

# Bite Performance in Clariid Fishes With Hypertrophied Jaw Adductors as Deduced by Bite Modeling

Anthony Herrel,<sup>1\*</sup> Dominique Adriaens,<sup>2</sup> Walter Verraes,<sup>2</sup> and Peter Aerts<sup>1</sup>

<sup>1</sup>Department of Biology, University of Antwerp (UIA), Antwerp, Belgium

<sup>2</sup>Institute of Zoology, University of Ghent, Ghent, Belgium

**ABSTRACT** Within clariid fishes several cranial morphologies can be discerned. Especially within anguilliform representatives an increase in the degree of hypertrophy of the jaw adductors occurs. The hypertrophy of the jaw adductors and skeletal modifications in the cranial elements have been linked to increased bite force. The functional significance of this supposed increase in bite force remains obscure. In this study, biomechanical modeling of the cranial apparatus in four clariid representatives showing a gradual increase in the hypertrophy of the jaw adductors (*Clarias gariepinus*, *Clariallabes melas*, *Channallabes apus*, and *Gymnallabes typus*) is used to investigate whether bite force actually increased. Static bite modeling shows that the apparent hypertrophy results in an in-

crease in bite force. For a given head size, the largest bite forces are predicted for *C. apus*, the lowest ones for *C. gariepinus*, and intermediate values are calculated for the other species. In addition, also in absolute measures differences in bite force remain, with *C. apus* biting distinctly harder than *C. gariepinus* despite its smaller head size. This indicates that the hypertrophy of the jaw adductors is more than just a correlated response to the decrease in absolute head size. Further studies investigating the ecological relevance of this performance difference are needed. *J. Morphol.* 253:196–205, 2002.

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**KEY WORDS:** biting; modeling; catfish; jaw adductors

The air-breathing catfishes or Clariidae are characterized by an elongated body, a dorsoventrally flattened head, small eyes, and a suprabranchial organ. Air-breathing catfishes are a diverse group that has radiated throughout Africa, the Middle East, and Southeast Asia (Teugels, 1996). The Central African clariids are characterized by a number of independent origins of elongated morphs with an anguilliform body shape (Boulenger, 1907; Pellegrin, 1927). Whereas many clariids, such as *Heterobranchius* and *Clarias*, typically live in large rivers and streams, the anguilliform clariids tend to occupy different habitats, with their elongated body form being linked to a burrowing lifestyle (Poll, 1959; Matthes, 1964; Nelson, 1994; Winemiller and Kelso-Winemiller, 1996).

Within clariid fishes several cranial morphotypes can be discerned, especially with relation to the hypertrophy of the jaw adductors in the anguilliform species (Fig. 1) (Cabuy et al., 1997). Although the hypertrophy of the jaw adductors and associated skeletal modifications in the cranial elements have been proposed to increase bite force (Cabuy et al., 1997), whether these modifications in cranial structure are indeed related to an increase in bite force has not been tested. And yet, a relation between jaw adductor size and bite force is implicitly assumed when discussing the ecological implications and evolutionary origins of the increase in jaw adductor size. Several factors, like dietary specialization, the use of the jaws for burrowing, aggressive interac-

tions, and even display have been suggested as possible explanations for the increase in the size of the jaw adductors (Cabuy et al., 1997). Alternatively, it has been proposed that the large relative size of the jaw adductors might be a correlated response to a decrease in head size, independent of the evolution of an anguilliform morphology. But without knowing the relation between adductor size and actual bite performance, these hypotheses remain purely speculative. Given that the functional properties (orientation of the muscles, 3-D skull configuration, physiological cross section, etc.) of the jaw system are crucial in understanding these relations, biomechanical modeling is an essential step in our understanding of this system.

In this study, we examine the functional properties of the jaw adductors in four species of clariids that show an increasing trend of hypertrophy. *Clarias gariepinus* is used as a generalized clariid that shows no obvious increase in jaw adductor size and is characterized by a bony enclosure of the dorsal

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\*Correspondence to: Anthony Herrel, Dept. Biology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Antwerp, Belgium.  
E-mail: aherrel@uia.ua.ac.be

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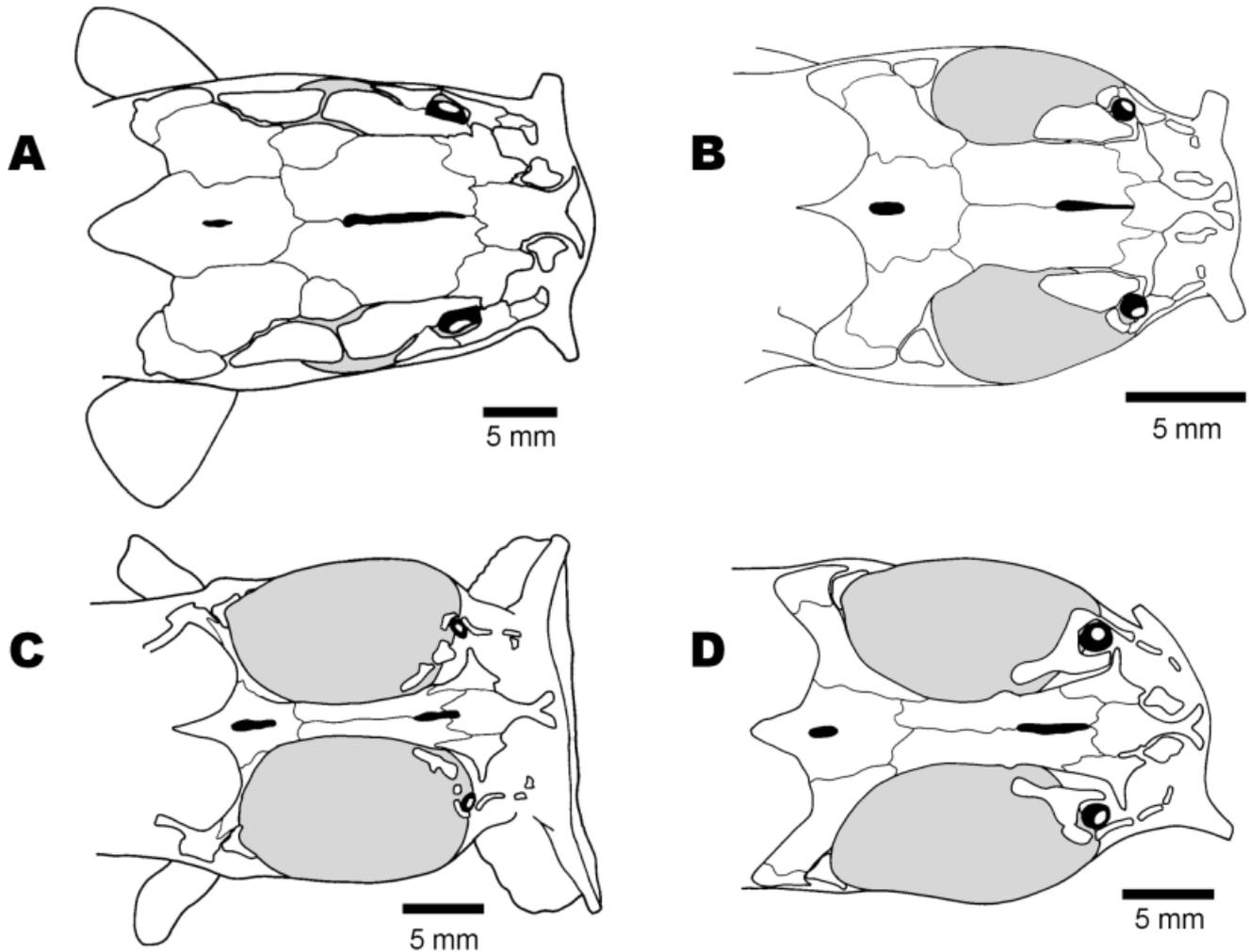


Fig. 1. Skull morphotypes in the Clariidae, showing the relation between the hypertrophy of the adductor mandibulae complex and bone reduction (dorsal view). The shaded area indicates the exposed adductor mandibulae complex. **A:** *Clarias gariepinus*. **B:** *Clariallabes melas*. **C:** *Gymnallabes typus*. **D:** *Channallabes apus*.

portion of the jaw adductors (Fig. 1A) (Adriaens and Verraes, 1996). *Clariallabes melas*, *Channallabes apus*, and *Gymnallabes typus* show an increased hypertrophy of the jaw adductors and a reduction of the bony elements of the skull covering the jaw adductors (Fig. 1B–D) (Cabuy et al., 1997). Based on biomechanical modeling, we investigate whether the apparent hypertrophy of the jaw adductors in these anguilliform morphs actually results in an increased relative and absolute bite performance. Only when a relation between adductor size and bite force is established can meaningful hypotheses concerning the ecological and evolutionary significance of the hypertrophy of the jaw adductors be proposed.

## MATERIALS AND METHODS

### Specimens

Three specimens of the species *Clarias gariepinus* (personal collection) (standard length, SL: 131–133

mm, skull length, SKL: 37–39 mm), *Clariallabes melas* (KMMA-38495-508) (SL: 84–104 mm, SKL: 14–20 mm), *Channallabes apus* (personal collection) (SL: 338–382 mm, SKL: 26–30 mm) and *Gymnallabes typus* (personal collection) (SL: 95–239 mm, SKL: 14–30 mm) were used in this study.

### Morphology

For each species three specimens were dissected. The jaw adductors ( $A_2A_3'$  and  $A_3''$ ) of both sides were removed and weighed (0.0001 g) (terminology of adductor mandibulae components follows Adriaens and Verraes [1996]). Next, the muscle bundles were immersed in an  $HNO_3$  30% solution for 24 h to dissolve the connective tissue. Fibers were gently teased apart using blunt-tipped glass needles, then transferred to and stored in a 50% glycerol solution. Twenty muscle fibers per bundle were selected ran-

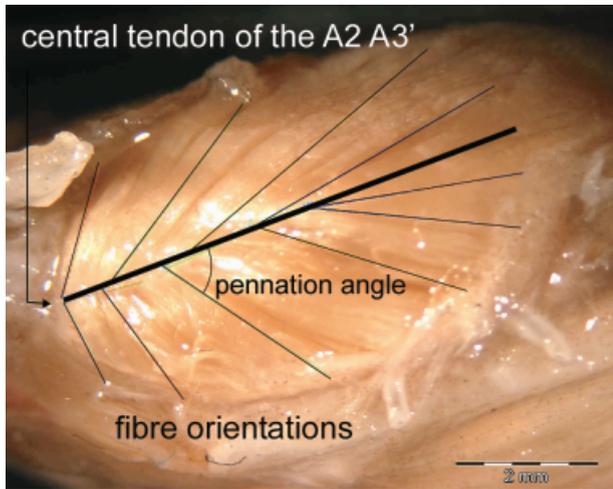


Fig. 2. Determination of the pennation angle (*Clari allabes melas*). The pennation angle of the  $A_2A_3'$  was determined by measuring the angle between the central tendon of the muscle (arrow on left) and the orientation of the muscle fibers. For every individual 20 angles were measured (see Table 2).

domly and drawn using a Wild M5 dissecting microscope with a camera lucida. The average fiber length per bundle was determined. The physiological cross section of each bundle was approximated by the ratio of the mass over the mean fiber length (i.e., a density for muscle tissue of  $1,000 \text{ Kg m}^{-3}$  was used). For all animals the pennation angle of the  $A_2A_3'$  was estimated by measuring the angle between the central tendon of the muscle and the muscle fibers at different locations across the muscle (Fig. 2). For every animal the angle was measured for 20 fibers.

### Bite Model

The analysis of biting in the species of fish examined relied on the computation of the static force equilibrium. The model used was a modified version of the one used by Herrel et al. (1998a,b). Muscle forces were scaled by their physiological cross section (250 KPa; Herzog, 1994), as it was shown that simulations with all fully active muscles give results (relative forces and force orientations) comparable to those of physiologically relevant mimics during feeding (i.e., simulations were muscle recruitment based on EMG recordings of these muscles during feeding; see Cleuren et al., 1995). Muscle orientation was defined by the 3D-coordinates of the centers of origin and insertion. Only the sagittal component, which depends on the degree of jaw depression, was taken into account, as for symmetrical biting the left and right transversal components are expected to cancel each other out. This spatial information was gathered from prepared skulls and dissections (note that this planar model can be regarded as three-dimensional in cases of symmetrical biting). Muscle forces were entered for one body side only and must

be regarded as an estimate of the forces actually involved in biting. Note that in the results the effect of the pennation angle is not taken into account in the calculations of the bite and joint forces (see Discussion).

For the simulations, the muscles were considered biarticular, crossing both the lower jaw–quadrate, and the hyomandibular–neurocranial joints. Calculation of the moment exerted by all jaw closers about the quadratomandibular joint allowed the magnitudes of the food reaction forces at selected bite points to be calculated (Fig. 3). This was done for a range of orientations of food reaction forces (set to vary between  $-30$  and  $-150^\circ$  with respect to the lower jaw; see Fig. 3), as the actual orientation of the food reaction force is often unpredictable and may depend on the shape, texture, and position of the food item, as well as the shape and position of the teeth. Biting points (= point of application of the food-reaction forces) at the anteriormost and posteriormost teeth were selected. Simulations were run at two gape angles:  $10^\circ$  and  $40^\circ$ .

Each food reaction force also exerts a moment about the hyomandibular–neurocranium joint, which must be balanced to maintain the preset static equilibrium condition. The moment required to counteract the effect of the food reaction force at this joint was determined (i.e., the reverse of the moment induced by the food reaction force; the required moment). Logically, biarticular muscles used for biting exert a moment about the hyomandibular–neurocranium joint as well. This moment was calculated. The difference between this moment and the required moment (i.e., remaining required moment) must therefore be provided by structures other than muscles (e.g., ligaments or bony structures). Conventionally, counterclockwise moments in fishes facing to the right are regarded as positive, clockwise moments negative. Segmental weights were not considered in the simulations since they are negligible compared to the other forces involved (less than 1% of the biting forces).

Using the food reaction forces and the muscle forces responsible for jaw closure, the magnitude and orientation of the forces exerted by the quadrate on the lower jaw were calculated (i.e., joint reaction forces). The joint forces are thus those forces acting from the lower jaw on the quadrate with the opposite sign and direction of the joint reaction forces. Notice that these forces must be regarded as the actual forces seen across the articulating surfaces, including the effect of muscular activity (so-called “bone on bone forces”; see Winter, 1990; Nigg, 1995).

### Statistical Analysis

To investigate whether species differed in their theoretical bite capacity, the forces calculated for food reaction forces oriented perpendicular to the lower jaw and the corresponding joint forces were

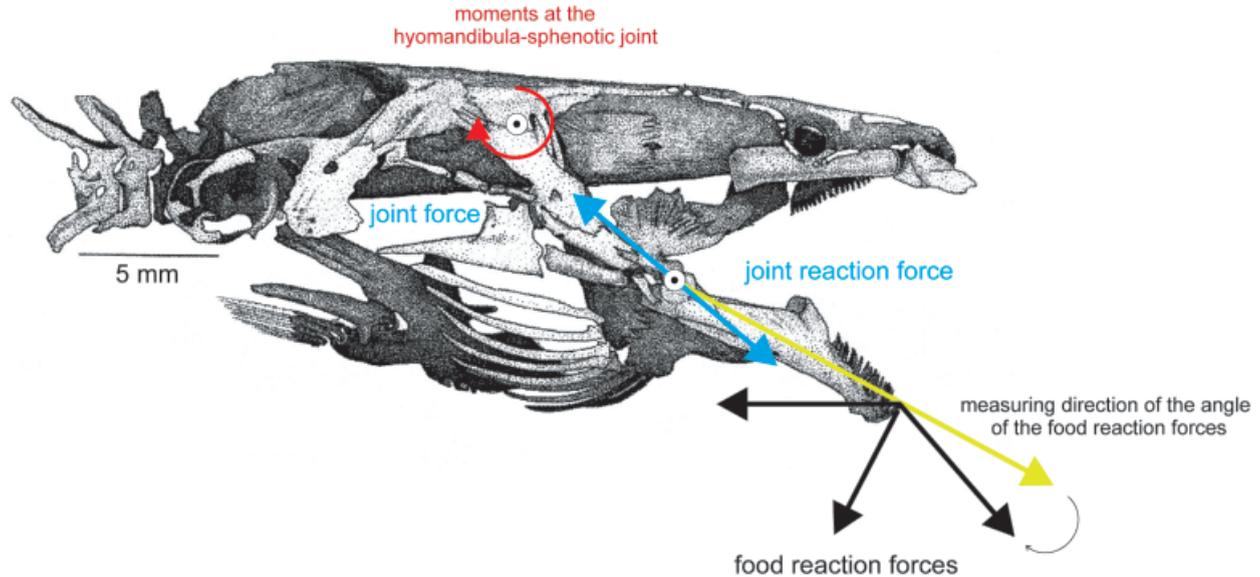


Fig. 3. Schematic representation of the output of the bite model using the skull of *Gymnallabes typus* for illustration. Action and reaction forces at the joints (blue vectors) and at an anterior bite point are represented. The orientation of the forces are measured relative to the line interconnecting the center of rotation and the tip of the lower jaw. Bite forces are calculated relative to the lower jaw and have the same magnitude but opposite orientation and sign to the food reaction forces. Moments at the hyomandibular-sphenotic joint (red) were calculated as well (see Materials and Methods). Modified after Cabuy et al. (1997).

used in a one-way ANOVA. Results were Bonferroni-corrected to account for multiple testing. All analyses were performed using Statistica (v. 5.0, Statsoft, Tulsa, OK).

## RESULTS

### Morphology

We will first give a brief overview of the most striking differences in the morphology of the skull and jaw adductors in the clariids examined in this study. For a more detailed description of the morphology of the cranial system, see Adriaens and Verraes (1996), Cabuy et al. (1997), and Devaere et al. (2001). Whereas the skulls of *Channallabes apus* and *Gymnallabes typus* are characterized by the absence of a bony protection covering the jaw muscles, the neurocranial bones of *Clarias gariepinus* form a closed broad roof (Fig. 1A). *Clariallabes melas* shows an intermediate morphology, where a gap between the rostral infraorbital series of bones and the caudal suprapreopercular series is present (Fig. 1B). Another conspicuous difference is the strong interdigitation between the bony processes on the hyomandibula and the sphenotic, found in *G. typus* and *C. apus*, but absent in *Clarias* and *Clariallabes*. Further differences involve the tooth rows (more posteriorly extended and larger in the hypertrophied morphs) and the coronoid process (larger in the clariids with hypertrophied jaw adductors, i.e., *G. typus* and *C. apus*). *Clariallabes melas* is in many respects intermediate between *C. gariepinus* and

the hypertrophied morphs, with the exception of the size of the teeth and the coronoid process.

The adductor mandibulae in clariids consists of an external  $A_2A_3'$  and a smaller  $A_3''$  part (see also Adriaens and Verraes, 1996). The  $A_2A_3'$  is extremely large in the hypertrophied morphs and covers the entire dorsolateral part of the head. It is a pennate muscle originating mainly on the infraorbital, frontal, sphenotic, and pterotic bones and inserting on the coronoid process of the lower jaw. The deeper  $A_3''$  is not pennate and originates on the frontal, sphenotic, pterospino, and parasphenoid bones. In *Clarias gariepinus* the origin of the  $A_2A_3'$  does not include the frontal, pterotic, and posttemporo-supracleithral bones.

### Biometrics

Whereas the relative mass of the  $A_2A_3'$  differs between species (although not significantly after Bonferroni correction Table 5) the relative mass of the  $A_3''$  does not seem to differ (Table 1). In contrast to our expectations, *Channallabes apus* has the largest relative adductor mass. The other species show a decrease in relative adductor mass from *Gymnallabes typus* to *Clarias gariepinus* (Table 1). Fiber lengths in both muscles are similar for all species (Tables 1, 5). Consequently, the relative physiological cross section differs only for the  $A_2A_3'$  (Table 1). Again, *C. apus* has the largest relative physiological cross section, followed by *G. typus*, *Clariallabes melas*, and *C. gariepinus*. Pennation angles of the

TABLE 1. Morphometric data of the jaw muscles

Species	AVG mass A <sub>2</sub> A <sub>3</sub> (g)	AVG mass A <sub>3</sub> ' (g)	AVG FL A <sub>2</sub> A <sub>3</sub> (mm)	AVG FL A <sub>3</sub> ' (mm)	AVG PXS A <sub>2</sub> A <sub>3</sub> (cm <sup>2</sup> )	AVG PXS A <sub>3</sub> ' (cm <sup>2</sup> )
<i>Clarias gariepinus</i>	0.0787 ± 0.01	0.0453 ± 0.01	4.49 ± 0.25	4.88 ± 0.50	0.18 ± 0.03	0.1 ± 0.001
<i>Clariallabes melas</i>	0.0320 ± 0.01	0.0087 ± 0.00	4.04 ± 0.59	3.81 ± 0.34	0.39 ± 0.03	0.12 ± 0.004
<i>Gymnallabes typus</i>	0.1087 ± 0.15	0.0187 ± 0.03	4.40 ± 1.15	3.62 ± 1.36	0.59 ± 0.11	0.11 ± 0.01
<i>Chanallabes apus</i>	0.3287 ± 0.16	0.0387 ± 0.02	5.26 ± 0.75	4.57 ± 0.57	1.27 ± 0.52	0.17 ± 0.01

The average mass, fiber length, and physiological cross section of the two most important jaw adductors are represented. AVG, average; FL, fiber length; PXS, physiological cross section.

A<sub>2</sub>A<sub>3</sub>' were highly variable in all species (Table 2). Although the range of pennation angles was similar in all species, the average angle was smallest in *C. gariepinus* and largest in *C. apus*, with the other species being intermediate (Table 2).

### Modeling — General

We first provide a short description of the forces associated with biting at a low gape angle (10°) and at a bite point (see Fig. 3) situated at the anterior-most teeth. Bite forces are lowest for food reaction forces oriented perpendicularly to the lower jaw in all species. Any deviation of this orientation results in an increase in bite force. Although intraspecific variation is present, *Chanallabes apus* generally has the largest scaled bite forces, followed by *Gymnallabes typus*, *Clariallabes melas*, and *Clarias gariepinus* (Table 3). Remarkably, *C. apus* also has larger average absolute bite forces compared to *C. gariepinus* (6.14 N vs. 1.09 N), despite its smaller average head size (27.33 mm vs. 38.33 mm). *Gymnallabes typus* (2.12 N) also bites more forcefully than *C. gariepinus* and *C. melas* (0.9 N) shows the lowest absolute bite forces. Note, however, that the average head size of these species is much smaller than that of *Clarias* and *Chanallabes* (*G. typus*: 19.43 mm; *C. melas*: 17.33 mm). Scaled joint forces are fairly large, especially in the two species with hypertrophied jaw adductors, and especially in *C. apus* (more than twice that of *Gymnallabes*) (Tables 3, 5). These forces are lowest for food reaction forces directed anteriorly and increase considerably as the orientation of the food reaction forces shifts posteriorly (Fig. 4). The orientation of these joint forces is slanted extremely posteriorly in all species. With the exception of *C. apus*, joint forces are oriented at an angle of about 160° for most of the range in food reaction force orientations. Although in *C. apus* joint

forces are directed slightly downwards, in all species the orientation of these forces is more or less in line with the quadrangle (see Cabuy et al., 1997; Adriaens and Verraes, 1998; Devaere et al., 2001, for descriptions of the skull in these species). The remaining moments calculated about the hyomandibular–neurocranium joint are largest for *C. apus* (0.38 ± 0.24 Nm), decrease slightly in *G. typus* (0.325 ± 0.58 Nm), and are lowest in *C. gariepinus* (0.028 ± 0.01 Nm) and *C. melas* (0.013 ± 0.01 Nm).

### Effect of Point of Application of the Food Reaction Forces

A posterior shift of the point of application of the bite forces results in an increase in bite forces in all species. This is hardly surprising, as this decreases the outlever of the system considerably (Wainwright, 1987, 1996; Westneat, 1995). The species with hypertrophied jaw adductors still bite considerably harder and the relation between the degree of hypertrophy and bite force remains (*Chanallabes apus* > *Gymnallabes typus* > *Clariallabes melas* > *Clarias gariepinus*; see Tables 3, 5). The effects of changes in the orientation of the food reaction forces on the magnitude of the bite and joint forces are similar to those described for an anterior bite point. The relative increase in bite force, as a result of the change in bite point, is largest for *G. typus*, where the forces are almost doubled. Joint forces are only slightly increased by the change in position of the bite point. Consequently, all species show relatively lower joint forces for a given bite force (by a factor of 1.5) for food particles positioned at the back of the tooth row. The jaw system in clariid fishes thus seems optimized for biting at the posterior teeth. Biting at the posterior teeth causes a slight posterior shift of the angle of the joint forces in all species (±5°). The remaining moments calculated about the hyomandibular–neurocranium joint are slightly higher in all species.

TABLE 2. Average pennation angles of the A<sub>2</sub>A<sub>3</sub>'

	<i>C. gariepinus</i>	<i>C. melas</i>	<i>G. typus</i>	<i>C. apus</i>
Average	27.35	44.37	50.72	35.14
STD	18.50	27.66	34.13	30.71
Min.	0.04	0.28	0.21	0.27
Max.	53.08	85.92	86.07	77.60

Table entries are pennation angles in degrees (see Fig. 2).

### Gape Effects

Opening the jaws from 10–40° causes a decrease in bite force of about 15% in all species for both bite points (Tables 4, 5). The differences in bite force among species remain and the clariids with hyper-

TABLE 3. Summary of the bite modeling at low gape angle ( $10^\circ$ )

Species	AVG BF 1	AVG BF 2	AVG JF 1	AVG JF 2
<i>Clarias gariepinus</i>	$1.2 \pm 0.18$	$1.63 \pm 0.24$	$6.33 \pm 0.92$	$6.31 \pm 0.92$
<i>Clariallabes melas</i>	$4.24 \pm 0.53$	$5.81 \pm 0.72$	$11.93 \pm 1.61$	$12.22 \pm 1.63$
<i>Gymnallabes typus</i>	$6.88 \pm 2.64$	$11.17 \pm 4.29$	$16.33 \pm 6.26$	$17.23 \pm 6.62$
<i>Chanallabes apus</i>	$13.81 \pm 5.71$	$18.12 \pm 7.50$	$35.72 \pm 14.82$	$36.84 \pm 15.27$

AVG BF 1, average bite force for food reaction forces oriented perpendicular to the lower jaw ( $90^\circ$ ) at bite point 1 (anteriormost teeth); AVG JF90 1, average bone-to-bone joint force for food reaction forces oriented perpendicular to the lower jaw at bite point 1; AVG BF 2, average bite force for food reaction forces oriented perpendicular to the lower jaw at bite point 2 (posteriormost teeth); AVG JF90 2, average bone-to-bone joint force for food reaction forces oriented perpendicular to the lower jaw at bite point 2.

trophied jaw muscles still bite more forcefully. Joint forces increase at higher gape angles but to a lesser degree as the decrease of the bite forces. This implies that biting at lower gape angles is more efficient as joint forces are lower for a given bite force. This pattern is similar and holds for both bite points and for all species examined. The observed patterns in the magnitude of the bite and joint forces, in response to changing orientation of the food reaction forces, are similar to the situation at low gape: bite forces are minimal for orientations perpendicular to the lower jaw and joint forces increase for food reaction forces pointing more posteriad. The orientation of the joint forces shifts anteriad, assuring a better alignment with the quadrade in all species. The remaining moments calculated are distinctly lower in all species (*Chanallabes apus*:  $0.274 \pm 0.18$  Nm; *Gymnallabes typus*:  $0.21 \pm 0.29$  Nm; *Clarias gariepinus*:  $0.004 \pm 0.002$  Nm) except *Clariallabes melas* ( $0.027 \pm 0.02$  Nm).

## DISCUSSION

Although the model used here to calculate bite forces must obviously be an oversimplification of reality, we feel that this approach does allow us to make biologically meaningful predictions of the effect of morphology on performance in the species studied. The static nature of our model, and the fact that pennation angles were not taken into account in our model are arguably the largest drawbacks of the approach taken here. Yet, as forceful biting (e.g., crushing) is typically a near-static process, determined by the nature of the food item, we feel that our model does give a good approximation of bite performance capacity in vivo. The pennation angle of a muscle, on the other hand, is an important component of the muscle architecture that might have a large effect on the forces calculated. Therefore, we determined pennation angles for the species studied. The problem, however, is that pennation angles of the jaw adductor ( $A_2A_3'$ ) in these fish are extremely variable (see Fig. 2, Table 2), making it extremely hard to assess the proportion of fibers with specific angles. Moreover, techniques typically used do not take into account the 3D aspect of the pennation angle, further complicating the interpre-

tation. Given that the ranges of fiber angles observed for the species examined are largely similar, we did not take into account the pennation angles in our model (it should be noted, however, that bite forces will be lower for all species). Even if the estimates of the average fiber angles are used to recalculate the maximal bite forces (at  $10^\circ$  and a posterior bite point, see Table 3), the relative performance of the species does not change drastically. *Clarias gariepinus* still has the lowest bite forces (1.45 N) and *Chanallabes apus* the highest (11.47 N), with the other species being intermediate (*Clariallabes melas*: 4.15 N; *Gymnallabes typus*: 9.13 N).

Despite these potential drawbacks, the results from bite modeling show that a relation exists between the apparent hypertrophy of the jaw adductors and bite force. However, the species that was thought to have the most extreme degree of hypertrophy (*Gymnallabes typus*, see Cabuy et al. [1997] based on morphological examination) did not show the largest bite forces. Still, a relation between adductor muscle mass, the corresponding physiological cross section of the muscle and the actual bite forces exists. Quite unexpectedly, the hypertrophy is almost exclusively restricted to the externalmost jaw adductor ( $A_2A_3'$ ) (Table 1). Space constraints on the deeper  $A_3''$  (which lies deep to both the m. levator arcus palatini and the  $A_2A_3'$ ) presumably prevent this muscle from showing a similar degree of expansion. The spatial competition with the surrounding muscles is already reflected in the elongated tendon sheet of the levator arcus palatini, with muscle fibers present only in the small part, which lies dorsal to the adductor mandibulae complex (Adriaens and Verraes, 1997). The scaled model output clearly shows large differences in potential bite force between the species examined here. The species with the largest calculated forces (*Chanallabes apus*) can theoretically bite with a force over 10 times greater than the generalized species (*Clarias gariepinus*). Moreover, the bite forces calculated on the basis of real (nonscaled) data are over six times higher in *C. apus*, despite its smaller absolute head size (27 vs. 38 mm). Bite forces are higher for all species when biting at the more posteriorly situated teeth. Correspondingly, it can be noted that in the species with hypertrophied jaw adductors the tooth

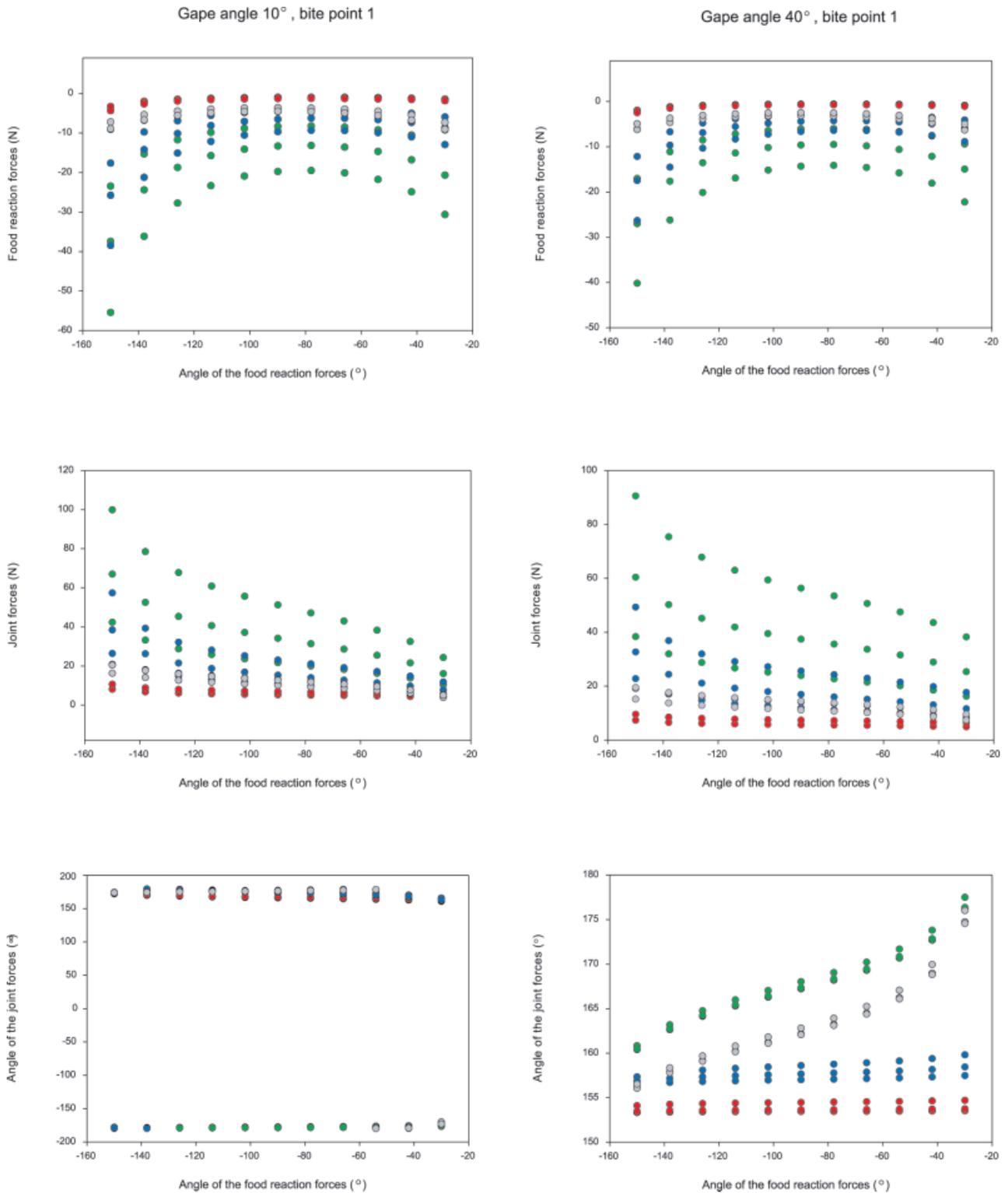


Fig. 4. Graphs representing the scaled food reaction forces, scaled joint forces and orientation of the joint forces for an anterior bite point at low (left) and at high (right) gape for the four species examined. The angle of the food reaction forces is plotted on the X-axis. This angle was set to vary in the model between  $-30^\circ$  and  $-150^\circ$ . *Channallabes apus*, green circles; *Gymnallabes typus*, blue circles; *Clariallabes melas*, gray circles; *Clarias gariepinus*, red circles.

TABLE 4. Summary of the bite modeling at high gape angle (40°)

Species	AVG BF 1	AVG BF 2	AVG JF 1	AVG JF 2
<i>Clarias gariepinus</i>	0.69 ± 0.10	0.93 ± 0.14	6.82 ± 0.98	6.88 ± 1.00
<i>Clariallabes melas</i>	2.89 ± 0.37	3.96 ± 0.50	13.25 ± 1.79	13.70 ± 1.84
<i>Gymnallabes typus</i>	4.70 ± 1.80	7.63 ± 2.92	18.16 ± 6.96	19.26 ± 7.39
<i>Chanallabes apus</i>	9.99 ± 4.14	13.11 ± 5.43	39.24 ± 16.29	40.78 ± 16.93

For an explanation of abbreviations, see Table 3.

rows are extended further posteriorly, thus increasing the functional capacity of the jaw system. Biting at the posterior teeth is also advantageous because of the fairly low joint forces produced.

The forces calculated at the jaw joint are fairly large and are clearly larger in the hypertrophied morphs. Although the orientation of these forces slightly deviates from one that allows the quadrate to brace the jaw posteriorly, the joint forces are largely aligned with the quadrate at higher gape angles. This indicates that forceful biting at higher gape angles (biting of fairly large prey) might be favored. However, as bite forces decrease at higher gapes a functional trade-off between bite capacity and the potential negative effects associated with large joint forces is present. When looking at the morphology of the jaw articulations in the clariids, no obvious adaptations can be linked to the increased joint forces (Fig. 5). However, in the anguilliform species, and especially *Chanallabes*, the mandibular joint supports the quadrate articulation much less (Fig. 5C). This may be a reflection of low variation in the angle of the joint forces in *Chanallabes*, whereas the latter may be high in *Clarias*, where the quadrate joint is largely surrounded by the mandibular articulation socket (Fig. 5A). The remaining moments calculated about the

hyomandibular-sphenotic joint (which need to be countered by physical structures, such as ligament or bone, to keep the skull in a static equilibrium) are larger in *Chanallabes apus* and *Gymnallabes typus*, which correlates well with the strong interdigitation of these to bones in these species (see Cabuy et al., 1997; Devaere et al., 2001). Based on the data of the bite modeling, predictions regarding feeding behavior can be made. Species with hypertrophied jaw adductor are expected to bite at the posterior teeth and at intermediate to large gape angles. Such a configuration optimizes bite performance while keeping the joint forces relatively low and in line with the bracing structures in the skull (i.e., the quadrate). A wider gape is also possible in the hypertrophied species, especially in *G. typus*, where apart from a short lower jaw, an extended skin fold surrounds the mouth. Unfortunately, no behavioral or kinematic data on the feeding behavior of these animals are available in the literature.

Although a rigorous framework for examining ecomorphological relations and the adaptive significance of morphological traits has been proposed (Arnold, 1983; Aerts et al., 2000), still, too often morphological data are used to speculate about evolutionary patterns. As the bite forces calculated in this article are an ecologically relevant indicator of performance of the jaw system, they may allow us to examine previously proposed adaptive hypotheses of the increase in jaw adductor size in some anguilliform clariids.

The most obvious hypothesis is that the increase in bite performance is linked to a dietary specialization. Unfortunately, dietary data on the fishes examined in this study are scarce. The diet of *Clarias gariepinus* is fairly well known and most authors agree that it is an opportunistic omnivore that feeds on zooplankton, aquatic insects, and terrestrial invertebrates (Groenewald, 1964; Clay, 1979). A distinct preference for animal prey such as fish and crustaceans seems to exist (Bruton, 1979; Clay, 1979). The few studies that have examined the diet in *Gymnallabes typus* indicate that it, too, is an omnivore. Insect larvae, ostracods, fish scales, termites, snail shells, and even plant material have been found in the stomach of this species (Matthes, 1964; Cabuy et al., 1997). Gut contents of *Clariallabes melas* indicate a diet of fish and the diet of *Chanallabes apus* apparently includes grasshoppers and other invertebrates (Matthes, 1964; Cabuy

TABLE 5. Summary of the univariate F-tests performed on the modeling data

Variable	F <sub>(3,8)</sub>	P
Mass A <sub>2</sub> A' <sub>3</sub>	4.41	0.04
Mass A <sub>3</sub>	2.63	0.12
FL A <sub>2</sub> A' <sub>3</sub>	1.40	0.31
FL A <sub>3</sub>	1.71	0.24
AVG PXS A <sub>2</sub> A' <sub>3</sub>	8.13	0.008*
AVG PXS A <sub>3</sub>	1.10	0.405
Gape angle 10°		
AVG BF 1	8.69	0.007*
AVG BF 2	8.10	0.008*
AVG JF 1	7.46	0.010*
AVG JF 2	7.49	0.010*
Gape angle 40°		
AVG BF 1	9.22	0.006*
AVG BF 2	8.61	0.007*
AVG JF 1	7.44	0.010*
AVG JF 2	7.46	0.011*

\*Significant at the P = 0.05 level after Bonferroni correction; for an explanation of abbreviations, see Tables 1–3.

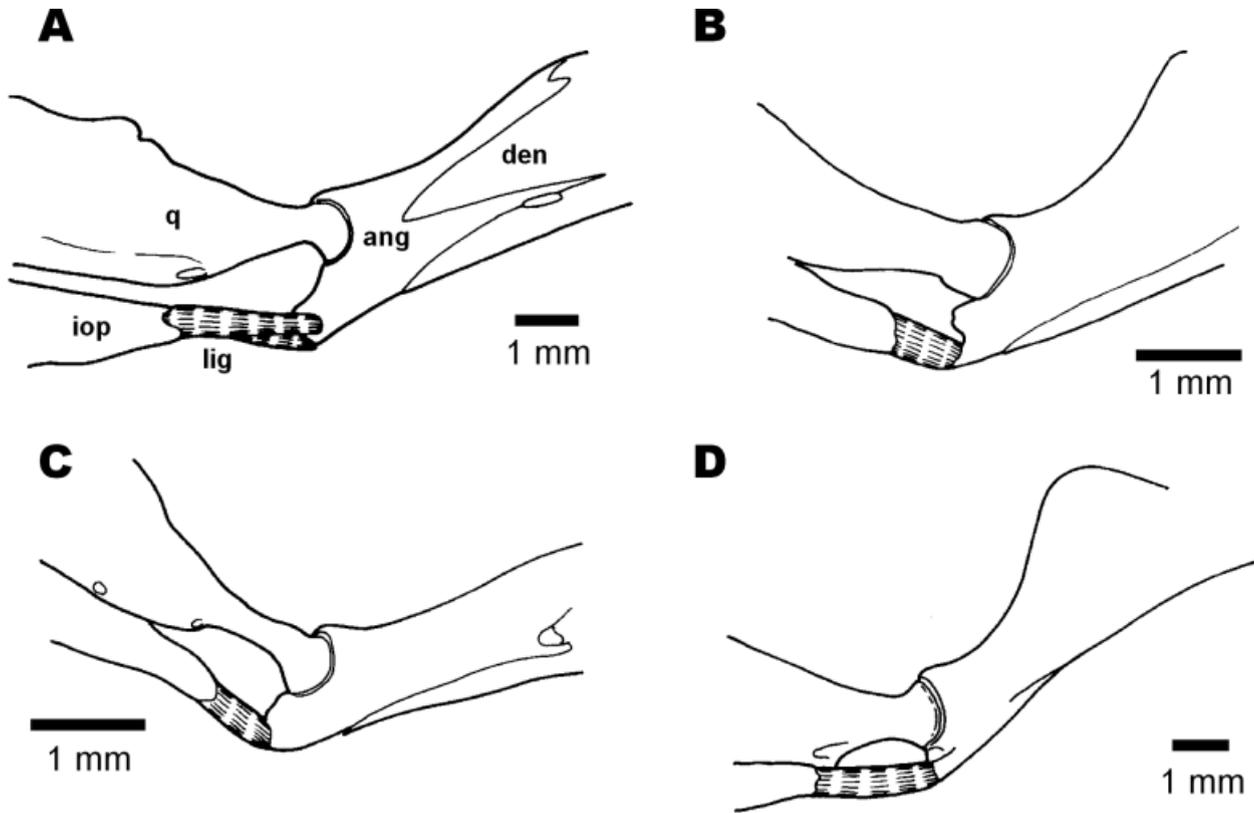


Fig. 5. Right lateral view of the jaw articulation in the four species of catfish. **A:** *Clarias gariepinus*. **B:** *Clariallabes melas*. **C:** *Gymnallabes typus*. **D:** *Channallabes apus*. ang, angular bone complex; den, dental bone complex; iop, interopercular bone; lig, interoperculo-mandibular ligament; q, quadrate.

et al., 1997). At first sight, all clariids thus seem opportunistic predators without an obvious need for large bite forces. However, it has been proposed that the increase in adductor size is the result of a decrease in general head dimensions, which is associated with the eel-like form of these species (Cabuy et al., 1997; Devaere et al., 2001). Although the absolute bite forces of the *C. gariepinus* specimens examined here are low, adult specimens (growing up to 1.5 m) would undoubtedly bite harder than the largest *Channallabes* specimens. Functionally, adult anguilliform clariids might thus need to increase the size of the jaw adductors (and thus bite force) to be able to eat the same wide range of prey types as *C. gariepinus*. Indeed, the few data available on forces needed to crush prey (Herrel et al., 1996, 1999) indicate that bite forces of about 15 N (as calculated for *C. apus*) would allow these fish to exploit a wide range of insect prey. However, there are some indications that the anguilliform clariids might be specializing on distinct prey types. The enlargement and orientation of the teeth in both *C. apus* and *G. typus* (see fig. 6 in Cabuy et al., 1997) indicate that they may be consuming fairly large prey on a regular basis. This is consistent with the results of this study, which show that the jaw system in these

anguilliform clariids seems to be optimized for biting at intermediate to large gape angles. Feeding on large prey might be associated with rotational or spin feeding, as observed in the eel (Helfman and Clark, 1986), or vigorous lateral head shaking (which has been observed in the laboratory). Both of these feeding modes induce large forces on the elements of the jaw suspension, which is reflected in the strengthening of the hyomandibular-neurocranium joint in anguilliform clariids with hypertrophied jaw muscles. It is interesting also that, within the anguilliform clariids, distinct differences in the degree of hypertrophy of the jaw adductors can be observed that may be related to differences in diet. Additional dietary data and observations on feeding behavior are essential to be able to prove or refute the above hypotheses.

Other, not mutually exclusive, functional advantages associated with the presence of hypertrophied jaw adductors are the use of the jaws in burrowing and during intra- or interspecific interactions. The use of the jaws for burrowing seems possible for *Channallabes apus*, as they are typically found in tunnels in muddy substrates and under rotten vegetation in shallow, muddy water (Lambert, 1960; Matthes, 1964; Adriaens and Herrel, pers. obs.).

*Gymnallabes typus*, on the other hand, has never been reported to burrow and observations by Cabuy et al. (1997) also indicate that they never observed burrowing in *G. typus* specimens in captivity. It thus seems more likely that both species use preexisting burrows and do not use their jaw apparatus for digging. It may be possible that burrowing in these species is possible by lateral undulations, where the head is pushed into the muddy and saturated soil, which would not require powerful jaws. Careful observations of these species in both captive and field circumstances are needed. Similarly, at present no indications are available that biting is used in intra- or interspecific interactions. Preliminary observations on the behavior of both *G. typus* and *C. apus* do not indicate intraspecific aggressive interactions. On the contrary, both species seem to exhibit a form of social behavior when kept in captivity. Again, careful observations and testing are required to refute or confirm these hypotheses.

The data gathered in this study cannot give conclusive evidence regarding the adaptive significance of the hypertrophy of the jaw adductors in anguilliform clariids such as *Channallabes apus* and *Gymnallabes typus*. Yet they establish the essential link between morphology and performance. The next obvious step is to link the performance data to ecological and behavioral variables such as diet, burrowing, and inter- or intraspecific interactions. Dietary data are currently being collected and may shed some light on the adaptive significance of increased bite performance.

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