fused in *A. adriaensis*), they are less mobile than the one in Loricariidae and Astroblepidae. The very high mobility of the lower jaws in Loricariidae (e.g. Lujan et al. 2012) may well have contributed to their successful radiation: mouth and jaw morphology differs vastly among the family.

Upper jaw teeth in chiloglanidines are chisel-like and more or less straight, but lower jaw teeth are curved and often spatulate, as are the loricariid and astroblepid teeth. The presence of a dentary tooth cup in the mochokid subgroup of *Acanthocleithron* + (*Synodontis* + *Microsynodontis* + Chiloglanidinae) (Vigliotta, 2008) again may have facilitated the evolution of a scraping feeding behaviour, as this enables a larger number of growing replacement teeth, quickly replacing teeth worn by scraping. This is seen in both Neotropical families as well, that also obviously wear down their teeth while scraping them. Again, only in Loricariidae a high degree of interspecific variation in tooth shapes is seen, including bendable teeth in several genera (Geerinckx et al. 2012).

With about 58 described species (Vigliotta, 2008), Afro-tropical chiloglanidines are substantially less numerous than their Neotropical counterparts: currently, about 700+ loricariid and 54 astroblepid species are known (Ferraris, 2007; Schaefer et al. 2011). Whether the Loricariidae + Astroblepidae clade benefitted from a longer history of diversification of the basic suckermouth bauplan, is unsure. The oldest known loricariid fossils date from the Miocene and are comparable to modern taxa (Gayet & Meunier, 2003); the stem group leading to Loricariidae, Astroblepidae, and their sister group Scoloplacidae is thought to have differentiated by the late Paleocene (López-Fernández & Albert, 2011). The chiloglanidine fossil record still appears blank; among Mochokidae, *Synodontis* fossils dated to early Miocene, and *Mochokus* fossils dated to late Miocene, have been reported (Otero et al. 2010; Pinton et al. 2011). Neotropical fish faunas encountered more tectonic events creating or changing mountainous habitats, possibly stimulating further transformation and diversification of the suckermouth habitus (Lundberg et al. 1998).

In the mochokid family, the transformation from generalist bottom feeders towards scrapers can be observed on a lower taxonomical scale, with genera substantially differing (e.g. *Mochokus* vs. *Atopochilus*). In the loricarioid clade, differences of comparable importance are observed between families only (e.g. Callichthyidae vs. Astroblepidae). Also, the mochokid lineage provides an opportunity to observe the more gradual transition from generalist bottom-feeding catfishes to scrapers: the facilitating traits visible in the chiloglanidine sister groups like *Synodontis* show how ancestral transitional stages might have functioned.

Studies on the morphological evolution of the Neotropical loricarioid lineage usually focus more on feeding capacities than on station-holding capacities (e.g. Schaefer & Lauder, 1986; Adriaens, 2003). Still, these authors considered possible facilitating interactions between station-holding and scraping. Mochokid diversity suggests that it is most plausible that, at least in the Afrotropical lineage, transitions towards scraping and towards station-holding co-evolved, facilitating each other. Recently, the importance of station-holding, or using sucker apparatuses for locomotion in fishes, has received renewed attention, illustrating how fish taxa reach, and stay in, such feeding grounds (e.g. Maie et al. 2013; De Meyer & Geerinckx, in press).

Acknowledgements

The sampling and on-site examination of specimens was possible thanks to a collaboration between the research group of Evolutionary Morphology of Vertebrates at Ghent University (Belgium), the Institut de Recherches Agronomiques et Forestières (I.R.A.F., Libreville, Gabon) and the Ichthyology Department at the Royal Museum for Central Africa (Tervuren, Belgium). The authors wish to thank I.R.A.F. collaborators Jean-Hervé Mve Beh and especially Auguste Mbonda for the invaluable assistance during the sampling. Funding was provided by a postdoctoral mandate to T.G. by FWO Vlaanderen.

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