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Analysis of ontogenetic changes in head shape and diet in a catfish with moderately enlarged jaw adductors (*Clariallabes melas*)

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ABSTRACT. Jaw adductor hypertrophy, or the presence of enlarged jaw-closing muscles, has arisen several times independently in African clariid catfish. Previous work has demonstrated that species characterized by enlarged jaw adductors may have unusual ways of foraging such as terrestrial foraging and prey capture, and often include a large proportion of hard and terrestrial prey in their diet. However, relatively little is known about species of the genus *Clariallabes* with an intermediate degree of jaw adductor hypertrophy. In the present study we present data on head shape and diet for a range of sizes of specimens of a poorly known species of *Clariallabes*, *C. melas*. Our data show that growth patterns in this species and the previously studied *C. longicauda* are similar in some ways (e.g. positive allometry of the growth of the jaw muscles) but different in others (negative allometry in hyoid width). However, *C. melas* has a smaller head for its body size in all dimensions. Due to the large number of empty stomachs we encountered, dietary data remain preliminary, but suggest a varied diet including both hard and soft prey. Our data show that a large amount of variation in head shape may exist even among related species and that species with jaw adductor hypertrophy generally show positive allometry in the growth of the jaw adductors and associated structures. Whether jaw muscle hypertrophy is an adaptive trait in clariid catfish awaits further comparative analyses testing for the evolutionary association between jaw adductor hypertrophy and the inclusion of hard prey into the diet.

KEY WORDS: fish, muscle, biting, suction, feeding, ontogeny

INTRODUCTION

In fish, the inclusion of hard prey into the diet (durophagy) is often associated with changes in dentition (e.g. Streelman & Albertson, 2006), the presence of enlarged pharyngeal or oral jaw adductor muscles (Wainwright, 1987; Hernandez & Motta, 1997), an overall increase in the robustness of the oral or pharyngeal jaws and the skull (Cabuy et al., 1999; Grubich, 2003) and in some species durophagy is associated with the presence of a specialized muscle activation pattern (Lauder, 1983; Korff & Wainwright, 2004). Interestingly, hypertrophy of the jaw adductors is often noted in populations showing a higher proportion of molluscs in the diet, suggesting an adaptive evolutionary response of the cranial morphology to diet (Turingan et al., 1995). Moreover, a strong plastic response in muscle size to an increase of molluscs in the diet has been demonstrated in some fish (Mittelbach et al., 1999).

Oral jaw adductor hypertrophy has arisen several times independently in African clariid catfish (Jansen et al., 2006; Devaere et al., 2007). Indeed, a recent study using combined morphological and molecular data suggests that an increase in jaw adductor size has originated at least four times independently (Devaere et al., 2007). Clariid catfish are, however, not known to be mollusc crushers and retain large pointed teeth on the jaws (Devaere et al., 2001). Among clariid catfish species, jaw adductor hypertrophy ranges from the normal dorsoventrally-compressed type with the jaw adductors largely covered by the cranial bones (*e.g.* within the genus *Clarias*), to a situation where most of the dorso-lateral cranial bones are strongly reduced to make space for the jaw adductor muscles (*e.g.* within the genus *Channallabes*) (Devaere et al., 2001). Although the species with more pronounced degrees of jaw adductor hypertrophy have been relatively well studied, little is known about species with an intermediate degree of jaw adductor hypertrophy, such as those of the genus *Clariallabes* (but see Wyckmans et al., 2007).

In other vertebrates, an increase in the size of the oral jaw adductor muscles is typically associated with an increase in bite force (Herrel et al., 2007a), and in many vertebrates an increase in bite force is associated with the inclusion of hard or large prey into the diet (Herrel et al., 2002; Aguirre et al., 2003; Herrel et al., 2005; Huber et al., 2009). However, at least for some groups such as lizards, it has been shown that sexual selection for increased fighting capacity may also lead to increased bite force (Lailvaux et al., 2004; Huyghe et al., 2005; Lappin & Husak, 2005) and sexual differences in the size of the jaw adductors (Herrel et al., 2007b). Moreover, in some burrowing mammals, high bite force may be associated with the ability to dig tunnels into hard soils rather than diet (Van Daele et al., 2009) suggesting that a multitude of selective pressures may be operating on jaw muscle size and bite force capacity.

Previous work on clariid catfish with enlarged oral jaw adductors has demonstrated that some of these species have unusual ways of foraging including terrestrial prey capture (Van Wassenbergh et al., 2006a), and that they include a large proportion of hard and often terrestrial prey in their diet (Huysentruyt et al., 2004). However, the species with the most extreme degree of jaw adductor hypertrophy appear to swallow their prey whole (Huysentruyt et al., 2004). Previous studies have shown that rapidly-growing and suction-feeding clariid species, such as *Clarias gariepinus* grow isometrically (Herrel et al., 2005). In contrast, the growth of jaw adductors and related structures shows positive allometry in a species with an intermediate degree of jaw hypertrophy, such as *Clariallabes longicauda* (Wykmans et al., 2007). In order to test the hypothesis that species with intermediate degrees of jaw hypertrophy are characterised by positive allometric growth, we analysed growth patterns in a species with an intermediate degree of jaw adductor hypertrophy (*Clariallabes melas*; Boulenger 1887). Moreover we compare patterns of growth in *C. melas* to those observed for its congener, *C. longicauda* (Boulenger, 1902) and present data on diet for a range of sizes of individuals of *C. melas*.

MATERIALS AND METHODS

Material examined

The 51 *Clariallabes melas* used in this study were obtained from the Royal Museum for Central Africa (RMCA - KMMA), Tervuren, Belgium. All specimens (30592-603-1 to 10; 68800-68802-1 to 2; 117776-117780-1 to 5; 119100-101-1 to 2; 29660; 46746-46747-1 to 2; 117770-117775-1 to 2; 178220-230-MEL15, 178220-230-1; 19072-19074-1; 38495-38508-1 to 2; 44916-917-1 to 2; 74381; 79220; 96646-96648-1 to 2; 98931; 119117; 138665; 73-68-P-566-574-1 to 8; 86-06-P-51-53-1 to 2; 88-01-P-1993; 88-01-P-1994-1995-1 to 2) were collected in the Congo River drainage. Fish included in this study range from 116 to 329mm total length and encompass juvenile (i.e. non-reproductive) and adult specimens.

Morphometrics

Body size (both total length and standard length) and head dimensions were measured using digital calipers (Mitutoyo CD-30C and CD-15B; ± 0.01mm). Head length was measured as the distance between the tip of the snout and the caudal edge of the occipital process. Head width and head height were measured just posterior to the jaw adductors.

The surface area taken up by the jaw adductors in dorsal view was determined using digital photographs of each specimen and is used here as a proxy for jaw adductor size (see Fig. 1; WYCKMANS et al., 2007). For our analyses, the average of the left and right sides was calculated. Additionally the maximal width of the head and the width of the neurocranium were determined on these pictures. Measurements were carried out using tpsDIG (version 1.40; ROHLF, 2004). A scale bar (1mm grid) was included in each photograph, allowing us to convert pixel measurements to metric units. These measures were taken as previous studies have shown them to be correlated with the inclusion of functionally-different prey into the diet in fish (WYCKMANS et al., 2007).

To determine the dimensions of a number of internal skeletal elements, X-ray photographs (dorsoventral view) were made using a Philips Optimus X-ray unit with image intensifier, coupled to a Redlake Imaging MotionPro high resolution digital video camera. On each photograph eight landmarks were digitized using Didge (version 2.2.0.; Cullum A.). Based on the X-Y coordinates, the length and width of the lower jaw and the hyoid, the length of the hyoid bars, the angle between the two hyoid bars and the width of the pectoral girdle were calculated (see Fig. 2; WYCKMANS et al., 2007). These measures are thought to reflect the ability of these fish to enlarge the oral cavity and thus their ability to capture elusive prey (VAN WASSENBERG et al., 2006c;d). As fish having wider pectoral girdles and longer and wider hyoids should be able to increase the volume of the oral cavity to a greater degree, they should be more successful in capturing elusive prey.

Diet

Stomach contents were removed *in situ* through a ventral incision, and preserved in a 70% aqueous ethanol solution. All prey items were sorted and identified using a binocular microscope (Wild M3Z). Because the majority of organisms found in the stomachs were crushed and/or digested, they were identified to the level of order or higher taxonomic level where appropriate.

The number of prey items found in every stomach was counted and for every prey item prey size was estimated. Intact prey items were measured using digital calipers (Mitutoyo CD-15B; ± 0.01mm). Non-intact prey items were grouped in size classes, from 0–45mm, at 5mm intervals. Average prey size, maximal prey size and the proportion of large prey (i.e. > 20mm) consumed were calculated for each individual fish. In addition, every prey group was weighed using an electronic microbalance (Mettler Toledo MT5; ± 0.001mg). For each prey group, a relative importance index (IRI) was calculated as an indicator of the significance of that particular prey group in the diet (HUYSENTRUYT et al., 2004): $IRI=(\%N+\%V)\times \%Oc$ where %N and %Oc are, respectively, the numeric abundance and the frequency of occurrence of a particular prey group. %V is the mass that particular prey group contributes to total prey mass. In addition, %IRI was calculated, being the proportion of IRI of each prey group in relation to the total IRI value.

Statistical analysis

To investigate size-related changes in morphology, $\log_{10}$ transformed morphological measures were regressed against the $\log_{10}$ transformed standard length. A two-tailed Student t-test was used to test for differences between the observed slopes obtained from the regression analyses and the slopes expected in the case of isometric growth (SOKAL & ROHLF, 1995). Isometry is the expected mode of growth for ectotherms growing throughout their life and has been demonstrated for non-specialized suction-feeding catfish (*Clarias gariepinus*; see HERREL et al., 2005). Analyses of covariance (ANCOVA) with standard length as covariate were used to test for differences in morphology between data presented here for *Clariallabes melas* and previously published data for *C. longicauda* (WYCKMANS et al., 2007). All analyses were performed using SPSS V15.

RESULTS

Ontogenetic changes in head size and shape in *Clariallabes melas*

All morphological traits examined are correlated with fish body size (all $R^2>0.120$ and $p<0.016$; Table 1). The observed ontogenetic changes in morphology, however, were not always consistent with those expected for a model of isometric growth. Whereas jaw adductor size (Student t-test, d.f.=50, t=2.02, $0.02<p<0.05$) increases faster, lower jaw width (Student t-test, d.f.=50, t=-2.57, $0.01<p<0.02$) and hyoid width (Student t-test, d.f.=47, t=-2.44, $0.01<p<0.02$) increase slower than predicted by geometric scaling models. Unexpectedly, the angle between the two hyoid bars decreases significantly during growth in *C. melas* (Student t-test, d.f.=47, t=-2.48, $0.01<p<0.02$).

Clariallabes melas versus *C. longicauda*

Significant interspecific differences were detected for all morphological traits examined. Taking into account the observed difference in average body size (SL) (one-way ANOVA; $F_{1,105}=10.36$; p=0.002), it is clear that *C. longicauda,* despite its smaller body size has a broader, more robust head and larger jaw adductor muscles than does *C. melas* (ANCOVA; all $p<0.002$; see Fig. 1).

TABLE 1

Table summarizing the scaling of head dimensions relative to body size in *Clariallabes melas*. d.f. = degrees of freedom; S.E. = standard error of the slope.

	EXPECTED SLOPE	OBSERVED SLOPE	S.E.	d.f.	t	P
Total length (mm)	1	0.990	0.010	50	-1.000	0.30 < P < 0.50
Cranial length (mm)	1	0.940	0.056	50	-1.071	0.20 < P < 0.30
Cranial width (mm)	1	1.005	0.057	45	0.088	> 0.90
Cranial depth (mm)	1	1.011	0.066	50	0.167	0.80 < P < 0.90
Neurocranial width (mm)	1	0.802	0.099	50	-2.000	0.05 < P < 0.10
Head width (mm)	1	1.005	0.067	47	0.075	> 0.90
Surface area jaw adductors (mm^2)	2	2.269	0.133	50	2.023	0.02 < P < 0.05
Width lower jaw (mm)	1	0.879	0.047	50	-2.574	0.01 < P < 0.02
Length lower jaw (mm)	1	0.978	0.063	50	-0.349	0.70 < P < 0.80
Width hyoid (mm)	1	0.883	0.048	47	-2.438	0.01 < P < 0.02
Length hyoid (mm)	1	1.111	0.088	47	1.261	0.20 < P < 0.30
Hyoid angle (°)	0	-0.149	0.060	47	-2.483	0.01 < P < 0.02
Width pectoral girdle (mm)	1	0.959	0.061	48	-0.672	0.50 < P < 0.70

TABLE 2

Table summarizing the diet of *Clariallabes melas*. **Occurrence** reflects the number of stomachs in which a particular prey group was observed; **prey number** reflects the total number of prey found; **mass** reflects the total prey mass of that prey category and **%IRI** indicates the relative importance of a prey group in the diet.

	OCCURRENCE		PREY NUMBER		MASS		%IRI
	#	%	#	%	mg	%	
Plant/unidentifiable	18	69.23					
Nematoda	2	7.69					
Gastropoda	1	3.85	2	3.23	3.61	1.99	0.85
Isopoda	1	3.85	8	12.90	2.00	1.10	2.26
Chilopoda	1	3.85	3	4.84	1.70	0.94	0.93
Insecta	4	15.38	4	6.45	0.55	0.30	4.35
Coleoptera (adult)	5	19.23	10	16.13	2.34	1.29	14.03
Coleoptera (larval)	1	15.38	12	19.35	46.90	25.81	29.55
Dictyoptera	1	3.85	2	3.23	3.14	1.73	0.81
Diptera (larval)	3	11.54	11	17.74	0.99	0.54	8.82
Ephemeroptera (larval)	1	3.85	1	1.61	0.26	0.14	0.28
Lepidoptera (larval)	2	7.69	2	3.23	66.51	36.60	13.17
Odonata (larval)	2	7.69	3	4.84	7.74	4.26	2.97
Teleostei	4	15.38	4	6.45	45.97	25.30	20.92

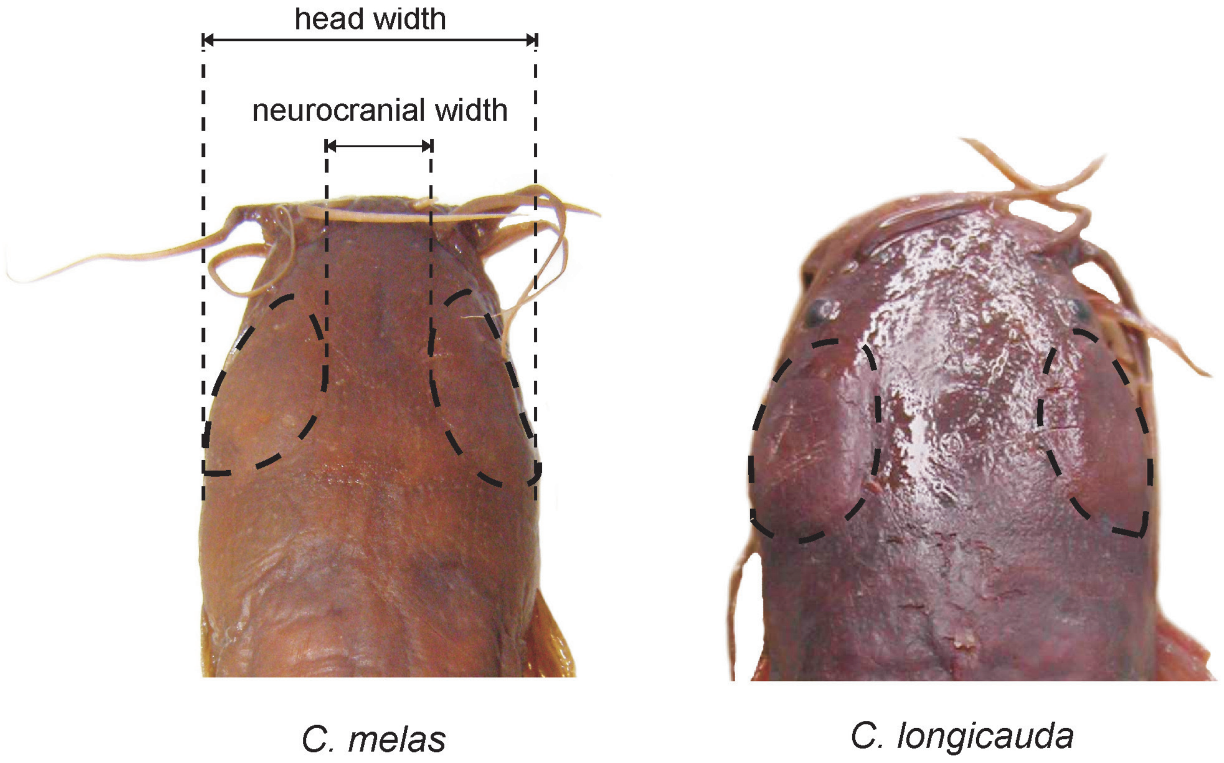

Fig. 1. – Pictures in dorsal view of the heads of *Clariallabes melas* (left) and *C. longicauda* (right). Indicated are the outlines of the jaw adductors, head width and neurocranial width. Note the more robust appearance of the head in *C. longicauda* compared to *C. melas*.

Diet in *Clariallabes melas*

Twenty (43.5%) of the 46 stomachs examined were empty and 13 (28.3%) contained only unidentifiable or plant matter. The content of the remaining 13 stomachs could be identified, although these also regularly contained some unidentifiable or plant matter, which was probably accidentally ingested. Table 2 summarizes the results of the stomach content analysis. The most important prey groups for *C. melas* are larval specimens of Coleoptera (%IRI=29.6), fish (%IRI =20.9), adult specimens of Coleoptera (%IRI=14.0) and larval specimens of Lepidoptera (% IRI=9.1). Over 30% of the preys retrieved from the stomachs were large (over 20mm in length). All hard-shelled prey retrieved from the stomachs had been effectively crushed, as was observed previously for *C. longicauda* (Wyckmans et al., 2007). Throughout ontogeny no changes in diet, or in the relationships between morphology and diet, could be demonstrated for *C. melas*.

DISCUSSION

Our data on cranial morphometrics for a size range of *Clariallabes melas* indicate that the jaw adductors become disproportionately bigger as fish grow; a phenomenon that was previously also observed for *C. longicauda* but is distinctly different from growth patterns observed for the non-hypertrophied *Clarias gariepinus* (Herrel et al., 2005). Interestingly, and in contrast to the patterns observed for *C. longicauda* (Wyckmans et al., 2007), jaw width and hyoid width within *C. melas* showed a negative allometry indicating that the heads in the large fish are characterized by large jaw muscles but relatively narrow jaws and hyoids. Why this is the case currently remains unclear, but we suggest that the relatively narrow hyoid may allow for a greater ventral excursion of the mouth floor due to rotation of the hyoid. All else being equal, rotation of a hyoid of a given length characterized by hyoid bars being closer together, as observed here for *C. melas*, will result in a greater ventral excursion of the

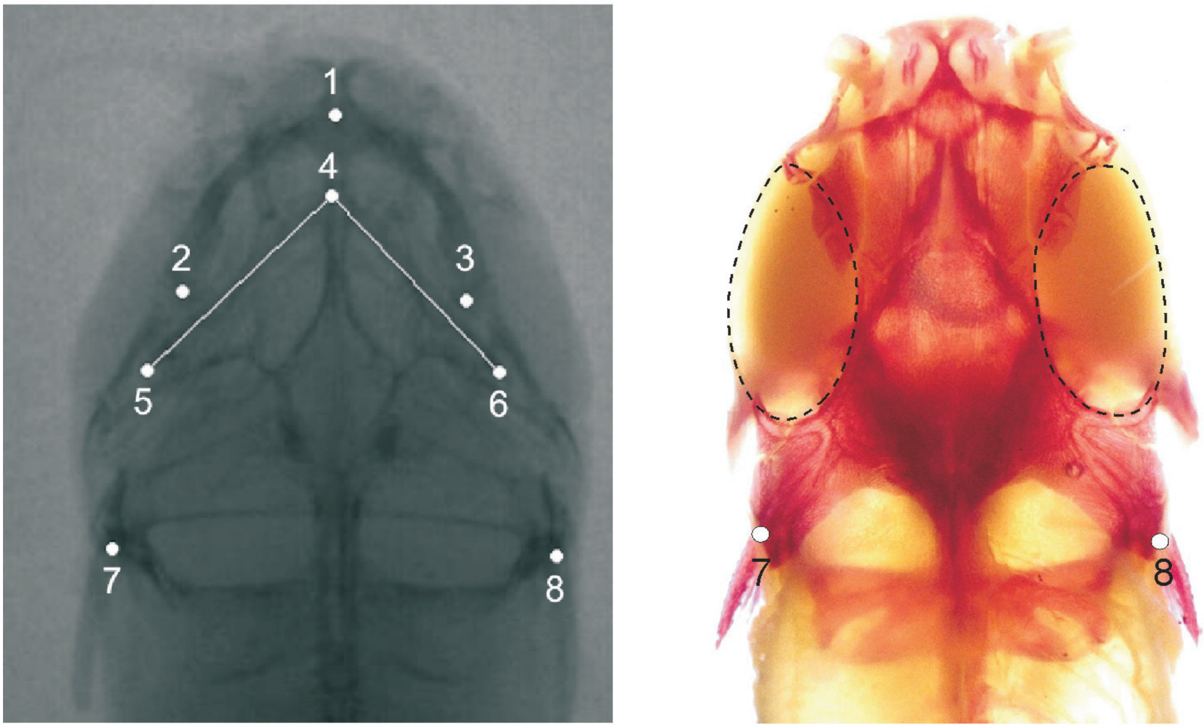

Fig. 2. – To the left a ventral view x-ray of the head of a *Clariallabes melas* is shown. On the X-ray the landmarks used to quantify head and jaw dimensions are indicated. To the right a dorsal view picture of a cleared and stained *C. melas* specimen is shown to illustrate the size of the jaw adductors. Note that the lower jaw and hyoid are not present in this specimen. (1) Lower jaw symphysis; (2, 3) caudal tips of the lower jaw; (4) hyoid symphysis; (5, 6) caudal tips of the hyoid; (7, 8) left and right pectoral fin articulation.

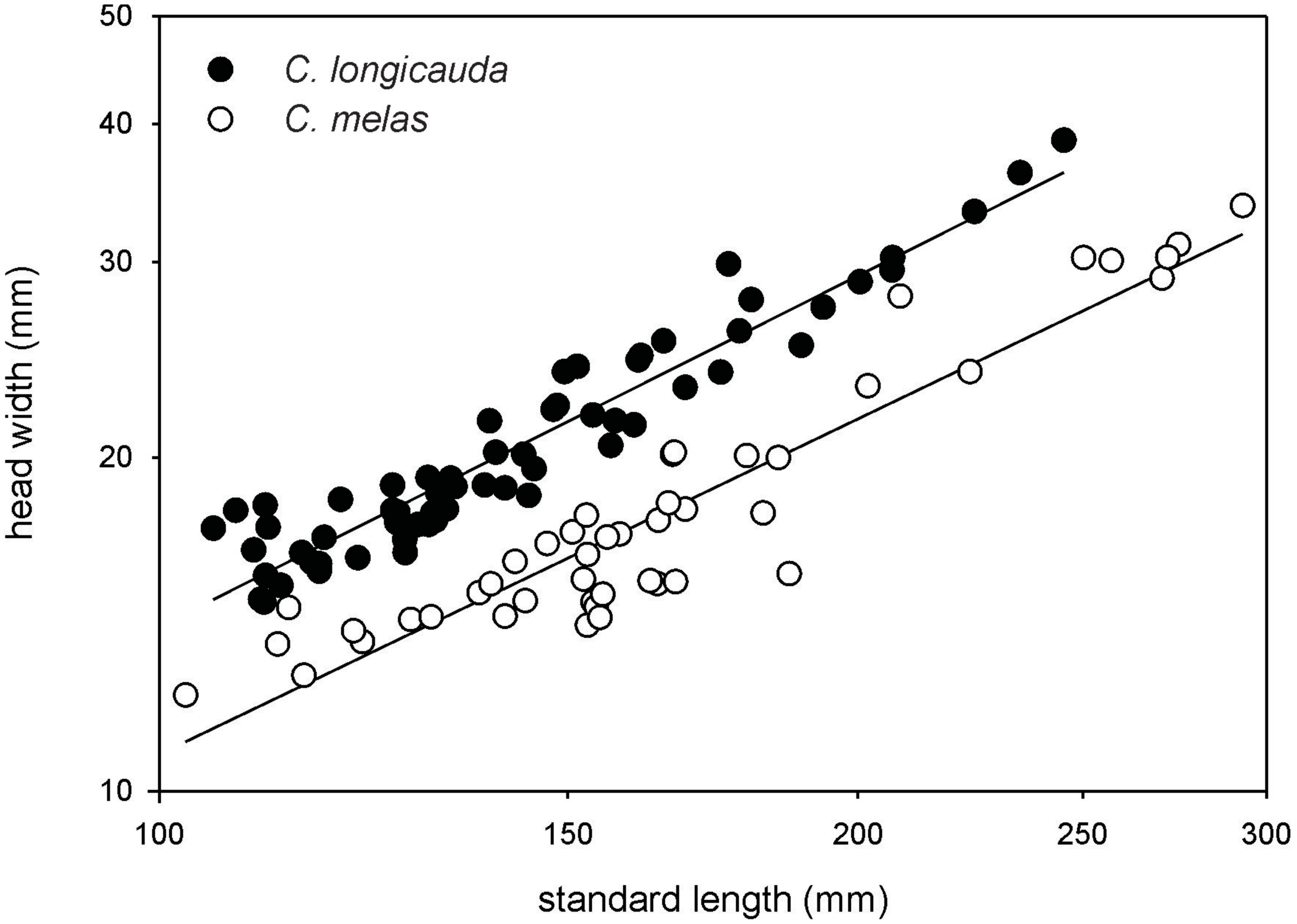

Fig. 3. – Scatterplot illustrating the differences in head width between *Clariallabes melas* and *C. longicauda*. For a given body size (standard length) *C. melas* has a significantly narrower head than *C. longicauda*.

mouth floor. Previously published kinematic data on suction feeding in clariid catfish with enlarged jaw adductors (including *Clariallabes*) do indeed suggest that the expansion of the buccal cavity is largely restricted to a ventrad rotation of the hyoid (VAN WASSENBERGH et al., 2004, 2006b;c) and consequently larger fish are expected to have an improved suction performance. An improvement of suction performance with size has been suggested previously also for *Clarias gariepinus* (VAN WASSENBERGH et al., 2005; 2006d). Although we suggest that larger *C. melas* might prey disproportionately more on relatively large and mobile prey such as teleost fish, our preliminary dietary data cannot confirm this. Additional dietary data are clearly needed to shed further light on the ecological significance of the observed ontogenetic changes in morphology.

Interestingly, our data indicate clear differences in morphology between the two *Clariallabes* species studied here. Even though *C. melas* is on average slightly larger than *C. longicauda* its head is clearly smaller and the jaw adductors are less developed for a given body size (Figs 1; 3). Although it is tempting to speculate about the ecological significance of this difference in morphology, our data for *C. melas* are insufficient to address this in a quantitative manner. Although the diet in *C. longicauda* appears more diverse, this may simply be an artifact of the small sample size in *C. melas*. In both species coleopterans and teleost fish are the most important food items with about 60-80% of the individuals having one or the other prey in their stomachs. Despite having smaller jaw adductors, the *C. melas* examined here crushed all hard prey as evidenced by the crushed molluscs, and crushed exoskeletons of insects and other arthropods, similar to the situation reported for *C. longicauda* (WYCKMANS et al., 2007). As many of the prey retrieved from the stomachs were large (30% over 20mm in length) this suggests an important role for the hypertrophied jaw adductors.

Our data illustrate how different species of clariid catfish with intermediate jaw adductor hypertrophy may differ dramatically in morphology and growth. Moreover, and in contrast to non-specialized suction-feeding catfish such as *Clarias gariepinus*, the growth of the head and structures functionally relevant to feeding is allometric. Although some tendencies for differences in diet can be discerned, these await further and more robust quantitative analyses. The fact that all hard prey were found crushed in the stomachs of the two *Clariallabes* species is in strong contrast to data for species with more extreme jaw adductor hypertrophy such as *Channalabes* or *Gymnallabes* where hard prey are apparently swallowed whole (HUYSENTRUYT et al., 2004). Thus, whereas the enlarged jaw adductors in these species with intermediate degrees of jaw specialization appear to provide a performance benefit in crushing hard prey, this does not appear to be the case in more specialized forms. Clearly further data on morphology and diet in species with enlarged jaw adductors such as *Platyallabes tihoni* (DEVAERE et al., 2005), *Dolichallabes microphtalmus* (DEVAERE et al., 2004) and their non-specialized sister taxa (DEVAERE et al., 2007) will be crucial to quantitatively test for evolutionary associations between morphology and diet in the group.

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