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Size-related changes in cranial morphology affect diet in the catfish *Clariallabes longicauda*

MARISA WYCKMANS[1]*, SAM VAN WASSENBERGH[1], DOMINIQUE ADRIAENS[2], RAOUL VAN DAMME[1] and ANTHONY HERREL[1]

[1]*Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerpen, Belgium*
[2]*Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium*

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Within the catfish family Clariidae, species exist with different degrees of jaw adductor hypertrophy. This jaw adductor hypertrophy has been related to bite performance, in turn suggesting a link to dietary specialization. Thus, an increase in the degree of hypertrophy will likely be reflected in an increase in the amount of hard prey in the diet. In the present study, we examine the ontogenetic scaling of cranial structure and diet in a species of catfish with a moderate degree of jaw adductor hypertrophy, *Clariallabes longicauda*. Additionally, we investigate whether the observed changes in the morphology of the feeding system during growth are linked to changes in diet. The fish examined demonstrate a strong positively allometric growth of the jaw adductors, of head height and of maximal head width, suggesting that larger fish can feed on larger and harder prey. Dietary data confirm these hypotheses and reveal an increase in maximal prey size consumed, the proportion of large prey in the diet, and average prey hardness during ontogeny. Moreover, the observed changes in the proportion of large prey consumed and prey hardness are correlated with an increase in lower jaw width and maximal head width, respectively. An increase in the amount of evasive prey in the diet with fish size is correlated with an increase in hyoid length. In summary, not only size dependent, but also size-independent variation of the feeding system was associated with ontogenetic changes in diet in *C. longicauda*. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 323–334.

ADDITIONAL KEYWORDS: feeding capacity – head shape – scaling – variation.

INTRODUCTION

Animals must live within the boundaries set by physical laws. The size of an organism is of crucial importance and has profound effects on its structure and function (Schmidt-Nielsen, 1984). Theoretical scaling models have been developed to understand the functioning of musculo-skeletal systems during growth, and to predict the effects of size on the functioning of musculo-skeletal systems in general (Hill, 1950; McMahon, 1973; Richard & Wainwright, 1995; West *et al*., 2003). In many of these models (Hill, 1950; Richard & Wainwright, 1995), geometric similarity, or maintenance of shape, is assumed. Although linear dimensions (e.g. jaw length) are expected to increase directly proportional to linear dimensions (e.g. body length, L), force generating capacity (being directly proportional to muscle cross sectional area) and segmental masses are expected to increase to the second and third power of linear dimensions, respectively.

There can, however, be important functional consequences of maintaining shape with increasing size. As a consequence of geometric similarity (maintenance of shape during growth), discrepancies between the available muscle force (proportional to L^2) and the force needed to accelerate a given segmental mass (proportional to L^3) arise, thus causing the accelerations to decrease as size increases. Although shape is being maintained with increases in size, function is not. Therefore, geometrically similar animals are not necessarily functionally equivalent. Functional equivalence in different-sized organisms only occurs when performance capability is maintained with

*Corresponding author. E-mail: marisawyckmans@hotmail.com

changes in size (Emerson, Greene & Charnov, 1994). Because ectotherms such as fish, amphibians and reptiles typically display indeterminate growth, they have been proposed as good systems in which to test the predictions of geometric scaling models (Meyers, Herrel & Birch, 2002; Deban & O'Reilly, 2005). Among ectotherms, fish have been the subject of most studies because they appear to maintain the shape of the cranial system during growth (Richard & Wainwright, 1995; Hernandez & Motta, 1997). However, a recent study by Herrel *et al*. (2005) demonstrated that, for the catfish *Clarias gariepinus* Burchell, 1882, neither the head, nor the cranial structures themselves scale according to geometric similarity models. Relative to head size, distinct changes in the mass and configuration of the feeding structures take place that appear to affect the functioning of the cranial system (Van Wassenbergh, Aerts & Herrel, 2005). A comparison of the functional consequences of changes in morphology during growth with published dietary data for this species suggested that the ontogenetic changes in morphology might be tightly linked to changes in diet (Herrel *et al*., 2005).

Besides the nonhypertrophied *C. gariepinus*, species with extremely well-developed jaw adductors, as well as intermediate forms, exist within the family Clariidae (air-breathing catfishes). Jaw adductor hypertrophy is assumed to have originated several times independently in clariids (Teugels & Adriaens, 2003) and has been related to an increased bite performance (Herrel *et al*., 2002). An obvious hypothesis is that this increase in bite performance is linked to dietary specialization, and such a relationship has been shown in other teleost families (Wainwright, 1996; Clifton & Motta, 1998; for Clariids, see also Huysentruyt *et al*., 2004). Within the Clariidae, however, most of our knowledge, both morphological and ecological, results from the nonhypertrophied (Bruton, 1979; Herrel *et al*., 2005) or extremely hypertrophied species (Cabuy *et al*., 1999; Devaere *et al*., 2001; Huysentruyt *et al*., 2004). Species with a moderate degree of jaw adductor hypertrophy remain largely unstudied, but kinematic studies suggest that prey are captured by a combination of suction feeding and biting. Prey items are sucked towards the mouth, during the expansion of the skull, after which the jaws are placed firmly onto the prey. Next, the head is swung to one side, thereby tearing loose attached pieces of prey (Van Wassenbergh *et al*., 2004). Thus, any change in the degree of hypertrophy of the jaw muscles can be expected to be reflected in the absolute and/or relative amount of large and hard prey into the diet. Changes in the size and shape of the elements related to buccal expansion should be related to the proportion of evasive prey into the diet.

Not only when comparing across species, but also during ontogeny, changes in the degree of jaw adductor hypertrophy can be observed in some species of catfish (Herrel *et al*., 2005). If this is a more general feature of cranial growth in catfish, then ontogenetic changes in diet are also expected in the more hypertrophied species such as *Clariallabes longicauda* Boulenger, 1902.

In the present study, we investigated the scaling of cranial structures and ontogenetic changes in the diet of a catfish species with a moderate degree of jaw adductor hypertrophy, *C. longicauda*. Additionally, we determined whether the observed changes in size and head morphology are correlated with changes in diet. Specifically, we expected an increase in the proportion of hard prey in the diet in fish with larger (both absolutely and relatively) heads and jaw muscles. Moreover, the proportion of evasive prey in the diet was expected to be related to changes in morphology that affect the expansion of the oral cavity during suction feeding (i.e. associated with the dimensions and shape of the hyoid and pectoral girdle). Finally, we tested whether the observed ontogenetic changes in diet are a consequence of changes in overall body size or rather are associated with specific shape changes in the cranial system of *C. longicauda*.

MATERIAL AND METHODS

MORPHOMETRICS

The 63 *C. longicauda* used in the study were obtained from the Royal Museum for Central Africa (RMCA–KMMA), Tervuren, Belgium. Specimens were predominantly collected in one of two localities in north-western Gabon and Cameroon (see Appendix). No geographical bias in morphology was detected upon inspection of the data.

Body size (both total length and standard length) and head dimensions were measured using digital calipers (Mitutoyo CD-30C and CD-15B; ±0.01 mm). 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 of the jaw adductors.

To estimate the size of the jaw adductors, the area taken up by the jaw adductors in dorsal view was determined from digital photographs of each specimen (Fig. 1), taken using a Nikon Coolpix 885 digital camera. The outline of the jaw adductors was indicated both on the left and the right side, and the enclosed surface area was calculated. As a measure of the jaw adductor size, the average of the left and right side was calculated. To validate these measurements, we dissected a small sample of fish ($N = 10$) of which the jaw adductors were removed. Muscles were blotted dry and weighed on an electronic microbalance (Mettler

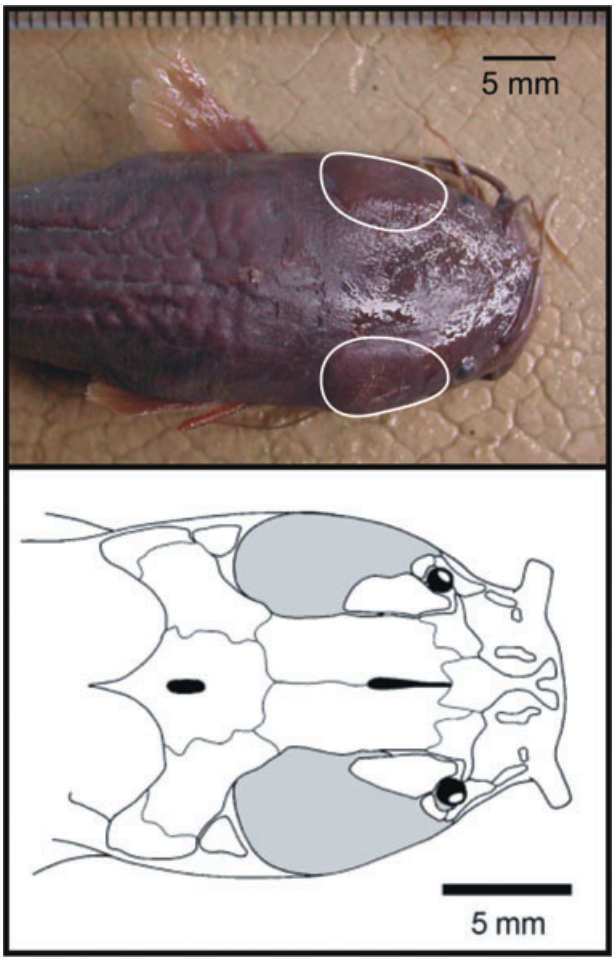

Figure 1. Dorsal view on the head of a *Clariallabes longicauda* specimen. The outlines of the jaw adductors are indicated in white.

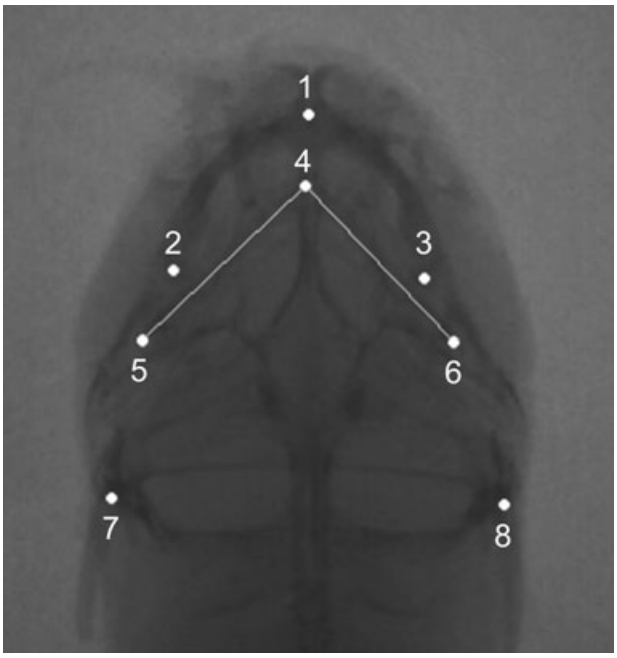

Figure 2. Dorsoventral X-ray photograph with the eight landmarks (white dots) that were digitized to determine the dimensions of the lower jaw, the hyoid and the pectoral girdle. White lines indicate the angle between the left and right hyoid bars. Numbers indicate the landmarks digitized: (1) lower 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.

Toledo MT5; ±0.001 mg). Regressions of surface area against muscle mass were highly significant ($r = 0.81$; $P < 0.01$). To test whether this correlation is the result of the covariance of these traits with size (fish with bigger heads will have larger muscles and larger surface areas), we regressed the traits against fish cranial length and calculated the residuals. The regression of the residual surface area against residual muscle mass was also highly significant ($r = 0.78$; $P < 0.01$), demonstrating that the surface area taken up by the jaw adductors in dorsal view is a good predictor of muscle mass in these fish.

Additionally, the maximal width of the head and the width of the neurocranium were both determined on these pictures. Neurocranium width was measured as the minimal width of the neurocranium, whereas maximal head width was measured as the maximal width across the jaw adductors. Measurements were carried out using tpsDIG32 (version 1.40; Rohlf, 2004). A scale bar (±1 mm) was included in each photograph, allowing the data to be converted to real units.

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) (Fig. 2) and the *x*- and *y*-coordinates for each point were exported to a spreadsheet. Based on the *x*- and *y*-coordinates, the length and width of the lower jaw and the hyoid, the angle between the two hyoid bars and the width of the pectoral girdle were calculated.

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 scope (type WILD M3Z). Because the majority of organisms found in the stomachs were crushed and/or digested, they were identified to the level of the 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 were measured using digital calipers (Mitutoyo CD-15B; ±0.01 mm). Non-intact prey were grouped in size classes, from 0–45 mm, at 5-mm intervals. Average prey size, maximal prey size and the proportion of large prey (i.e. > 20 mm) consumed was calculated for each individual fish. In addition, every prey group was weighed using an electronic microbalance (Mettler Toledo MT5; ±0.001 mg).

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 of *C. longicauda* (Huysentruyt *et al*., 2004):

$$\mathrm{IRI} = (\%N + \%V) \times \%Oc$$

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.

Not only the taxonomic diversity, but also the ecological and functional diversity of the diet was assessed. To do so, prey items were divided into a number of ecological/functional classes: (1) Hard (H) – Intermediate (I) – Soft (S); (2) Terrestrial (T) – Aquatic (A); and (3) Evasive (E) – Non-evasive (NE). These classifications were only made for prey that could be identified to the level of the order.

Based on previous measurements of prey hardness (Herrel *et al*., 1999, 2001; Verwaijen, Van Damme & Herrel, 2002; Aguirre *et al*., 2003), every prey item was classified as being either hard (i.e. adult Coleoptera, Hymenoptera, larval Trichoptera, Isopoda, Gastropoda and Vertebrata), of intermediate hardness (i.e. Ephemeroptera, Hemiptera, Odonata, Orthoptera and Diplopoda) or soft (all other prey). Prey hardness was estimated for each prey item using the following regressions (Verwaijen *et al*., 2002):

$$\text{Hard: } \log_{10}[\text{prey hardness}\,(N)] = 1.582 \times \log_{10}[\text{prey size}\,(\text{mm})] - 1.365$$

$$\text{Intermediate: } \log_{10}[\text{prey hardness}\,(N)] = 1.780 \times \log_{10}[\text{prey size}\,(\text{mm})] - 1.942$$

$$\text{Soft: } \log_{10}[\text{prey hardness}\,(N)] = 0.997 \times \log_{10}[\text{prey size}\,(\text{mm})] - 1.379$$

For all intact prey, the actual prey length was used to calculate prey hardness; for non-intact prey, the middle of the size class to which the prey item was assigned was used as an indicator of prey length. In addition, an average prey hardness value was calculated for each individual.

To classify organisms as being evasive or non-evasive, the assumption was made that terrestrial prey had fallen into the water where they could easily be captured by the fish. Consequently, all terrestrial prey groups were classified as being non-evasive. An overview of the classification of the different prey into functional categories is provided in Table 1.

Finally, the proportion of prey belonging to each ecological/functional class was calculated in three different ways: numeric (number of prey), volumetric (mass), and based upon the frequency of occurrence (i.e. number of stomachs containing prey of a particular ecological/functional class in relation to the total number of full stomachs). This was carried out both for each individual and for the species as a whole.

Statistical analysis

To investigate ontogenetic changes in morphology, $\log_{10}$-transformed morphological measures were regressed against the $\log_{10}$-transformed standard length. A two-tailed Student's *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).

Next, the $\log_{10}$-transformed average and maximal prey size, proportion of large prey consumed, average prey hardness, prey number (absolute), and prey mass (proportional) in each ecological/functional class were regressed against the $\log_{10}$-transformed standard length to investigate ontogenetic changes in diet.

Finally, we investigated which morphological variable(s) could account for dietary variation using multiple regression analyses. The $\log_{10}$-transformed average and maximal prey size, the proportion of large prey consumed, average prey hardness, prey number (absolute), and prey mass (proportional) in each ecological/functional class were regressed against the morphological variables. The morphological variables used were the $\log_{10}$-transformed standard length and the residual values of all other $\log_{10}$-transformed measures relative to the $\log_{10}$-transformed standard length. In the case of ontogenetic changes in diet, the residuals of the dietary variables (relative to standard length) were regressed against the morphological variables.

RESULTS

Ontogenetic changes in head size and shape

All morphological traits examined (Table 2) were highly correlated with fish body size (all $R^2 > 0.614$ and $P < 0.0001$), except for the angle between the two hyoid bars ($R^2 = 0.04$ and $P = 0.155$). The observed

Table 1. Diet composition of *C. longicauda*. The taxonomic classification is based on stomach analyses for 47 individuals. The ecological/functional classification is based on a subgroup of 39 individuals

TAXONOMIC CLASSIFICATION Prey type	No. of stomachs	No. of prey	Mass (mg)	% IRI	Functional category
Plant/unidentifiable**	37				
Invertebrata					
Nematoda**	1				
Annelida	2	2	8.714	0.08	S-NE-A
Gastropoda	3	217	7.929	7.76	H-NE-A
Arthropoda*	6	12	0.807	0.86	
Araneae	2	4	59.522	0.29	S-NE-T
Decapoda	3	4	135.984	0.80	S-E-A
Isopoda	3	4	5.350	0.17	H-NE-T
Chilopoda	2	2	2.644	0.06	S-NE-T
Diplopoda	1	1	0.187	0.01	I-NE-T
Insecta*	19	29	17.503	7.07	
Coleoptera (ad)	10	22	540.255	11.34	H-NE/E-T/A
Coleoptera (la)	6	12	548.139	6.17	S-NE-T
Dictyoptera	3	3	0.563	0.11	I-NE-T
Diptera (ad)	7	7	2.731	0.61	S-NE-T
Diptera (la)	6	74	59.675	5.84	S-NE-A
Hemiptera	3	8	8.314	0.32	I-NE-T
Hymenoptera	14	19	73.804	4.82	H-NE-T
Isoptera	4	28	6.324	1.37	S-NE-T
Isoptera**	2				
Lepidoptera (ad)	1	1	15.529	0.04	S-NE-T
Lepidoptera (la)	5	6	465.487	4.12	S-NE-T
Mecoptera	1	1	0.383	0.01	S-NE-T
Odonata (ad)	1	1	21.210	0.05	I-NE-T
Odonata (la)	16	26	162.594	9.14	I-E-A
Orthoptera	7	8	113.635	1.95	I-NE-T
Siphonoptera	1	1	1.145	0.01	S-NE-T
Trichoptera	2	3	2.185	0.08	S-NE-T
Eggs (insect)	1	10	5.268	0.13	S-NE-A
Vertebrata					
Teleostei	10	10	1507.895	25.57	H-E-A
Eggs (fish)	4	152	96.042	7.83	S-NE-A
Anura	2	2	1034.751	3.39	H-E-A
Total	47	669	4904.569		

ECOLOGICAL/FUNCTIONAL CLASSIFICATION
Number of stomachs with prey size in this class (number of stomachs with average prey size in this class)

0–5 mm	5–10 mm	10–15 mm	15–20 mm	> 20 mm
15 (6)	29 (12)	21 (10)	8 (3)	18 (8)

Hard – Intermediate – Soft

	No. of stomachs	No. of prey	Mass (mg)	% IRI
Hard	29	275	3171.863	58.15
Intermediate	24	45	305.967	5.94
Soft	25	308	1408.429	35.91

Evasive – Non-evasive

	No. of stomachs	No. of prey	Mass (mg)	% IRI
Evasive	27	52	3376.291	35.47
Non-evasive	31	576	1509.968	64.53

Terrestrial – Aquatic

	No. of stomachs	No. of prey	Mass (mg)	% IRI
Terrestrial	30	120	1330.461	23.17
Aquatic	30	508	3555.798	76.83

*prey group not accounted for in ecological/functional part of the table.
**prey group for which only frequency of occurence was calculated. IRI, relative importance index.
S, soft; I, intermediate; H, hard; E, evasive; NE, non-evasive; A, aquatic; T, terrestrial.

Table 2. Overview of the minimum and maximum values, averages and standard deviations (SD) for all morphological traits examined

Variable	Minimum	Maximum	Mean	SD
Total length (mm)	119.10	276.16	162.28	36.57
Standard length (mm)	105.52	245.33	145.39	32.72
Head length (mm)	19.89	51.97	28.26	6.74
Head width (mm)	14.82	38.66	20.94	5.30
Head height (mm)	8.43	28.46	13.13	4.11
Neurocranium width (mm)	5.66	20.50	10.22	2.63
Maximum head width (mm)*	16.05	53.32	25.28	7.60
Jaw adductor size (mm^2)	22.36	336.80	77.07	63.02
Lower jaw length (mm)	5.06	14.53	7.91	2.10
Lower jaw width (mm)	8.57	24.12	12.59	3.07
Hyoid length (mm)	3.93	13.32	7.50	1.79
Hyoid width(mm)	11.78	29.03	15.81	3.88
Hyoid angle (°)	81.27	138.51	92.94	10.50
Pectoral girdle width (mm)	12.47	32.25	17.81	4.22

*measured across jaw adductors.

Table 3. Results of Student's *t*-test used to test for differences between observed slope and expected slope (geometric scaling)

Variable	Expected slope	Observed slope	SE
Total length (mm)	1	0.994	0.007
Head length (mm)	1	1.000	0.037
Head width (mm)	1	1.051	0.041
Head height (mm)	1	1.208	0.068
Neurocranium width (mm)	1	0.876	0.088
Max. head width (mm)*	1	1.185	0.059
Jaw adductor size (mm^2)	2	2.712	0.143
Lower jaw length (mm)	1	0.964	0.088
Lower jaw width (mm)	1	0.946	0.059
Hyoid length (mm)	1	0.831	0.087
Hyoid width(mm)	1	0.935	0.056
Hyoid angle (°)	0	0.067	0.047
Pectoral girdle width (mm)	1	0.938	0.059

*measured across jaw adductors.
SE, standard error.
Bold variables are significantly different from predictions of geometric similarity.

ontogenetic changes in morphology, however, were not always consistent with those expected for a model of isometric growth (Table 3). Notably, jaw adductor size (Student's *t*-test, d.f. = 61, $t = 4.98$, $P < 0.01$; Fig. 3), maximal head width (Student's *t*-test, d.f. = 61, $t = 3.14$, $P < 0.01$) and head height (Student's *t*-test, d.f. = 61, $t = 3.06$, $P < 0.01$) increased faster than predicted by geometric scaling models. Thus, distinct changes in head shape occur during growth in *Clariallabes longicauda*.

DIET: GENERAL

Sixteen (25.4%) of the 63 stomachs examined were empty and six (9.5%) contained only unidentifiable or plant matter. The content of the remaining 41 stomachs could be identified, although these too regularly contained some unidentifiable or plant matter. Table 1 summarizes the results of the stomach content analysis. In the taxonomic part of Table 1, an overview of all prey groups (based on the 47 stomachs

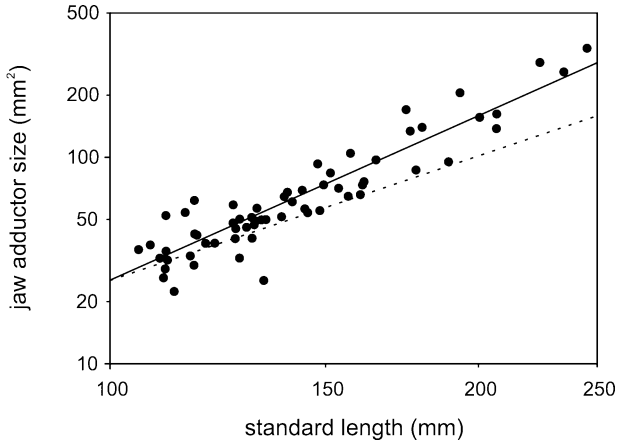

Figure 3. Log-log plot of jaw adductor size against standard length. Jaw adductor size scales with significant positive allometry (full line, slope of 2.71). The dashed line represents the expected slope of 2 under a model of geometric similarity (Table 3).

with content) is given. It shows that the three most important prey groups for *C. longicauda* were fish (% IRI = 25.6), adult Coleoptera (% IRI = 11.3) and larval Odonata (% IRI = 9.1). The ecological/functional part of Table 1 is based on 39 stomachs with identifiable content and shows how the prey are divided over the different ecological/functional and size classes. An important part of the diet consisted of hard prey (% IRI = 58.2). Although prey of intermediate hardness were found in a similar number of stomachs compared to soft prey, there was a large difference in importance (% IRI = 5.9 for intermediate versus 35.9 for soft prey). Furthermore, both non-evasive (% IRI = 64.5) and aquatic prey (% IRI = 76.8) were important components of the diet of *C. longicauda*. In 80% of the stomachs, the average prey size was smaller than 20 mm.

Size-related changes in diet

Size-related changes in diet were detected for a number of prey characteristics. Notably, the proportion of large prey (> 20 mm) ($R^2 = 0.14$, $P = 0.021$), the maximal prey size consumed ($R^2 = 0.10$, $P = 0.047$), the average prey hardness ($R^2 = 0.10$, $P = 0.045$), the proportion of hard and soft prey ($R^2 = 0.10$, $P = 0.047$ and $R^2 = 0.19$, $P = 0.006$, respectively), the proportion of evasive and non-evasive prey (both $R^2 = 0.16$; $P = 0.012$), and the proportion of terrestrial and aquatic prey (both $R^2 = 0.16$; $P = 0.012$) changed with increasing fish size. Whereas the average prey hardness and the proportion of hard, evasive and aquatic prey in the diet increased with fish body size, the proportion of soft, non-evasive and terrestrial prey consumed decreased with increasing fish body size.

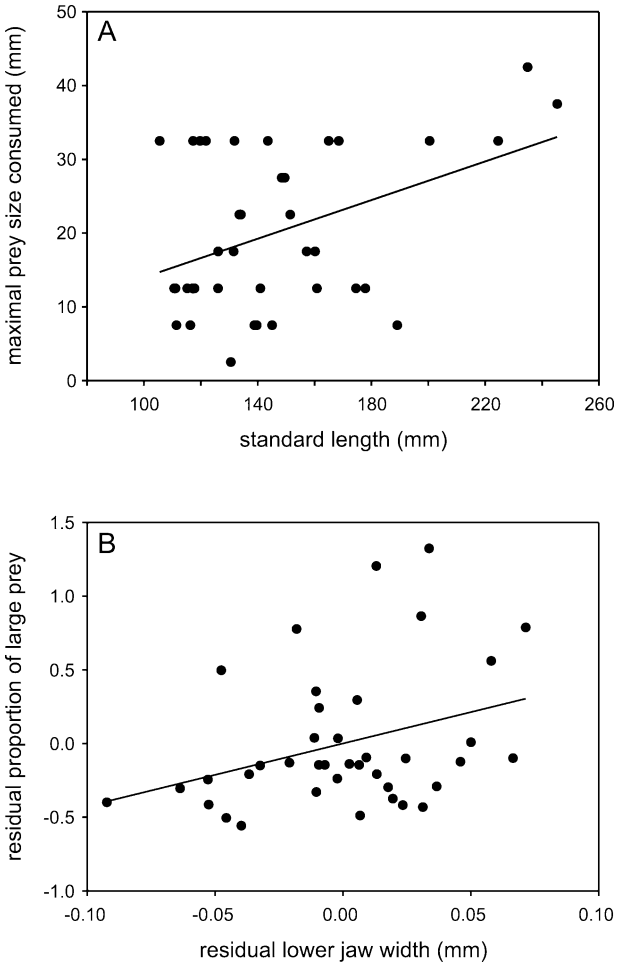

Figure 4. A, maximal prey size consumed plotted against fish standard length. B, the residual proportion of large prey in the diet increases with relative lower jaw width.

Relationships between morphology and diet

Multiple regression analyses indicated that variation in dietary variables in most cases could be explained by distinct changes in morphological variables (Table 4). The relative proportion of large prey consumed increased with relative lower jaw width (residuals relative to standard length) (slope = 4.94 ± 1.97; $R^2 = 0.149$; $P = 0.02$; see also Fig. 4). Fish with a relatively broad lower jaw for a given size thus consume relatively more large prey.

Relative prey hardness and relative maximal head width (residuals relative to standard length) are positively related (slope = 4.51 ± 1.86; $R^2 = 0.141$; $P = 0.02$; see also Fig. 5). Thus, fish with a relatively broad head for a given size consume relatively harder

Table 4. Results of multiple regression analyses of dietary variables against morphological variables. Note that only significant regressions are listed here. Note also that results of non-evasive and terrestrial prey are not shown as these mirror those for evasive and aquatic prey, respectively. It should be mentioned, however, that for the number of non-evasive prey no significant correlations with morphology were detected

Dietary variable	Morphological variable	R^2	Slope	SE
% large prey consumed*	Lower jaw width (res)	0.255	4.954	1.993
	Standard length		1.823	0.777
% large prey consumed (res)*	Lower jaw width (res)	0.149	4.943	1.965
Average prey hardness	Maximum head width** (res)	0.222	4.507	1.881
	Standard length		1.731	0.840
Average prey hardness (res)	Maximum head width** (res)	0.141	4.507	1.855
Hard				
% mass	Lower jaw width (res)	0.326	8.208	2.494
	Standard length		2.286	0.969
% mass (res)	Lower jaw width (res)	0.238	8.212	2.448
Soft				
% mass	Standard length	0.378	–2.974	0.839
	Head width (res)		–8.273	2.875
% mass (res)	Head width (res)	0.192	–8.285	2.837
Evasive				
Number of prey	Hyoid length (res)	0.149	6.133	2.447
% mass	Standard length	0.309	2.940	0.980
	Pectoral girdle width (res)		5.007	1.949
% mass (res)	Pectoral girdle width (res)	0.159	5.007	1.923
Aquatic				
% mass	Standard length	0.395	2.976	0.944
	Lower jaw length (res)		4.490	1.850
	Pectoral girdle width (res)		3.885	1.909
% mass (res)	Lower jaw length (res)	0.263	4.492	1.825
	Pectoral girdle width (res)		3.886	1.882

*prey size > 20 mm.
**measured across jaw adductors.
SE, standard error; res, residual values, relative to standard length.

prey. The relative proportion of hard prey in the diet was positively related to relative lower jaw width (slope = 8.21 ± 2.45; $R^2 = 0.24$; $P = 0.002$). Consequently, for the proportion of soft prey in the diet, a negative relationship with head width was observed (slope = –8.29 ± 2.84; $R^2 = 0.19$; $P = 0.006$).

The relative proportion of evasive prey was related to relative pectoral girdle width (slope = 5.01 ± 1.92; both $R^2 = 0.16$ and $P = 0.01$). The absolute number of evasive prey in the diet, on the other hand, was positively related to relative hyoid length (slope = 6.13 ± 2.45; $R^2 = 0.15$; $P = 0.017$; Fig. 6). The presence of evasive prey in the diet thus appears to be associated with shape differences in the pectoral girdle and hyoid.

Finally, the relative proportion of aquatic prey in the diet was positively related to relative lower jaw length and pectoral girdle width (both $R^2 = 0.26$; lower jaw length: slope = 4.49 ± 1.83; $P = 0.019$ and pectoral girdle width: slope = 3.89 ± 1.88; $P = 0.046$).

DISCUSSION

Ontogenetic diet switches in fishes and other ectotherms appear to be a universal phenomenon. Why do fish switch diet as they grow? The most common explanation is that ontogenetic diet switches reflect the changing feeding abilities or energetic demands of fish as they grow. Most, but not all diet switches of carnivorous species involve increases in the average size of prey with increasing predator size (Keast, 1985; Osenberg & Mittelbach, 1989). As fish grow, they are able to eat larger prey, and bigger prey become more profitable. Increasing prey size will usually lead to taxonomic changes and these changes are manifested as ontogenetic diet switches (Wainwright & Richard, 1995). An example of a shift in diet during ontogeny in a clariid catfish (the taxonomic group of our study species *Clariallabes longicauda*) has been reported for *C. gariepinus*

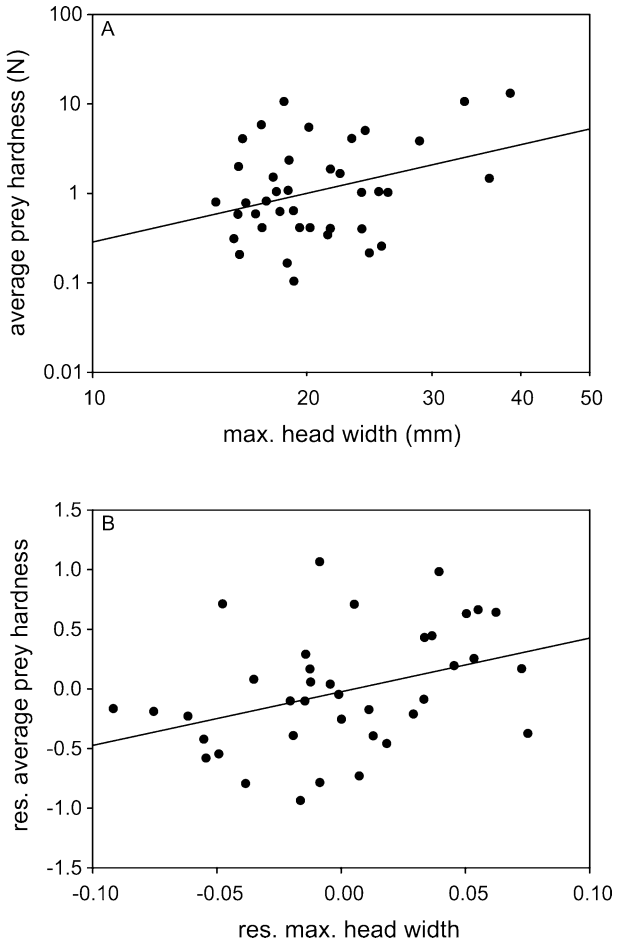

Figure 5. Log-log plot of the average prey hardness against maximal head width (i.e. measured across jaw adductors), represented as absolute and (A) relative (B) values. Average prey hardness significantly increases with increasing maximal head width (Table 4).

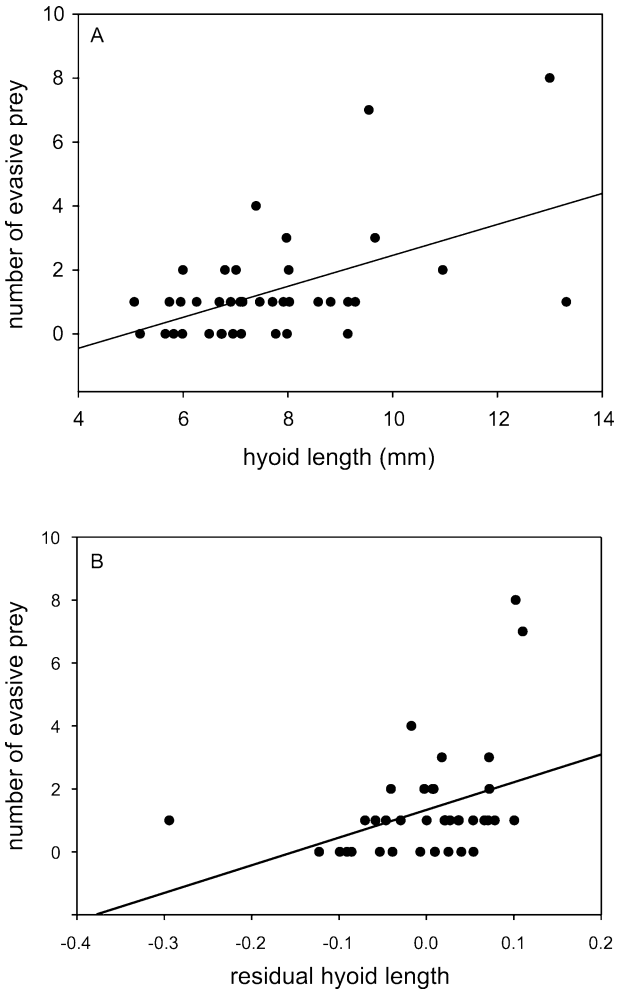

Figure 6. A, plot of the number of evasive prey against hyoid length. The number of evasive prey increases significantly with increasing hyoid length (Table 4). B, note how also relative hyoid length is significantly correlated with the number of evasive prey in the diet (Table 4).

(Bruton, 1979). The study showed that crustaceans, insects and larval fishes make up the bulk of the diet for small *C. gariepinus*, whereas the diet of larger conspecifics is primarily composed of adult fish.

Moreover, mouth size is usually positively related to prey size (Wainwright & Richard, 1995; Hugueny & Pouilly, 1999; Sibbing & Nagelkerke, 2001; Bouton, De Visser & Barel, 2002). The dimensions of the lower jaw affect the volume of the buccal cavity (Bouton *et al.*, 2002). Therefore, larger fish (with larger mouths) are expected to feed on larger prey. Indeed, in *C. longicauda*, maximal prey size and the proportion of large prey consumed both increase with predator size. However, in the largest *C. longicauda* specimens, an amount of relatively small prey (< 20 mm) is also found. Because large individuals apparently consume both small and large prey items, the expected increase in average prey size with predator size is not present.

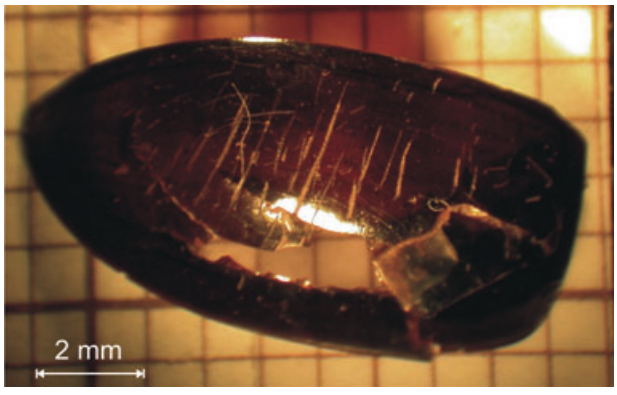

Figure 7. A coleopteran elythrum showing clear bite marks as an example of a crushed prey item (one square = 1 mm^2).

As the cross-sectional area of the jaw adductor muscles increases during growth, larger animals will be able to bite harder compared to smaller individuals. Furthermore, the present study demonstrates that *Clariallabes longicauda* adds significantly to this increase in maximal bite force during ontogeny by showing a positive allometric growth of the jaw muscles (Fig. 3). Consequently, it was not unexpected to find that the average hardness of the prey included in the diet increases with size in this catfish (Table 4). Moreover, almost all prey items, including the hard ones, were crushed (Fig. 7). Interestingly, this observation is in contrast to those made by Huysentruyt *et al*. (2004) who demonstrated that, although the extremely hypertrophied clariids *Gymnallabes alvarezi* Günther, 1867 and *Channallabes apus* Günther, 1873 mainly feed on Coleoptera (hard prey), these prey are typically swallowed whole. At least in *C. longicauda*, however, it appears that the size of the jaw muscles through their effect on bite performance likely lie at the basis of dietary specialization (Herrel *et al*., 2002; Huysentruyt *et al*., 2004). This is in close agreement with what has been demonstrated in ecomorphological studies of other fish taxa (Wainwright, 1996; Clifton & Motta, 1998). Such allometric growth in the jaw adductors co-occurring with an increase in the number of hard prey taken has also been observed previously for a closely related species (*C. gariepinus*; Herrel *et al*., 2005) and a more distantly related teleost species (*Archosargus probatocephalus* – Sparidae, Walbaum, 1792; Hernandez & Motta, 1997). Our observation that larger *C. longicauda* have relatively broader and higher heads (Table 3) is probably related to this relative increase in jaw adductor size during ontogeny because broader jaw muscles need to be 'accommodated' inside the head of the fish (Barel, 1983).

Interestingly, also the proportion of evasive prey in the diet of *C. longicauda* increased with increasing predator size (Table 4). Again, this was according to our predictions because a similar result was also obtained for the closely related *C. gariepinus* (Bruton, 1979); in this species, the size and number of evasive prey in the diet increases considerably with increasing fish size. Functionally, this makes sense because a fish of twice the length can theoretically produce a volume-increase eight-fold greater than that of the fish half its size, and will thus be able to displace a considerably larger amount of water towards and into the mouth. Moreover, a study on the scaling of suction performance in *C. gariepinus* has shown that larger catfish can engulf prey from a larger distance, and that the suction-induced water flow can drag larger prey into the mouth compared to smaller catfish (Van Wassenbergh, Aerts & Herrel, 2006).

As suggested by Wainwright & Richard (1995), changes in specific morphological variables can often explain much of the observed variation in dietary variables. Therefore, variation in the diet within the examined individuals may also occur as a consequence of interindividual variation in morphology independent of differences in body size. Indeed, a positive relationship between the proportion of large prey consumed and lower jaw width was found, even after excluding the effects of absolute body size (Fig. 4B). Similarly, we found a positive relationship between average prey hardness and maximal head width (Fig. 5B). As noted above, individuals with relatively broader heads will also have larger jaw adductors and therefore be able to exert larger bite forces. Yet, not only bite performance, but also suction performance appears to depend on size-independent changes in the shape of the components of the cranial system: the number of evasive prey was positively related to the relative hyoid length (Fig. 6). Because the most important part of the expansion of the bucco-pharyngeal cavity in *C. longicauda* is due to ventral rotation of the hyoid (Van Wassenbergh *et al*., 2004), a relatively larger hyoid will probably be advantageous in generating suction. Furthermore, a relatively broader pectoral girdle provides a larger area of attachment for the hypaxial muscles, the most important muscles for generating suction (Van Wassenbergh *et al*., 2006). This potentially explains the observed relation between diet (amount of evasive prey) and morphology (hyoid length and pectoral girdle width). These results indicate that not only exponential increases in size of musculo-skeletal components because of growth, but also more subtle variation in the characteristics of the head components between similar sized individuals can result in altered feeding capacities.

In conclusion, the data obtained in the present study show distinct ontogenetic changes in head size and shape in the catfish *C. longicauda* that are correlated to changes in diet. Larger fish have disproportionately well developed jaw adductors and eat more hard prey. Whereas the extremely hypertrophied clariids, *G. alvarezi* and *C. apus*, have a specialized feeding system and mainly eat hard prey (Huysentruyt *et al*., 2004), the present study demonstrates that even a small degree of jaw adductor hypertrophy has functional consequences that are reflected in the diet of the species. Similar to *C. gariepinus* (Bruton, 1979), larger *C. longicauda* have the potential to generate larger volume-increases of the bucco-pharyngeal cavity and eat a larger proportion of evasive prey. Furthermore, a relationship between the size of the mouth and the proportion of large prey consumed was observed for *C. longicauda*. Clearly, not only the exponentially-increasing effects of growth, but also size-independent variation in the

characteristics of the head components between individuals results in altered feeding capacities, indicating the importance of cranial shape to diet in these fish.

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REFERENCES

Aguirre LF, Herrel A, Van Damme R, Matthysen E. 2003. The implications of food hardness for diet in bats. *Functional Ecology* **17:** 201–212.

Barel CDN. 1983. Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Netherlands Journal of Zoology* **33:** 357–424.

Bouton N, De Visser J, Barel CDN. 2002. Correlating head shape with ecological variables in rock-dwelling haplochromines (Teleostei: Cichlidae) from Lake Victoria. *Biological Journal of the Linnean Society* **76:** 39–48.

Bruton MN. 1979. The food and feeding behaviour of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of cichlids. *Transcripts of the Zoological Society of London* **35:** 47–114.

Cabuy E, Adriaens D, Verraes W, Teugels GG. 1999. Comparative study on the cranial morphology of *Gymnallabes typus* (Siluriformes: Clariidae) and their less anguilliform relatives, *Clariallabes melas* and *Clarias gariepinus*. *Journal of Morphology* **240:** 169–194.

Clifton KB, Motta PJ. 1998. Feeding morphology, diet and ecomorphology relationships among five Caribean labrids (Teleostei, Labridae). *Copeia* **4:** 953–966.

Deban SM, O'Reilly JC. 2005. The ontogeny of feeding kinematics in a giant salamander *Cryptobranchus alleganiensis*: Does current function or phylogenetic relatedness predict the scaling patterns of movement? *Zoology* **108:** 155–167.

Devaere S, Adriaens D, Verraes W, Teugels GG. 2001. Cranial morphology of the anguilliform clariid *Channallabes apus* (Günther, 1873) (Teleostei: Siliruformes): are adaptations related to powerful biting? *Journal of Zoology London* **255:** 235–250.

Emerson SB, Greene HW, Charnov EL. 1994. Allometric aspects of predator–prey interactions. In: Wainwright PC, Reilly SM, eds. *Ecological morphology: integrative organismal biology*. Chicago, IL: University of Chicago Press, 123–139.

Hernandez LP, Motta PJ. 1997. Trophic consequences of differential performance in the sheepshead, *Archosargus probatocephalus* (Teleostei, Sparidae). *Journal of Zoology London* **243:** 737–756.

Herrel A, Adriaens D, Verraes W, Aerts P. 2002. Bite performance in clariid fishes with hypertrophied jaw adductors as deduced by bite modeling. *Journal of Morphology* **235:** 196–205.

Herrel A, Spithoven L, Van Damme R, De Vree F. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13:** 289–297.

Herrel A, Van Damme R, Vanhooydonck B, De Vree F. 2001. The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79:** 662–670.

Herrel A, Van Wassenbergh S, Wouters S, Adriaens D, Aerts P. 2005. A functional morphological approach to the scaling of the feeding system in the African catfish, *Clarias gariepinus*. *Journal of Experimental Biology* **208:** 2091–2102.

Hill AV. 1950. The dimensions of animals and their muscular dynamics. *Science Progress* **150:** 209–230.

Hugueny B, Pouilly M. 1999. Morphological correlates of diet in an assemblage of West African freshwater fishes. *Journal of Fish Biology* **54:** 1310–1325.

Huysentruyt F, Adriaens D, Teugels GG, Devaere S, Herrel A, Verraes W, Aerts P. 2004. Diet composition in relation to morphology in some African anguilliform clariid catfishes. *Belgian Journal of Zoology* **134:** 41–46.

Keast A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environmental Biology of Fishes* **12:** 119–129.

McMahon TA. 1973. Size and shape in biology. *Science* **179:** 1201–1204.

Meyers JJ, Herrel A, Birch J. 2002. Scaling of morphology, bite force and feeding kinematics in an iguanian and a scleroglossan lizard. In: Aerts P, D'Aout K, Herrel A, Van Damme R, eds. *Topics in functional and ecological vertebrate morphology*. Maastricht: Shaker Publishing, 47–62.

Osenberg CW, Mittelbach GG. 1989. Effects of body size on the predator–prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monographs* **59:** 405–432.

Richard BA, Wainwright PC. 1995. Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *Journal of Experimental Biology* **198:** 419–433.

Rohlf FJ. 2004. *tpsDIG32 version 1.40.* Available at http://life.bio.sunysb.edu/morph/index.html

Schmidt-Nielsen K. 1984. *Scaling: why is animal size so important?* Cambridge: Cambridge University Press.

Sibbing FA, Nagelkerke LAJ. 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries* **10:** 393–437.

Sokal RF, Rohlf FJ. 1995. *Biometry*. New York, NY: WH Freeman.

Teugels GG, Adriaens D. 2003. Taxonomy and phylogeny of Clariidae: an overview. In: Arratia G, Kapoor BG,

Chardon M, Diogo R, eds. *Catfishes*, Vol. 1. Enfield, CT: Science Publishers Inc., 465–487.

Van Wassenbergh S, Aerts P, Herrel A. 2005. Scaling of suction-feeding kinematics and dynamics in the African catfish, *Clarias gariepinus*. *Journal of Experimental Biology* **208:** 2103–2114.

Van Wassenbergh S, Aerts P, Herrel A. 2006. Scaling of suction feeding performance in the catfish *Clarias gariepinus*. *Physiological and Biochemical Zoology* **79:** 43–56.

Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2004. Effects of jaw adductor hypertrophy on buccal expansions during feeding of air breeding catfishes (Teleostei, Clariidae). *Zoomorphology* **123:** 81–93.

Verwaijen D, Van Damme R, Herrel A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* **16:** 842–850.

Wainwright PC. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* **77:** 1336–1343.

Wainwright PC, Richard BA. 1995. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* **44:** 97–113.

West GB, Savage VM, Gillooly JF, Enquist BJ, Woodruff WH, Brown JH. 2003. Why does metabolic rate scale with body size? *Nature* **421:** 713.

APPENDIX

Overview of the localities where *Clariallabes longicauda* specimens were collected.

Collection number (Royal Museum for Central Africa)	Number of specimens	Locality
73-16-P-6375-380	4	Olounou, Cameroon
73-16-P-6408-412	4	Olounou, Cameroon
73-16-P-6469-472	1	Olounou, Cameroon
73-16-P-6518-555	6	Olounou, Cameroon
73-16-P-6556-587	9	Olounou, Cameroon
73-16-P-6659-660	1	Olounou, Cameroon
73-16-P-6664-665	1	Olounou, Cameroon
73-02-P-2255	1	Elang, river Sanaga, Cameroon
73-18-P-3311-313	3	Elogo, river Nyong, Cameroon
76-14-P-687	1	Mieri, river Doume, Cameroon
76-14-P-839	1	Kombetiko, river Nguesse, Cameroon
77-32-P-17-32	3	Méséa, river Bom, Cameroon
77-32-P-124-143	3	Bassin Doumé, Cameroon
95-042-P-0811-0813	3	Bassin Dja, Cameroon
179114-115	2	Tchibanga, river Nyanga, Gabon
98-029-P-0944	1	Nyame Pende creek, Gabon
99-056-P-0001-0004	3	Ebeigne, river Otubitang, Oyem, Gabon
A0-049-P-0123-0140	13	Ebeigne, river Woleu, Oyem, Gabon
A0-049-P-0141-0142	2	Ebeigne, river Woleu, Oyem, Gabon
A0-049-P-0144	1	Mifoumou (Nefarge), Oyem, Gabon