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## Effects of jaw adductor hypertrophy on buccal expansions during feeding of air breathing catfishes (Teleostei, Clariidae)

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**Abstract** Some species of Clariidae (air breathing catfishes) have extremely well developed (hypertrophied) jaw closing muscles that increase the maximal biting force of these species. As these enlarged jaw muscles tightly cover the suspensoria, which are firmly connected to the neurocranium, we expect diminished lateral expansions during suction for species with hypertrophied jaw muscles. In turn, this could imply a reduced suction performance for these species. Compared to *Clarias gariepinus*, which has relatively small jaw closers, *Clariallabes longicauda* shows a clear hypertrophy of the jaw adductors. A kinematic analysis of prey capture in these two species is presented here. As predicted, *Clariallabes longicauda* shows less lateral expansion (average abduction of the hyoids of 19.0°) than *Clarias gariepinus* (abduction of 31.1°). However, our data indicate that the decrease in lateral expansion capacity in the species with excessive adductor development is compensated for by a larger and faster ventral expansion of the buccal cavity by depression of the hyoid.

**Keywords** Catfish · Feeding · Functional morphology · Jaw adductors · Hypertrophy · Cranial expansions

### Introduction

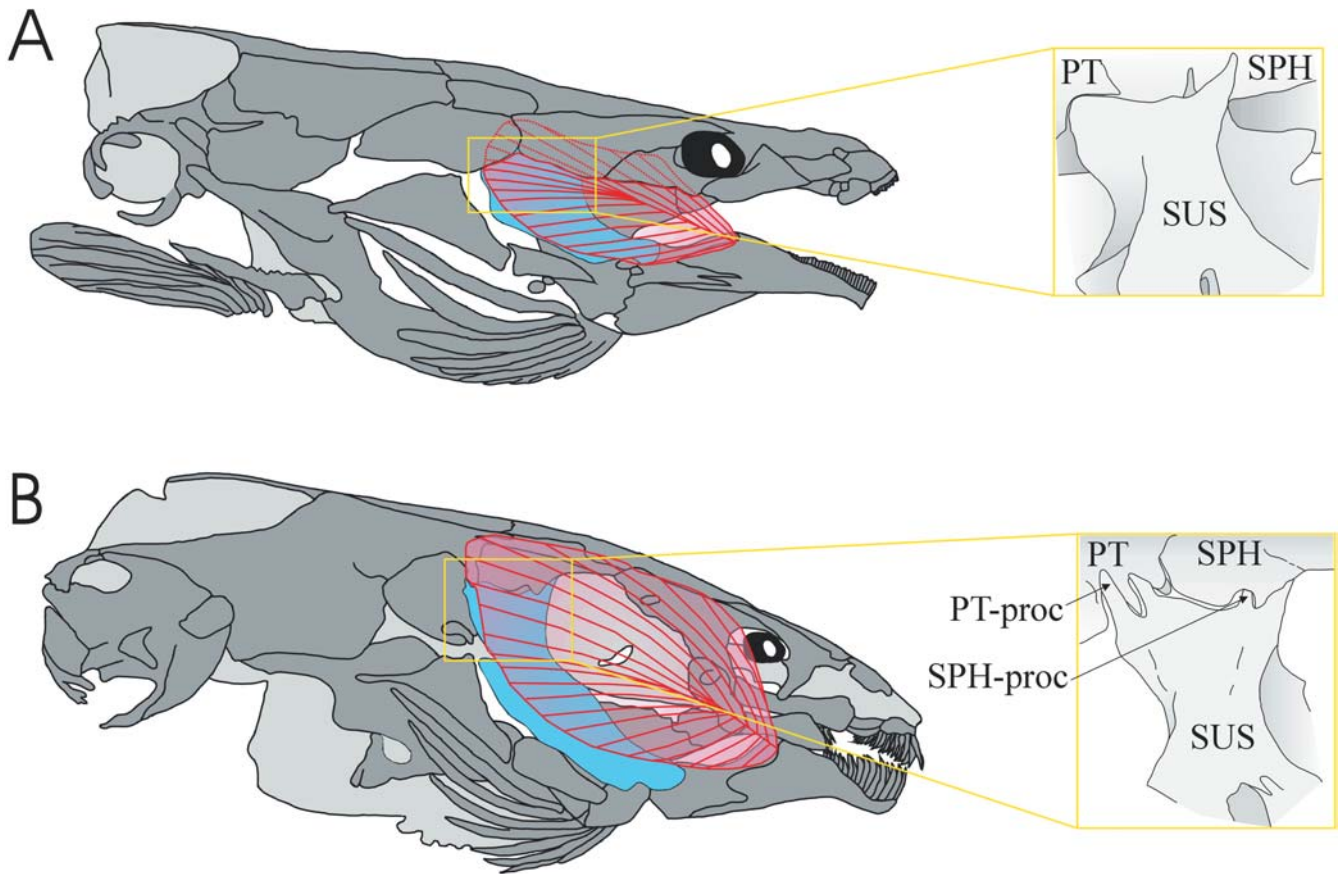
Siluriformes (catfishes) are an important component of the fish fauna of tropical limnic systems. It is a very diverse group with over 2,500 described species (Teugels 1996). Representatives of the air breathing catfishes or

Clariidae are found in Africa, the Middle East and South-East Asia. They are characterised by an elongated body, a dorsoventrally flattened head, small eyes and a suprabranchial organ (Teugels 1996). Within the Clariidae, several species have developed unusually large (hypertrophied) jaw closing muscles (*m. adductor mandibulae A2A3'*). Species like *Gymnallabes typus* Günther, 1867 (Cabuy et al. 1999) and *Channallabes apus* Günther, 1873 (Devaere et al. 2001) show an excessive growth of the jaw adductors of which the physiological cross-sectional area is respectively more than three and seven times higher for a given skull length, compared with the non-hypertrophied species *Clarias gariepinus* Burchell, 1822 (Herrel et al. 2002). According to phylogenetic studies, this hypertrophy of the jaw adductors is a derived feature for clariid catfishes (Teugels and Adriaens 2003).

Biomechanical modelling showed that species with such enlarged jaw closers can (at least theoretically) produce a higher maximal biting force (Herrel et al. 2002). Given this increased bite performance, it was not surprising that diet analyses found an altered feeding pattern for species that possess hypertrophied jaw adductors with a special preference for coleopterans, which are hard prey (F. Huysentruyt, personal communication). Moreover, also other morphological characteristics of the clariids with jaw adductor hypertrophy are regarded as adaptations related to the increased biting force (Cabuy et al. 1999; Devaere et al. 2001; see also Barel 1983; Turingan and Wainwright 1993). A noticeable characteristic in this respect is the stronger interdigitation of the suspensorium (hyomandibula) with the neurocranium (sphenotic and pterotic). The suspensorium (which in teleost fishes suspends the lower jaw, the hyoid bars and the opercular bone) in clariid species with jaw closer hypertrophy has a series of well-developed processes onto the neurocranium (Cabuy et al. 1999; see Fig. 1B). As during biting reaction forces of the food exert a moment about a transversal axis at the level of the suspensorium–neurocranium joint (Herrel et al. 2002), the stronger connection of these two bones may function to counter

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**Fig. 1A, B** Lateral view of the skulls of *Clarias gariepinus* (A) (modified from Adriaens and Verraes 1996) and *Clariallabes longicauda* (B). The pink surface represents the adductor mandibulae A2A3' (hypertrophied in *Clariallabes*) which almost entirely covers the suspensorium (in blue). The physiological cross-sectional area of this A2A3' of *Clariallabes longicauda* is about twice that of *Clarias gariepinus* [Herrel et al. 2002; data for

*Clariallabes melas* (Boulenger, 1887)]. Note that the upper part of this jaw closing muscle of *Clarias* is covered by the skull roof. A detailed view on the articulation of the suspensorium with the neurocranium is presented on the right (A modified from Cabuy et al. 1999), illustrating the interdigitations in *Clariallabes longicauda*. PT Pterotic, PT-proc pterotic process, SPH sphenotic, SPH-proc sphenotic process, SUS suspensorium

the larger moments that are caused by the increase in bite force.

Exerting bite forces onto the prey is only one aspect of feeding in Clariidae. Suction feeding is generally used to draw the prey towards the mouth (Bruton 1979). Suction feeding in actinopterygian fishes is characterised by a three-dimensional expansion and subsequent compression of the buccopharyngeal cavity, which is driven by complex movements of several musculoskeletal elements of the cranial system (Muller et al. 1982; Muller and Osse 1984). Unfortunately, experimental data on suction feeding mechanisms of siluriforms are almost completely lacking in the literature (but see Alexander 1970).

Given the morphology of the head in clariid catfishes with hypertrophied jaw adductors, we expect a diminished lateral expansion of the skull during suction feeding compared to the non-hypertrophied clariids. There are two reasons to expect this:

1. The jaw adductor muscle almost completely covers the lateral side of the head (Fig. 1). A considerable growth

of this viscoelastic mass inserting both on suspensorium and neurocranium can potentially constrain the abduction (lateral swing) of the suspensorium.

2. The stronger connection (through interdigitating processes) of the suspensorium with the neurocranium (Fig. 1) can also limit the abduction of the suspensorium.

If this reduced lateral expansion actually occurs in species with jaw closer hypertrophy, we further predict either a decrease in suction performance capacity or a compensation for the decrease in lateral expansion by creating a larger and/or faster ventral expansion. As the depression of the mouth floor by the hyoid apparatus is the most important ventral expansion for generating suction (Alexander 1970; Lauder 1985) this compensation will most likely take place at this level. On the other hand, the hyoid also participates in lateral expansions by pushing the suspensoria outwards when the sternohyoid musculature is contracted. If the suspensorium abduction is hindered for the above reasons, increased abduction

forces exerted by the musculus sternohyoideus and m. levator arcus palatini via the hyoid onto the suspensorium can compensate for the potentially increased mechanical resistance to this movement.

In order to test the potential consequences of jaw closer hypertrophy on the cranial expansions during suction feeding in clariid catfishes, a kinematic analysis of the prey captures by two species (*Clarias gariepinus* and *Clariallabes longicauda* Boulenger, 1902) was performed. Whereas *Clarias gariepinus* has relatively small jaw closers and a relatively flat suspensorium–neurocranium articulation (Fig. 1A) *Clariallabes longicauda* has hypertrophied jaw adductors and a strongly interdigitated suspensorium–neurocranium articulation (Fig. 1B). The interspecific differences in prey capture kinematics are determined, with special emphasis to the variables of lateral expansion and hyoid movements.

## Materials and methods

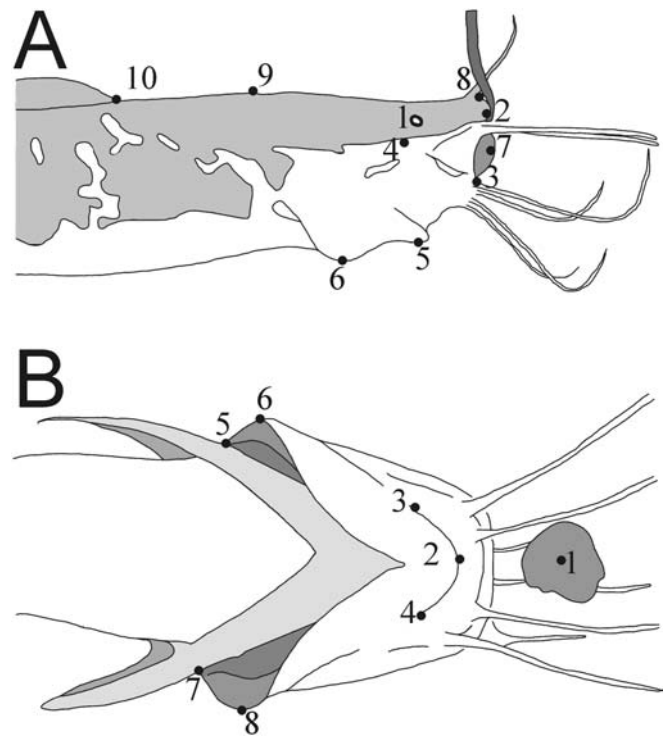
### Animals

Ten adult specimens (six *Clarias gariepinus* and four *Clariallabes longicauda*) were used in the experiments. The *Clarias* specimens were aquarium-raised specimens of which larval stages were initially obtained from the Laboratory for Ecology and Aquaculture (Catholic University of Leuven). Specimens of *Clariallabes longicauda* were caught in Northern Gabon. Cranial lengths of the *Clarias gariepinus* specimens were 44.4, 44.7, 47.5, 47.5, 51.7 and 56.6 mm. The *Clariallabes longicauda* individuals had cranial lengths of 32.4, 34.7, 35.7 and 49.0 mm. Cranial length (CL) was defined as the distance between the rostral tip of the premaxilla and the caudal tip of the occipital process. The animals were kept separate in 20-l test aquaria and were trained to capture the presented food inside a narrow, projecting corridor (25 cm length, 8 cm width, 15 cm water height) of the aquarium (which forced the animals to feed in a position perpendicular to the camera). The thin Plexiglas walls (2 mm) of the corridor minimised the amount of X-ray absorption during cineradiography.

To measure the properties of the sternohyoideus muscles, three specimens (preserved in 70% alcohol) for each species were dissected. The muscles of both sides were removed and weighed (0.0001 g). The average muscle fibre length was approximated by taking the average of lengths of the most medially positioned fibre, a central muscle fibre and the most laterally situated fibre. Muscle and muscle fibre orientation were determined from myological drawings (Adriaens and Verraes 1997; Van Meir, personal communication). The force transmission of this muscle, resulting in suspensorial abduction was calculated according to De Visser and Barel (1996) in a two-dimensional representation of their model.

### Prey

Previous research on feeding of fishes revealed the capacity of fishes to change (modulate) the prey capture kinematics in function of the prey type (Liem 1980, 1993; Lauder 1981; Wainwright and Lauder 1986; Nemeth 1997; Ralston and Wainwright 1997; Ferry-Graham 1998; Ferry-Graham et al. 2001). To reduce the chance that interspecific differences are the result of differences in behavioural modulation between both species, two different prey types were used: (1) a piece of cod fillet (*Gadus morhua* Linnaeus, 1758) of about 3 cm<sup>3</sup> and (2) a North Sea shrimp (*Pandalus borealis* Krøyer, 1838). Both prey types were attached to a thin, plastic-coated steel wire and were suspended about 5 cm above the bottom of the corridor. The cod was pinned onto the steel wire, while the shrimp

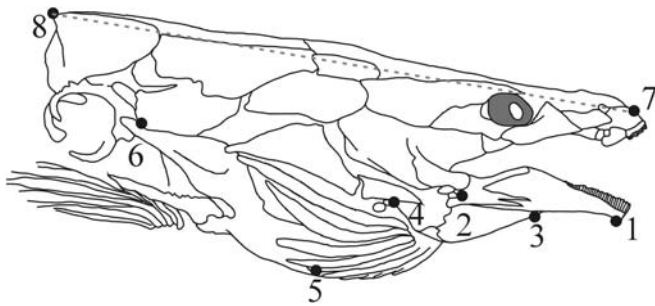


**Fig. 2A, B** Anatomical landmarks digitised on the lateral (A) and ventral (B) high-speed video images of *Clarias gariepinus*. Identical landmarks were digitised on images of *Clariallabes longicauda*. **A** Lateral landmarks: 1 middle of the eye, 2 upper jaw tip, interior side, 3 lower jaw tip, interior side, 4 jaw articulation, 5 tip of the hyoid, 6 most ventrally positioned point of the branchiostegal membrane, 7 prey, 8 rostral tip of the skull roof, 9 caudal tip of the skull roof, 10 anterior tip of the caudal fin. The measured angular variables are: gape angle (2-4-3) and neurocranial elevation (8-9-10). The linear variables are: gape distance (2-3), hyoid depression (1-5) and branchiostegal depression (6-perpendicular distance to 8-9). **B** Ventral landmarks: 1 prey, 2 hyoid symphysis, 3, 4 most caudally discernible points on the hyoid bars, 5, 7 base of pectoral spine, 6, 8 lateral tip of the branchiostegal membrane. The measured angular variable is the hyoid expansion (3-2-4). The measured linear variable is the branchiostegal expansion [distance of the segment through 6 (or 8) that intersects perpendicularly with the line through 5 (or 7) perpendicular with 5-7]

was clipped around its middle. These prey were selected because: (1) fish and crustaceans are the most abundant prey found in stomachs of wild *Clarias gariepinus* (Bruton 1979) and also *Clariallabes longicauda* could be trained to feed on these prey, (2) the attached prey types elicit suction feeding behaviour and (3) both prey clearly differ in form and attachment strength.

### High-speed video recordings

High-speed video recordings (250 frames s<sup>-1</sup>) were made from a lateral and ventral position, using a Redlake Imaging Motionscope digital high-speed video camera (shutter 1/2,500). Two floodlights (600 W) provided the necessary illumination. Only those prey capture sequences that were approximately perpendicular to the camera lens were selected and retained for further analysis. To do so, lateral recordings in which skull roof, skull bottom or origin of the maxillary barbel of the opposite side of the fish were visible, as well as ventral recordings in which the side of the skull was visible, were discarded. For each individual, ten lateral and ten ventral



**Fig. 3** Positions of the radio-opaque markers used in cineradiography, as seen from a lateral view on *Clarias gariepinus* (modified after Cabuy et al. 1999): 1 rostral tip of the lower jaw, 2 the caudal tip of the lower jaw, near the articulation with the quadrate, 3 rostral and 4 caudal tip of the cleithrum, 5 ventrorostral tip of the cleithrum, 6 dorsocaudal of the cleithrum, close to the articulation with the posttemporo-supracleithrum, 7 rostral of the upper jaw, 8 caudal tip of the processus occipitalis. Points 7 and 8 are fixed neurocranium points. The *dashed line* represents the reference line for following angle variables: 1-2 lower jaw angle, 3-4 hyoid angle and 5-6 angle of the cleithrum

recordings (each consisting of five cod and five shrimp captures) were analysed. For one *Clarias gariepinus* individual, however, only four (instead of five) ventral recordings with cod as prey could be analysed. Anatomical points were digitised on the recorded images (Fig. 2) using Didge (version 2.2.0; Alistair Cullum), and the horizontal ( $x$ ) and vertical ( $y$ ) coordinates for each point were exported to a spreadsheet. To improve the accuracy of the digitisations, each point was digitised separately throughout the entire prey capture sequence.

#### Cineradiographic recordings

For two individuals of *Clarias gariepinus* (47.5 and 51.7 mm CL) and two individuals of *Clariallabes longicauda* (32.4 and 34.7 mm CL) lateral X-ray film recordings (50 frames  $s^{-1}$ ) were made on Eastman 7231 Plus-X negative film (16 mm). X-rays were generated by a Siemens Tridoros 880 Optimatic (90 kV, 2 ms pulses). A Sirecon 2 image intensifier (17 cm diameter) with an Arriflex 16 mm ST camera (with a 70-mm lens) was placed at a distance of 1 m from the X-ray source. For each individual, ten recordings (five with cod and five with shrimp as prey) were analysed. Before the cineradiography, small metal markers were inserted subcutaneously or into the cranial bones at specific locations using hypodermic needles (Fig. 3). During implantation of these radio-opaque markers, the animals were anaesthetised with MS222 (Sandoz). The placement of the markers was checked using dorsoventral and lateral X-ray photographs, on which also measurements of the hyoid position and length were made for both species. Cineradiographic films were projected (Vanguard Instruments projector) on a HIPAD-digitiser, the position of each marker was digitised, and horizontal ( $x$ ) and vertical ( $y$ ) coordinates of each point were recorded for each frame. The coordinates were recalculated to a frame of reference moving with the neurocranium, with the horizontal axis parallel to the roof of the buccal cavity. Angles describing the position of the lower jaw, hyoid and cleithrum were measured with respect to this plane. Clockwise rotations are negative when fish are facing towards the right.

#### Kinematic variables

After digitisation of the sequences, the coordinates of each point were used to calculate the variables of interest. The kinematic plots allowed us to analyse movements of the lower jaw tip, hyoid tip, branchiostegal membrane and neurocranium on the high-speed

video recordings. After data filtering (Butterworth low-pass filter) and differentiation, peak velocities of jaw and hyoid movements were determined. On the cineradiographic recordings, movements of the lower jaw, hyoid, cleithrum (pectoral girdle) and neurocranium were analysed.

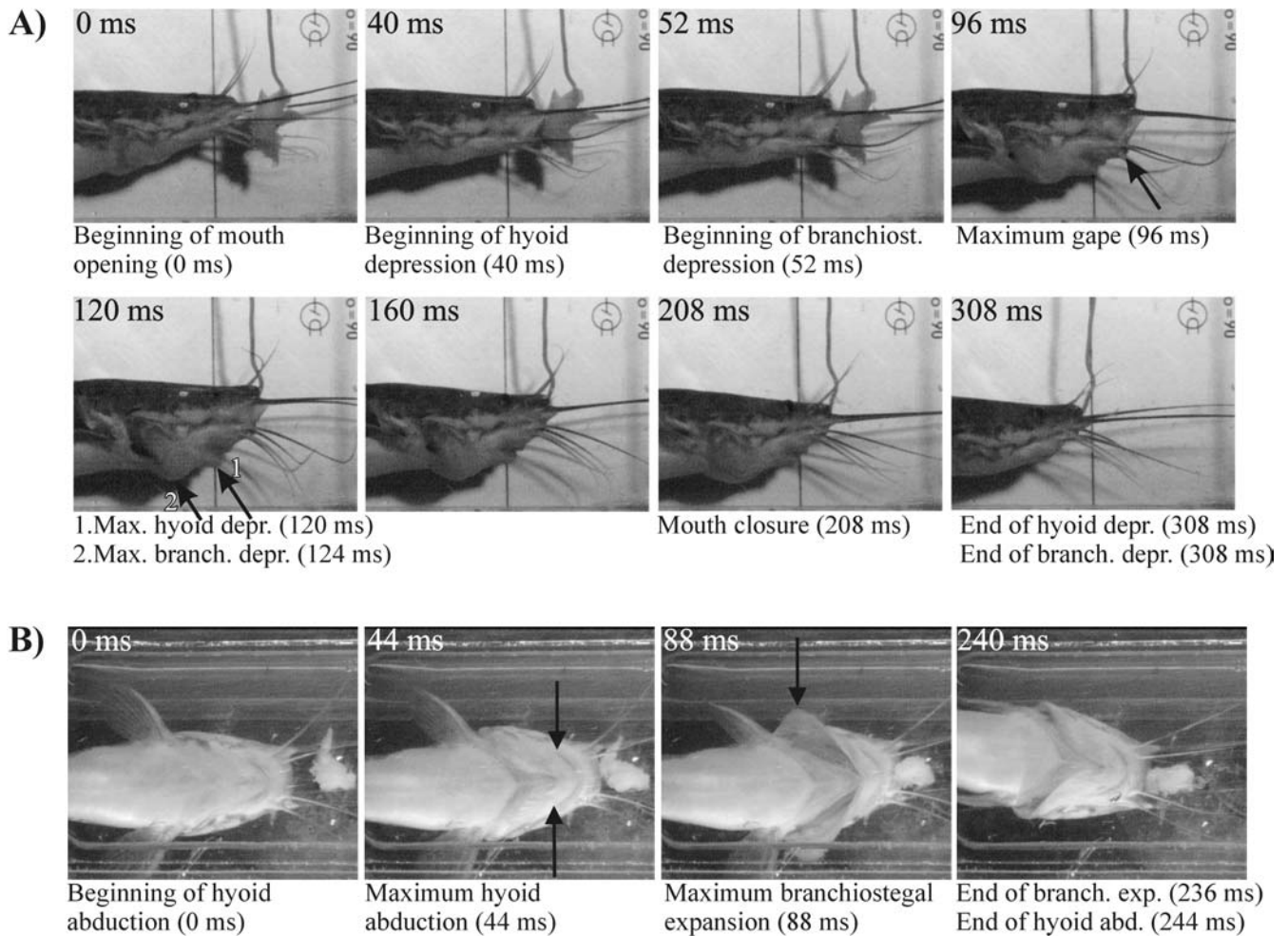
For the lateral high-speed video recordings, the following kinematic variables were analysed: the time (after the beginning of the mouth opening) at which (1) mouth opening, (2) hyoid depression and (3) branchiostegal depression (a) starts, (b) attains its maximal excursion and (c) ends; the displacement variables of (1) maximum gape angle (2) total hyoid depression (maximal depression minus starting position), (3) total depression of the branchiostegal membrane (maximum depression minus starting position) and (4) total neurocranial elevation; the velocity variables are (1) the maximal jaw opening velocity, (2) maximal jaw closing velocity, (3) maximal hyoid depression velocity and (4) maximal hyoid elevation velocity. Also the total duration of the entire prey capture sequence (beginning of mouth opening until end of recovery) was calculated from the timing variables. All timing variables of the lateral recordings are relative to the beginning of the mouth opening.

For the ventral high-speed video recordings, the following kinematic variables were analysed: the time at which (1) lateral hyoid expansion and (2) lateral branchiostegal expansion (a) starts, (b) attains its maximal excursion and (c) ends; displacements and angles including (1) the width of the hyoids at start (angle), (2) maximal width of hyoids (angle), (3) maximal lateral expansion of the hyoids (angle, maximal width minus starting width) and (4) the lateral expansion of the branchiostegal membrane (maximal excursion minus starting position); the velocity variables of (1) average angular hyoid abduction velocity and (2) average angular hyoid adduction velocity. All timing variables of the ventral recordings are relative to the beginning of the lateral expansion of the hyoids.

Cineradiographic recordings allowed us to analyse the movements of the hyoid, the cleithrum, the lower jaw and the neurocranium. Note that there were individual differences caused by the fact that the number of discernible markers differed among individuals. Although the same marking treatment was carried out for all of the test animals, some of the markers changed position, or were expelled from the skull between the period of marking and the recording sessions. As a result, data on hyoid movements are lacking for one *Clariallabes longicauda* individual. Marker placement was checked after each recording session.

#### Statistics

To test for effects of species and prey type on feeding kinematics, a principal components analysis (PCA) was performed on the kinematic variables of (1) the lateral high-speed video recordings and (2) the ventral high-speed video recordings. Two-way MANCOVAs were performed on the individual averages (within each prey type) of the varimax rotated principal component scores (PC scores) of the first two principal components, with species and prey type as independent variables. After comparing the eigenvalues of the principal components with 'broken stick' values, only the first two principal components were retained for further analysis (Jobson 1992). To compensate for body size differences between the individuals, cranial length was taken as a covariate in the MANCOVA (Richard and Wainwright 1995). Species effects were also tested univariately (ANCOVA). In that case, a sequential Bonferroni test was performed to adjust the significance level for these results. In all other cases, the significance level of  $P=0.05$  was used. All PC scores, as well as all kinematic variables used in (co)variance analyses were normally distributed (Kolmogorov-Smirnov test). To account for the scaling effects in interspecific comparison tests, linear displacements and angular and linear velocities were compared using two-way ANCOVAs (with cranial length as covariate). The (size-independent) angular displacement variables were compared by two-way ANOVAs. For all the analyses, the statistical package Statistica (v. 5.0; Statsoft, Tulsa) was used.



**Fig. 4A, B** Selected video frames from a representative lateral (A) and ventral (B) prey capture sequence for one individual of *Clarias gariepinus* feeding on an attached piece of cod. Numbers above the frame represent time in milliseconds relative to the beginning of the mouth opening for lateral images, or the beginning of the hyoid

expansion for the ventral images (time 0 ms). Below the frames, some important events are given with the exact time (in parentheses) at which these took place. Arrows indicate maximal excursions of the structures indicated

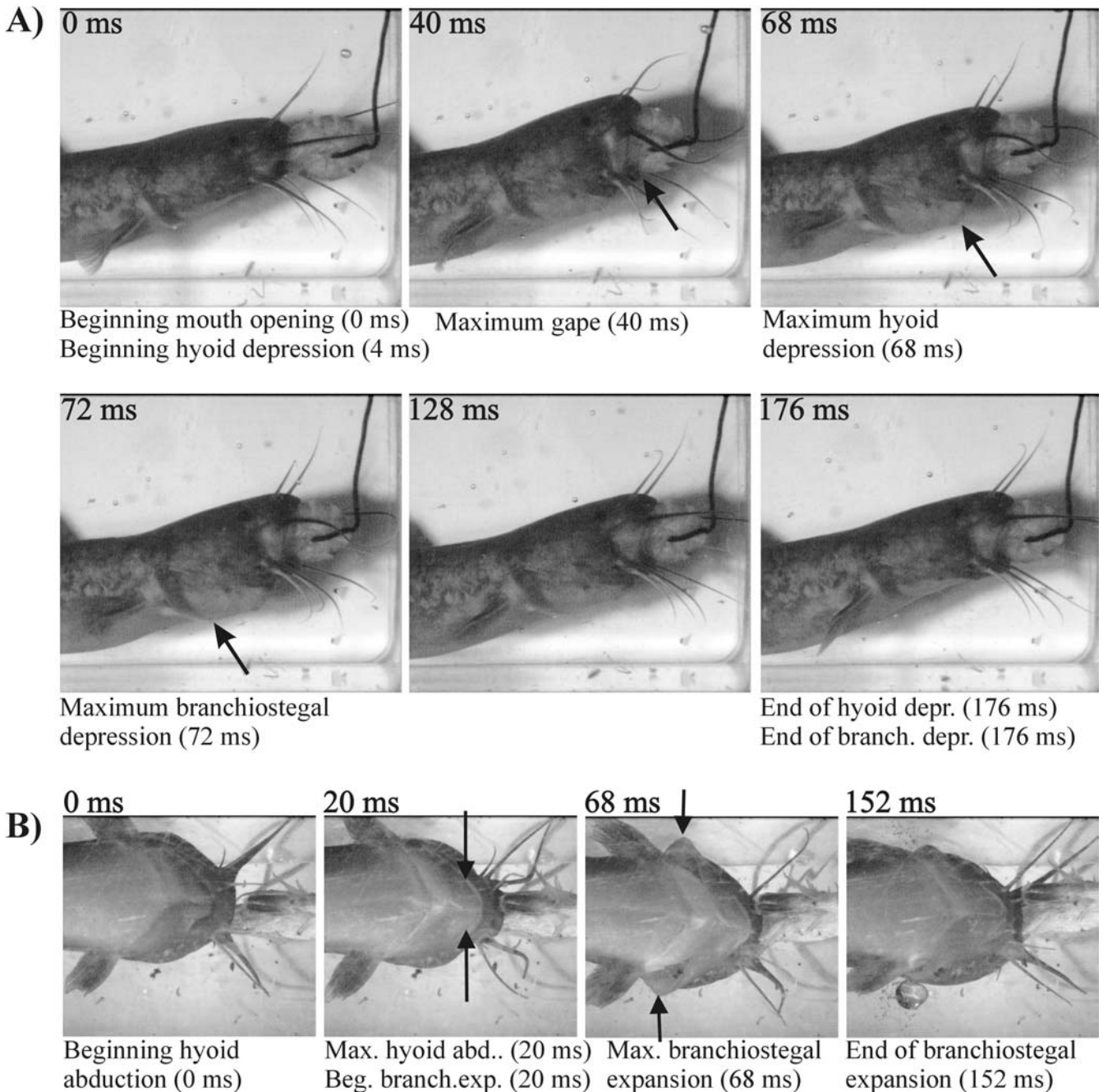
## Results

### Prey capture

The prey are captured by a combination of suction feeding and biting. In most cases, after the expansion of the skull, during which the prey is sucked towards the mouth, the jaws are placed firmly onto the prey (Figs. 4, 5). Next, the head is swung to one side, thereby tearing loose the attached pieces of food. Sometimes, when striking on a piece of cod, the suction was sufficient to draw the entire prey into the mouth. Touching of the prey with some of the barbels sometimes preceded the strike. While in most cases barbel touching was passive, occasional active touching could be discerned (one or two barbels being moved towards the prey). During prey capture, food items are approached relatively slowly. The maximum swimming speed during the strike never exceeded 0.22 m/s ( $n=100$  including both species). As

predicted for siluriform fishes in general (Alexander 1965), no protrusion of the upper jaws took place.

Both on lateral and ventral views, a rostrocaudal expansion wave is visible, which is typical for aquatic, suction feeding vertebrates (Muller and Osse 1984; Van Leeuwen and Muller 1984; Lauder 1985). In *Clarias gariepinus* for example, maximum gape (on average after 75 ms) precedes maximum hyoid depression (on average after 100 ms) and maximum branchiostegal depression (on average after 110 ms; Fig. 6). Rotation of the cleithrum (visible in the radiographic recordings) starts at the same time or shortly after the hyoid rotation. The cleithrum rotates (during retraction)  $-23.2 \pm 1.5^\circ$  (mean  $\pm$  standard error) in *Clarias gariepinus* and  $-23.0 \pm 1.3^\circ$  in *Clariallabes longicauda*. The opposite rotations of the hyoid and the cleithrum, by which these elements return to their initial positions, continue after mouth closure. The ventral recordings show a clear lateral expansion of the hyoids that is shortly followed by the highly mobile



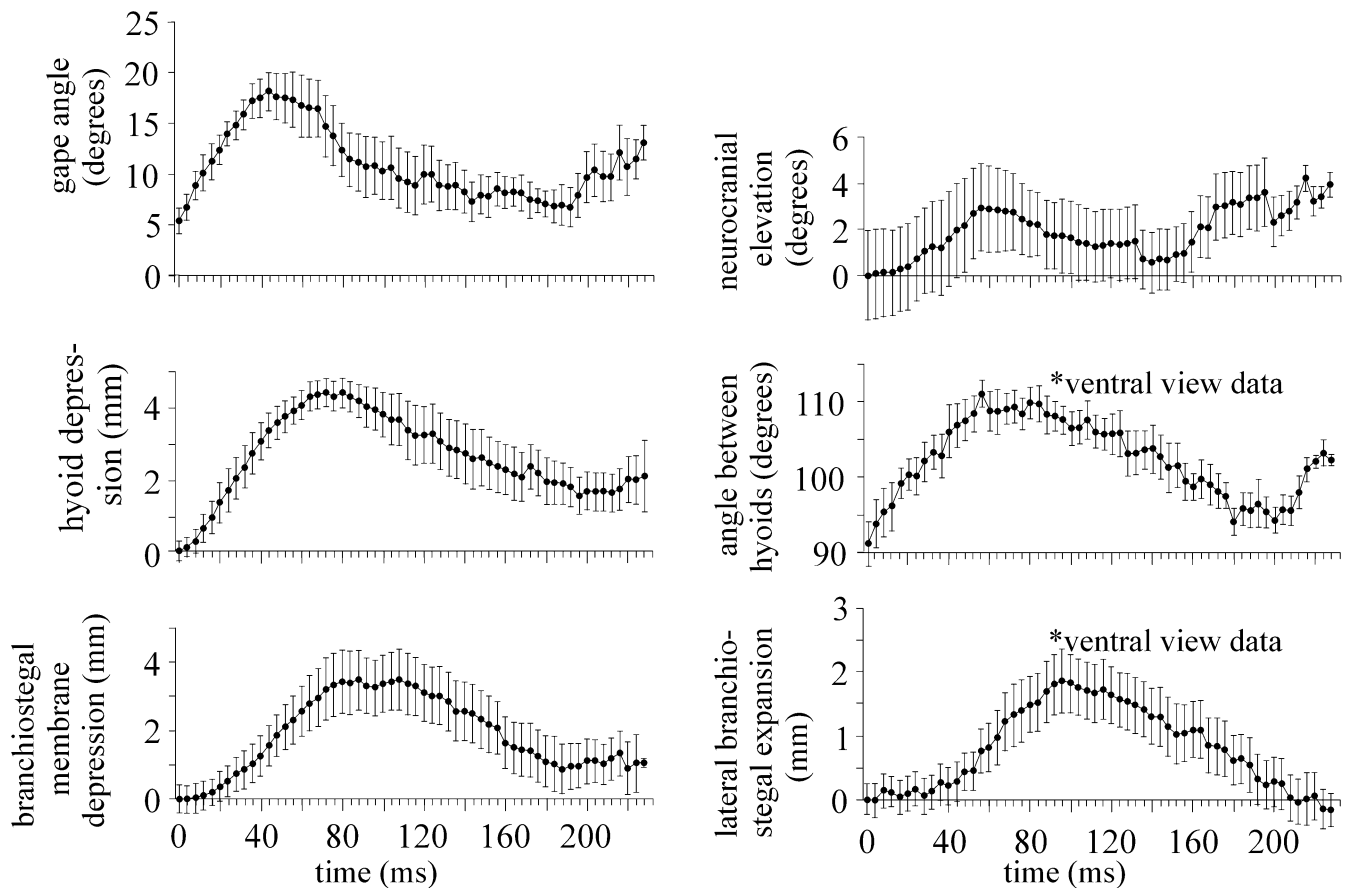
**Fig. 5A, B** Selected video frames from a representative lateral (**A**) and ventral (**B**) prey capture sequence for one individual of *Clariallabes longicauda* feeding on an attached shrimp. Numbers above the frame represent time in milliseconds relative to the beginning of the mouth opening for lateral images, or the beginning

of the hyoid expansion for the lateral images (time 0 ms). Below the frames, some important events are indicated with the exact time (in parentheses) at which these took place. Arrows indicate maximal excursions of the structures indicated

branchiostegal membranes. The total duration of the prey captures (the time from the beginning of the mouth opening until the recovery of the branchiostegal expansion) is 0.225 s for *Clarias gariepinus* and 0.196 s for *Clariallabes longicauda*. *Clariallabes longicauda* tends to feed at higher maximal gapes (gape angle:  $58.0 \pm 1.6^\circ$ , gape distance:  $0.179 \pm 0.009$  CLs) compared to *Clarias gariepinus* (gape angle:  $33.1 \pm 1.3^\circ$ , gape distance:

$0.340 \pm 0.010$  CLs). Examples of prey capture sequences of *Clarias gariepinus* and *Clariallabes longicauda* are given in Figs. 4 and 5, respectively.

Prey capture kinematics of *Clarias gariepinus* and *Clariallabes longicauda* are far from stereotyped. For the same prey, individual fish show an extensive variation in the timing and magnitude of the prey capture movements. The total duration of the strike, for example, varied from



**Fig. 6** Mean kinematic profiles, with standard error bars, of selected kinematic variables during prey capture in one individual *Clarias gariepinus* (cranial length=46.10 mm, total length=182.20 mm). Ten

capture events (five fish and five shrimp) are included in each profile. Time zero is defined as the beginning of mouth opening

208 to 376 ms and from 200 to 456 ms for two of the *Clarias gariepinus* individuals. The maximum gape distance varied from 11.8 to 17.8 mm and from 10.8 to 16.2 mm for these two individuals. This is also illustrated by the relatively large standard errors on the mean kinematic profiles of one individual (Fig. 6).

The average neurocranial elevation is  $6.3 \pm 0.8^\circ$  in *Clarias gariepinus* and  $10.6 \pm 1.0^\circ$  in *Clariallabes longicauda*, although during several strikes both species reached neurocranial elevations of more than  $25^\circ$ .

#### General interspecific comparison

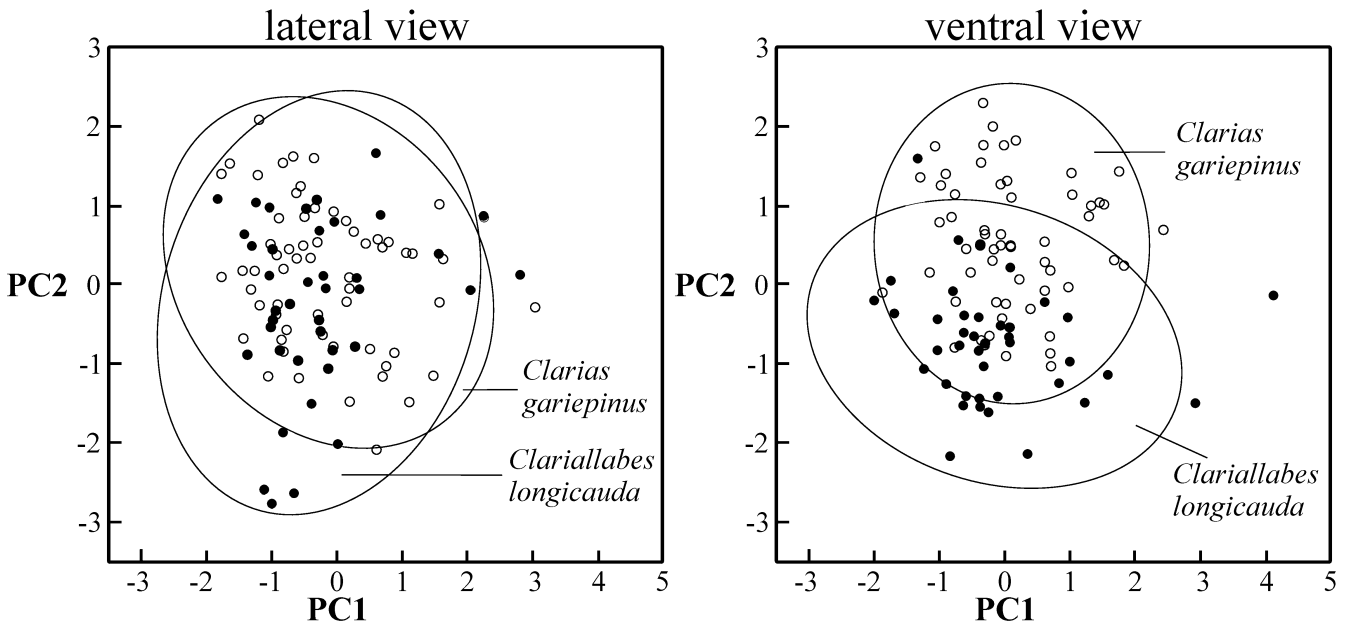
To determine whether the prey captures of *Clarias gariepinus* and *Clariallabes longicauda* are kinematically distinct, the two species were compared using a principal component analysis (Fig. 7; Table 1).

The two species do not differ significantly based on the movements observed on the lateral external images (two-way MANCOVA, Rao's  $R_{2,14}=4.02$ ,  $P=0.26$ ). Consequently, it is not possible to make a clear distinction between the general prey capture kinematics of both species from the lateral view data.

On the basis of the movements observed on the ventral images, however, both species do differ significantly (two-way MANCOVA, Rao's  $R_{2,14}=7.15$ ,  $P=0.007$ ). This difference is significant for PC1 (one-way ANCOVA,  $F_{1,15}=4.63$ ,  $P=0.048$ ) as well as for PC2 (one-way ANCOVA,  $F_{1,15}=13.8$ ,  $P=0.0021$ ). PC1 mainly represents variation in the timing of the hyoid expansion and the branchiostegal expansion, while PC2 mainly represents variation in the starting angle between the hyoid bars and in the total dilatation of the hyoid (Table 1). Apparently, the most important differences in prey capture kinematics, by which it is possible to distinguish prey captures of both catfish species, are the lateral movements of the hyoid bars seen from the ventral view. Indeed, *Clariallabes longicauda* has larger hyoid angles at the start of the prey capture sequence ( $101.0 \pm 1.1^\circ$  versus  $86.4 \pm 1.2^\circ$  for *Clarias*) and showed less lateral expansion of the hyoid ( $19.0 \pm 1.2^\circ$  versus  $31.1 \pm 1.2^\circ$  for *Clarias*) (Table 2).

#### Lateral expansions

As mentioned, *Clariallabes longicauda* shows less lateral expansion during suction feeding compared to *Clarias*



**Fig. 7** Plots of the principal component scores of the first two principal components (*PC1* and *PC2*). Principal component analyses were performed on the data sets of the lateral (*left graph*) and ventral recordings (*right graph*). Principal component scores were subdivided by species (*white points* = *Clarias gariepinus*, *black points* = *Clariallabes longicauda*) and plotted with the 95%

confidence limit ellipses for each species. Covariance analysis (MANCOVA) showed that *Clarias gariepinus* and *Clariallabes longicauda* do not differ significantly in lateral prey capture kinematics. However, they do differ significantly in ventral prey capture kinematics on both *PC1* and *PC2*

**Table 1** Results from the principal component analysis on two data sets: (a) lateral external and (b) ventral external recordings. Factor loadings exceeding 0.70 are indicated in *bold*. (*B* Branchiostegal membrane, *dep* depression, *elev* elevation, *exp* expansion, *H* hyoid, *max* maximum, *N* neurocranium, *M* mouth, *vel* velocity)

	Lateral external		Ventral external	
	PC1	PC2	PC1	PC2
Eigenvalue	7.85	2.46	3.59	2.48
Percentage of total variance	46.2	14.5	32.7	22.5
Broken stick	3.44	2.44	3.02	2.02
Time max gape	<b>0.804</b>	0.283	Time max H exp	<b>0.896</b>
Time end gape	<b>0.870</b>	0.253	Time end H exp	<b>0.908</b>
Time begin H dep	0.165	0.104	Time begin B exp	0.426
Time max H dep	<b>0.834</b>	0.337	Time max B exp	<b>0.754</b>
Time end H dep	<b>0.902</b>	0.167	Time end B exp	<b>0.793</b>
Time begin B dep	0.504	0.030	Begin angle H	-0.106
Time max B dep	<b>0.783</b>	0.342	Max angle H	-0.009
Time end B dep	<b>0.893</b>	0.243	Total exp H	0.105
Total duration	<b>0.919</b>	0.199	Total B exp	0.167
Max gape	-0.036	-0.354	Average vel H exp	-0.614
Total H dep	0.588	-0.501	Average vel H add	-0.247
Total B dep	0.149	0.009		
Total N elev	0.059	0.121		
Peak vel M open	-0.378	-0.659		
Peak vel M closing	0.310	<b>0.757</b>		
Peak vel H dep	-0.278	<b>-0.793</b>		
Peak vel H elev	0.246	<b>0.741</b>		

*gariepinus*. This lateral expansion was measured by the increase in the angle between the hyoid bars (also referred to as the dilatation or widening of the hyoid) during the expansive phase of the feeding event. The average hyoid dilatation is reduced in *Clariallabes longicauda* ( $19.0 \pm 1.2^\circ$ ) compared to *Clarias gariepinus* ( $31.1 \pm 1.2^\circ$ ) (Table 2). The maximal observed values for lateral expansions are also lower in *Clariallabes longicauda* ( $41.2^\circ$  versus  $51.2^\circ$  for *Clarias gariepinus*). In *Clariallabes*

*longicauda*, the hyoid starts its lateral expansion on average with a larger angle between the hyoid bars ( $101.0 \pm 1.1^\circ$  versus  $86.4 \pm 1.2^\circ$  for *Clarias gariepinus*, see Table 2), but merely reaches similar maximal angles ( $119.9 \pm 1.1^\circ$  versus  $117.6 \pm 0.8^\circ$  for *Clarias gariepinus*). The average velocities of hyoid abduction (as well as adduction velocities) tend to be larger in *Clarias gariepinus* (Table 2). As the dilatation of the hyoids is directly coupled to the abduction of the suspensoria, and



**Table 2** Interspecific comparison of the hyoid movements. Significant *P* values after sequential Bonferroni adjustment are indicated in *bold*. The high-speed video data include six individuals of

*Clarias* and four of *Clariallabes*. The cineradiographic data include two individuals of *Clarias* and one of *Clariallabes*. (CL Cranial lengths, ° degrees)

	<i>Clarias gariiepinus</i>	<i>Clariallabes longicauda</i>	Statistics	Significance
Lateral (high-speed video)				
Average hyoid depression (CL)	0.152±0.006	0.210±0.001	ANCOVA, $F_{1,15}=4.63$	<i>P</i> =0.048
Maximal hyoid depression (CL)	0.26	0.33	ANCOVA, $F_{1,15}=4.54^a$	<i>P</i> =0.049
Mean peak velocity of hyoid depression (CL/s)	2.77±0.13	5.56±0.40	ANCOVA, $F_{1,15}=7.77$	<i>P</i> =0.014
Maximal peak velocity of hyoid depression (CL/s)	5.69	12.38	ANCOVA, $F_{1,15}=5.77^a$	<i>P</i> =0.030
Mean peak velocity of hyoid elevation (CL/s)	1.79±0.09	2.46±0.21	ANCOVA, $F_{1,15}=1.87$	<i>P</i> =0.19
Maximal peak velocity of hyoid elevation (CL/s)	3.82	7.42	ANCOVA, $F_{1,15}=1.02^a$	<i>P</i> =0.33
Lateral (cineradiographic film)				
Average starting angle hyoid (°) <sup>b</sup>	12.2±2.2	0.0±2.5	ANOVA, $F_{1,2}=11.5$	<i>P</i> =0.077
Average peak angle hyoid (°) <sup>b</sup>	-43.3±2.8	-49.8±3.3	ANOVA, $F_{1,2}=1.69$	<i>P</i> =0.32
Maximal peak angle hyoid (°) <sup>b</sup>	-62.5	-70.3	ANOVA, $F_{1,2}=4.33^a$	<i>P</i> =0.17
Average total rotation hyoid (°)	-55.6±2.6	-49.8±3.5	ANOVA, $F_{1,2}=12.7$	<i>P</i> =0.071
Ventral (high-speed video)				
Average starting angle hyoids (°)	86.4±1.2	101.0±1.1	ANOVA, $F_{1,16}=20.9$	<b><i>P</i>=0.00031</b>
Average peak angle hyoids (°)	117.6±0.8	119.9±1.1	ANOVA, $F_{1,16}=1.50$	<i>P</i> =0.24
Average hyoid dilatation (°)	31.1±0.8	19.0±1.2	ANOVA, $F_{1,16}=20.2$	<b><i>P</i>=0.00037</b>
Maximal hyoid dilatation (°)	51.2	41.2	ANOVA, $F_{1,16}=10.3^a$	<i>P</i> =0.0055
Average abduction velocity (°/s)	404±22	347±38	ANCOVA, $F_{1,15}=6.46$	<i>P</i> =0.0226
Maximal abduction velocity (°/s)	943	1,146	ANCOVA, $F_{1,15}=6.00^a$	<i>P</i> =0.027
Average adduction velocity (°/s)	315±25	232±21	ANCOVA, $F_{1,15}=8.87$	<i>P</i> =0.0094
Maximal adduction velocity (°/s)	1,251	602	ANCOVA, $F_{1,15}=4.30^a$	<i>P</i> =0.056

<sup>a</sup> Individual maxima for both prey types included

<sup>b</sup> Angle with respect to the roof of the buccal cavity

given the configuration of the hyoids at the starting position of the feeding event, the larger and faster abduction of the hyoids can be translated into a larger and faster suspensorium abduction.

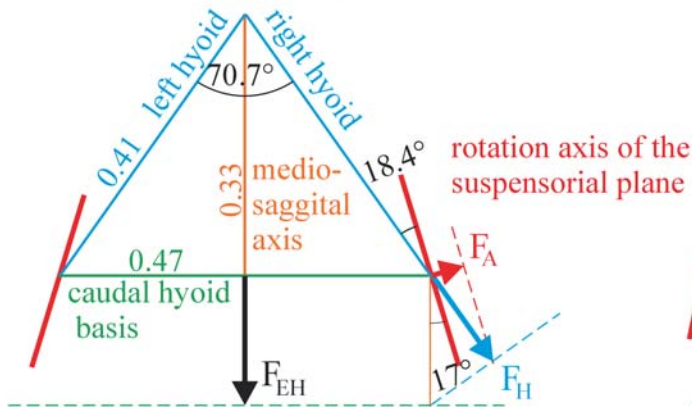
### Hyoid movements

The hyoid movements for both species, analysed from lateral and ventral views, are compared in Table 2. For a given skull size, a more extensive lowering of the mouth floor by the hyoid is observed in *Clariallabes longicauda* (0.210±0.001 CLs) compared to *Clarias gariiepinus* (0.152±0.006 CLs). The speed by which the hyoid depression lowers the mouth floor is also larger in *Clariallabes longicauda*. The cineradiographic recordings show angular depressions of the hyoid that start shortly after the beginning of the lower jaw depression (also observed for larval *Clarias gariiepinus* by Adriaens et al. 2001). In *Clarias gariiepinus*, the hyoid starts its rotation in most cases (17 out of 20) slightly elevated (12±2.2°) with respect to a plane parallel to the roof of the buccal cavity (Fig. 3) and shows an average rotation of -55.6±2.6°. In *Clariallabes longicauda*, the hyoid starts its rotation parallel with the roof of the buccal cavity (0.0±2.5°) and rotates on average -49.8±3.5°. The maximal angle of hyoid depression is on average larger in *Clariallabes longicauda* (49.8±3.3° versus 43.3±2.8° in *Clarias gariiepinus*).

### Discussion

Several studies have proposed that the anatomical changes enhancing biting forces could decrease the amount of suction (Barel 1983; De Visser and Barel 1996, 1998; Bouton et al. 1999; see also Ferry-Graham et al. 2001). Fishes whose jaw apparatus is highly specialised for biting are distinct in many aspects of their cranial morphology (see, for example, Barel 1983) and muscle activity patterns during feeding (Alfaro et al. 2001) from fishes that only use suction feeding. This indicates a potential incompatibility of optimising both functions. Furthermore, recent models have suggested a functional trade-off between biting and suction performance mediated by modifications of the hyoid apparatus (De Visser and Barel 1996, 1998). In these studies, it is argued that cichlid fishes that are able to produce high biting forces cannot have the left and right hyoid bars close to one another medially. In this condition in which the hyoid bars include only a small angle, the depression of the hyoid apparatus initially causes no outward rotation of the suspensorium, suction is presumed to be most efficient. However, no experimental data have yet demonstrated these predictions. It is also unknown if the same architectural differences in the cranial system are present in other groups of fishes besides cichlids. Although never mentioned in literature, the morphological differences between species with and without jaw adductor hypertrophy illustrated in Fig. 1 can also have a direct effect on suction feeding mechanics by limiting lateral expansion of the buccal cavity. In the present study, we tested

## *Clarias gariepinus*



**Fig. 8** Schematic planar representation of the hyoid's starting configuration (blue lines) and the interconnection with the suspensorium (red lines represent the rotation axis) from a dorsoventral view in *Clarias gariepinus* and *Clariallabes longicauda*. Specific distances (in cranial lengths) and angles are given for both species. For a given expansion force in the hyoid plane ( $F_{EH}$ , black arrow),

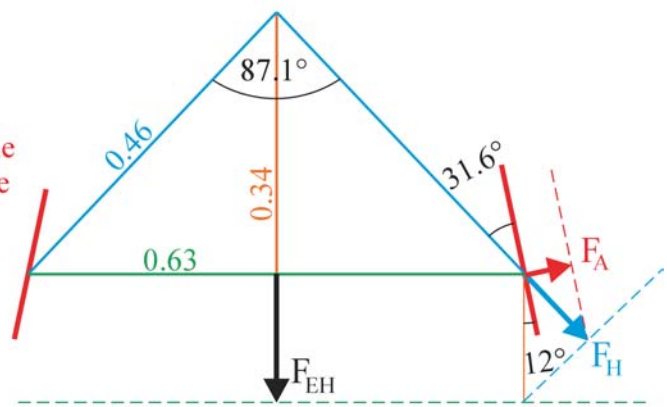
whether the increase of the jaw closing muscle dimensions combined with fortifications of the connection of the suspensorium to the neurocranium reduce the potential for lateral expansion of the buccal cavity in clariid catfishes.

### Differences in lateral expansion

As predicted, the lateral expansion capacity is reduced during suction feeding in the species with hypertrophied jaw closers (*Clariallabes longicauda*) compared to the species without this hypertrophy (*Clarias gariepinus*). Most likely, this effect is caused by the striking morphological differences illustrated in Fig. 1. The presence of an increased jaw muscle mass covering a large part of the side of the skull, combined with the reinforced articulation of the suspensorium with the neurocranium, apparently has consequences on the buccal expansion mechanics during suction feeding in these clariid catfishes.

The average speed of dilatation of the hyoid apparatus, which is directly coupled to the lateral expansions, is also reduced in the species with the jaw adductor hypertrophy (Table 2). We suggest that this reduced abduction velocity is caused by the enlarged adductor muscles, rather than by the interdigitating bony processes at the suspensorial articulation surface. Given the viscoelastic nature of the jaw closers and the fact that this muscle extends beyond the boundaries of the suspensorium, deformation of this muscle mass as a result of suspensorium abduction will have a speed-reducing effect on this movement. On the other hand, the “locking” of the suspensorial articulation through interdigitation processes would probably only limit the maximal rotation capacity of the suspensorium

## *Clariallabes longicauda*



the force component along the hyoid ( $F_H$ , blue arrow) and the force resulting in suspensorial abduction ( $F_A$ ) are shown. In *Clariallabes longicauda*,  $F_A$  at the beginning of the hyoid retraction is expected to be about 40% higher compared to *Clarias gariepinus* (see also Table 3)

presumably without interfering with the speed of expansion. Notably, also the opposite movement, the adduction of the hyoid bars and consequent adduction of the suspensorium, has a reduced average velocity in *Clariallabes longicauda* compared to *Clarias gariepinus* (Table 2).

### Abduction forces

The hyoid apparatus plays a crucial role in the expansive phase of the suction feeding event, not only because of its contribution to the depression of the mouth floor and (indirectly) to the opening of the mouth, but also because it participates in the lateral expansion of the oral cavity (i.e. suspensorium abduction; Lauder 1985; Aerts et al. 1987; Aerts 1991; De Visser and Barel 1996). Contraction of the sternohyoideus muscle results in retraction and depression of the hyoid and produces important passive reaction forces at the level of the interconnection of the hyoid with the suspensorium. It is commonly assumed that during strenuous activities such as suction feeding the abduction forces originate mainly from the hyoid (Alexander 1970; Aerts 1991). Therefore, the position of the hyoid is an important determinant of the distribution of the expansive forces over the expansion movements (De Visser and Barel 1996).

When comparing the shape and the position of the hyoid apparatus of *Clarias gariepinus* and *Clariallabes longicauda*, we expect larger abduction forces to be transmitted by the hyoid onto the suspensorium in the latter species (Fig. 8). The starting configuration of the hyoids, as well as the orientation of the rotation axis of the suspensorial plane differ between both species. *Clariallabes longicauda* has a broader hyoid with a larger

**Table 3** Properties of the sternohyoideus muscles of *Clarias gariepinus* and *Clariallabes longicauda*. All values are represented in cranial lengths (CL) to enable the comparison. Effective physiological cross-section=mass $\times$ cos(fibre inclination)/fibre length

Species	Mass (10 <sup>-6</sup> CL <sup>3</sup> ) <sup>a</sup>	Average fibre length (CL) <sup>a</sup>	Average muscle fibre inclination (degrees) <sup>b</sup>	Effective physiological cross-section (10 <sup>-6</sup> CL <sup>2</sup> )
<i>Clarias gariepinus</i>	2.4 $\pm$ 0.2	0.267 $\pm$ 0.01	13.5	8.6
<i>Clariallabes longicauda</i>	10.6 $\pm$ 1.9	0.292 $\pm$ 0.09	23.9	33.1

<sup>a</sup>  $n=3$ <sup>b</sup> Angle with respect to the mediosagittal axis of the skull, which represents the line of action of the sternohyoideus

angle between the hyoid bars (87.1 $\pm$ 4.0 $^\circ$  versus 70.7 $\pm$ 3.3 $^\circ$  in *Clarias gariepinus*) and a rotation axis of the suspensorial plane that is more parallel to the mediosagittal axis of the skull (12 $^\circ$  versus 17 $^\circ$  in *Clarias gariepinus*). Both features contribute to a larger angle between the hyoid bars and the suspensorial rotation axis and by this means also to an increased transmission of the retraction force of the hyoids to forces resulting in suspensorial abduction (Fig. 8).

Not only the transmission of forces from the hyoid onto the suspensorium is expected to be larger in *Clariallabes longicauda*, but also the retraction forces themselves ( $F_{EH}$  in Fig. 8). When comparing the properties of the sternohyoideus muscle, the muscle that retracts the hyoid (Table 3), a considerably higher muscle mass is found for *Clariallabes longicauda* compared to *Clarias gariepinus*. Even though the sternohyoideus muscle fibres are slightly longer and on average more inclined (Table 3), the over four times higher mass of this muscle (for a given skull length) will cause a more forceful retraction of the hyoid (during sternohyoideus activity) for this species (effective physiological cross-section of 33.1 10<sup>-6</sup> CL<sup>2</sup> versus 8.6 10<sup>-6</sup> CL<sup>2</sup> for *Clarias gariepinus*).

As the abduction forces exerted by the hyoid onto the suspensorium are thus larger in the species with the reduced lateral expansion (*Clariallabes longicauda*), this difference cannot be explained by differential abduction forces. This result further strengthens the notion that the lateral expansions are constrained or counteracted by structures increasing the mechanical resistance to this movement.

#### Compensating effects on buccal expansions

A reduced lateral expansion does not necessarily imply a reduced suction feeding efficiency. The observed decrease in the magnitude and the velocity of the lateral expansion in *Clariallabes longicauda* compared to *Clarias gariepinus* can be compensated for by more extensive and faster ventral expansions (lowering of the floor of the mouth). This would not be surprising, as the simultaneous lateral expansion of the hyoid and the ventral lowering of the mouth floor by the hyoid causes a mechanical trade-off between lateral and ventral buccal expansions. If there is no lateral expansion, the hyoid apparatus will maintain its initial configuration. In that case, its full mediosagittal

length can contribute to the lowering of the mouth floor. The other extreme would be a lateral expansion that abducts the hyoid apparatus so that both hyoid bars lie in each other's extensions. In that case, there will be no hyoid depression at all (see also Diogo and Chardon 2000).

As expected, the reduced dilatation of the hyoids in *Clariallabes longicauda* (19.0 $\pm$ 1.2 $^\circ$  versus 31.1 $\pm$ 1.2 $^\circ$  for *Clarias gariepinus*) goes along with a more extensive depression of the mouth floor by the hyoid (0.210 $\pm$ 0.001 CLs versus 0.152 $\pm$ 0.006 CLs for *Clarias gariepinus*). However, the difference in mouth floor depression is too large (38%) to be explained solely by the differences in hyoid dilatation. If the hyoid apparatus with initially a similar mediosagittal length (0.33 $\pm$ 0.02 CLs in *Clarias gariepinus* and 0.34 $\pm$ 0.03 CLs in *Clariallabes longicauda*) is dilated as observed (Table 2) and equally depressed to an angle of -45 $^\circ$  (relative to the roof of the buccal cavity), an increase of only 7% in mouth floor depression can be expected. Therefore an additional factor, besides this mechanical consequence of the reduced hyoid dilatation, must have contributed to the increased mouth floor depression by the hyoid in *Clariallabes longicauda*. This factor most likely involves an increased angular depression of the hyoid apparatus. Indeed, the cineradiographic data point out that the hyoid is depressed to larger angles with respect to the roof of the skull in *Clariallabes longicauda* compared to *Clarias gariepinus*. The combined effect of the reduced shortening of the hyoid by lateral expansions and an increased angular depression of the hyoid can cause substantially larger mouth floor depressions.

Suction in fishes implies the generation of a water flow into the mouth cavity. Consequently, suction feeding performance can be estimated by two variables: (1) the total volume of the water drawn into the buccal cavity, which is related to the magnitude of buccal expansions, and (2) the velocity of the water entering the mouth, which is related to the rate of expansion of the buccal cavity and the size of the oral aperture (Muller et al. 1982; Van Leeuwen and Muller 1984; Wainwright et al. 2001). As mentioned, the reduced magnitude of the lateral expansions are (at least partly) compensated for by the larger depression of the mouth floor by the hyoid. Yet, as *Clariallabes longicauda* also has a reduced average velocity of this lateral expansion (see Table 2), this can still result in a reduced velocity of the water sucked in. Moreover, *Clariallabes longicauda* feeds using larger

maximal gape distances ( $0.340 \pm 0.010$  CLs versus  $0.179 \pm 0.009$  CLs for *Clarias gariepinus*), which also reduces the speed of water inflow. Therefore, the observed higher peak velocity of hyoid depression in *Clariallabes longicauda* (see Table 2) will be of great importance to preserve a sufficient speed of the water entering the mouth.

## Conclusion

Buccal expansions during suction feeding clearly differ between the species without hypertrophied jaw adductors (*Clarias gariepinus*) and the species with hypertrophied jaw adductors (*Clariallabes longicauda*). The predicted consequence (i.e. the reduced lateral expansion in the species that exhibits these enlarged adductors) is confirmed, even despite the fact that the abduction forces exerted by the hyoid onto the suspensorium are larger in this species. The reduced lateral expansion is compensated for by a more extensive and faster lowering of the mouth floor by the hyoid. Therefore, the results of the present study support the notion that features of the cranial system in favour of an increased biting force (larger adductor muscles, stronger bony connections between skeletal elements) will have consequences on suction feeding mechanics (though not necessarily on suction feeding performance). Thus, morphological specialisation has consequences on other functions performed by the same system, as the same structures have to participate in different functions (for example, prey capture, swallowing, aquatic respiration, air breathing). In other words, changing the features of one of the components of the system can alter the mechanics of several, structurally coupled functions of this system. Not only effects on prey capture mechanics, but also on other functions performed by the complex cranial system, such as aquatic respiration and air breathing can be expected. Air breathing catfishes (Clariidae), exhibiting a rich structural diversity, are particularly suitable to investigate the effects of variation in morphology (degree of jaw adductor hypertrophy) in a complex integrated system (cranial musculoskeletal apparatus of teleost fish).

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## References

- Adriaens D, Verraes W (1996) Ontogeny of cranial musculature in *Clarias gariepinus* (Siluroidei: Clariidae): the adductor mandibulae complex. *J Morphol* 229:255–269
- Adriaens D, Verraes W (1997) Ontogeny of the hyoid musculature in the African catfish, *Clarias gariepinus* (Burchell, 1822) (Siluroidei: Clariidae). *Zool J Linn Soc* 121:105–128
- Adriaens D, Aerts P, Verraes W (2001) Ontogenetic shift in mouth opening mechanisms in a catfish (Clariidae, Siluriformes): a response to increasing functional demands. *J Morphol* 247:197–216
- Aerts P (1991) Hyoid morphology and movements relative to abducting forces during feeding in *Astatotilapia elegans* (Teleostei: Cichlidae). *J Morphol* 208:323–345
- Aerts P, Osse JWM, Verraes W (1987) Model of jaw depression during feeding in *Astatotilapia elegans* (Teleostei: Cichlidae): mechanisms for energy storage and triggering. *J Morphol* 194:85–109
- Alexander RMCN (1965) Structure and function in catfish. *J Zool Lond* 148:88–152
- Alexander RMCN (1970) Mechanics of the feeding action of various teleost fishes. *J Zool Lond* 162:145–156
- Alfaro ME, Janovetz J, Westneat MW (2001) Motor control across trophic strategies: muscle activity of biting and suction feeding fishes. *Am Zool* 41:1266–1279
- Barel CDN (1983) Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Neth J Zool* 33:357–424
- Bouton N, Witte F, Van Alphen JJM, Schenk A, Seehausen O (1999) Local adaptations in populations of rock-dwelling haplochromines (Pisces: Cichlidae) from southern Lake Victoria. *Proc R Soc Lond B* 266:355–360
- Brunton 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. *Trans Zool Soc Lond* 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*. *J Morphol* 240:169–194
- Devaere S, Adriaens D, Verraes W, Teugels GG (2001) Cranial morphology of the anguilliform clariid *Channallabes apus* (Günther, 1873) (Teleostei: Siluriformes): are adaptations related to powerful biting? *J Zool Lond* 255:235–250
- De Visser J, Barel CDN (1996) Architectonic constraints on the hyoid's optimal starting position for suction feeding of fish. *J Morphol* 228:1–18
- De Visser J, Barel CDN (1998) The expansion apparatus in fish heads, a 3-D kinetic deduction. *Neth J Zool* 48:361–395
- Diogo R, Chardon M (2000) Anatomie et fonction des structures céphaliques associées à la prise de nourriture chez le genre *Chrysichthys* (Téléostei: Siluriformes). *Belg J Zool* 130:21–37
- Ferry-Graham LA (1998) Effects of prey size and mobility on prey-capture kinematics in Leopard sharks *Triakis semifasciata*. *J Exp Biol* 201:2433–2444
- Ferry-Graham LA, Wainwright PC, Westneat MW, Bellwood DR (2001) Modulation of prey capture kinematics in the Cheek-lined Wrasse *Oxycheilinus digrammus* (Teleostei: Labridae). *J Exp Zool* 290:88–100
- Herrel A, Adriaens D, Verraes W, Aerts P (2002) Bite performance in clariid fishes with hypertrophied jaw adductors as deduced by bite modelling. *J Morphol* 253:196–205
- Jobson JD (1992) Principal components, factors and correspondence analysis. In: Fienberg S, Olkin I (eds) Applied multivariate data analysis, vol 2. Categorical and multivariate methods. Springer, Berlin Heidelberg New York, pp 345–482
- Lauder GV (1981) Intraspecific functional repertoires in the feeding mechanism of the characoid fishes *Lebiasina*, *Hoplias*, and *Chalceus*. *Copeia* 1981:154–168
- Lauder GV (1985) Aquatic feeding in lower vertebrates. In: Hildebrand M, Bramble DM, Liem KF, Wake DB (eds)

- Functional vertebrate morphology. Belknap (Harvard University Press), Cambridge, MA, pp 210–229
- Liem KF (1980) Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am Zool* 20:295–314
- Liem KF (1993) Ecomorphology of the teleostean skull. In: Hanken J, Hall BK (eds) *The skull*, vol 3. Functional and evolutionary mechanisms. University of Chicago Press, Chicago, pp 422–452
- Muller M, Osse JWM (1984) Hydrodynamics of suction feeding in fish. *Trans Zool Soc (Lond)* 37:51–135
- Muller M, Osse JWM, Verhagen JHG (1982) A quantitative hydrodynamical model of suction feeding in fish. *J Theor Biol* 95:49–79
- Nemeth DH (1997) Modulation of buccal pressure during prey capture in *Hexagrammos decagrammus* (Teleostei: Hexagrammidae). *J Exp Biol* 200:2145–2154
- Ralston KR, Wainwright PC (1997) Functional consequences of trophic specialization in pufferfishes. *Funct Ecol* 11:43–52
- Richard BA, Wainwright PC (1995) Scaling the feeding mechanism of largemouth Bass (*Micropterus salmoides*): kinematics of prey capture. *J Exp Biol* 198:419–433
- Teugels GG (1996) Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): an overview. *Aquat Living Resour* 9(hors série):9–34
- Teugels GG, Adriaens D (2003) Taxonomy and phylogeny of Clariidae. An overview. In: Arratia G, Kapoor AS, Chardon M, Diogo R (eds) *Catfishes*, vol I. Science Publishers, Enfield, pp 465–487
- Turingan RG, Wainwright PC (1993) Morphological and functional bases of durophagy in the queen triggerfish, *Ballistes vetula* (Pisces, Tetraodontiformes). *J Morphol* 215:101–118
- Van Leeuwen JL, Muller M (1984) Optimum sucking techniques for predatory fish. *Trans Zool Soc Lond* 37:137–169
- Wainwright PC, Lauder GV (1986) Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zool J Linn Soc* 88:217–228
- Wainwright PC, Ferry-Graham LA, Waltzek TB, Carroll AM, Hulsey CD, Grubich JR (2001) Evaluating the use of ram and suction during prey capture by cichlid fishes. *J Exp Biol* 204:3039–3051