

The retroarticular process, streptostyly and the caecilian jaw closing system

Adam P. Summers^{a,*}, Marvalee H. Wake^b

^a*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA*

^b*Department of Integrative Biology and Museum of Vertebrate Zoology, 3060 VLSB, University of California, Berkeley, CA 94720-3140, USA*

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Abstract

Caecilians have two functionally separate sets of jaw closing muscles. The jaw adductor muscles are parallel fibered muscles positioned close to the jaw joint and their lever mechanics suggests they are well suited to rapidly closing the jaws. A second set of muscles, the hypaxial interhyoideus posterior (IHP), levers the jaws closed by pulling on the retroarticular process (RA) of the lower jaw. Models of the lower jaw point out that the angle and length of the RA has a profound effect on the closure force exerted by the IHP. The caecilian skull is streptostylic – the quadrate-squamosal apparatus (QSA) moves relative to the rest of the skull, a condition that seems at odds with a well-ossified cranium. Modeling the contribution of this streptostylic suspension of the lower jaw shows that rotational freedom of the QSA amplifies the force of the IHP by redirecting force applied along the low axis of the lower jaw. Measurements from several species and life stages of preserved caecilians reveal a large variation in predicted bite force (as a multiple of IHP force) with age and phylogeny.

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Introduction

Caecilians are fossorial, limbless amphibians with a circumtropical distribution (Taylor, 1968). The architecture of the caecilian skull appears particularly well suited to burrowing, exhibiting tight sutures and fusion of skeletal elements (Wake, 1993). In spite of their robust skull there is a surprising degree of cranial kinesis (streptostyly) in the quadrate-squamosal apparatus (Wake and Hanken, 1982), and though the quadrate does not rotate to any great degree, it may be relatively

free to do so (Fig. 1). Streptostyly has evolved several times in tetrapods, serving to increase gape in lizards and snakes, and also allowing the lower jaw to move relative to the origin of the adductor muscles in order to alter the leverage of these jaw closers (Gans, 1961, 1966; Herrel et al., 2000). The development and functional significance of streptostyly in caecilians has been speculated on (Marcus et al., 1933; Wake and Hanken, 1982; Straub, 1985; Wilkinson and Nussbaum, 1997; summarized by Wake, 2003), but specific tests of the effects of streptostyly have not been done.

Neither of the two reasons mentioned above for the evolution of streptostyly would seem to pertain to caecilians: most do not eat particularly large prey items

*Corresponding author.

E-mail address: asummers@uci.edu (A.P. Summers).

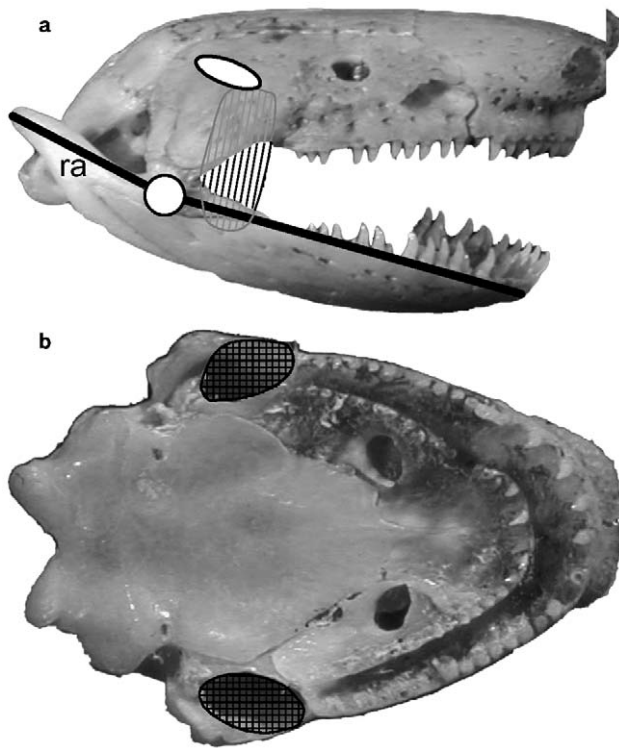


Fig. 1. The skull of a caecilian. (a) Lateral and (b) ventral view of *Dermophis mexicanus*. The position of the jaw adductors is shown by hatching. The adductors are largely overlain by dermal bone. A circle is drawn on the joint between the lower jaw and the quadrate, and the position of the mobile area between the quadrate and the squamosal is indicated by an oval.

(they are elongate, but not large in cross-section; see Gaborieau and Measey, 2004; Measey et al., 2004; O'Reilly, 2000; Presswell et al., 2002; Wake, 1980, 1983, and references therein) and their jaw adductors are relatively small, with origin and insertion quite close to the jaw joint (Bemis et al., 1983; Nussbaum, 1983; O'Reilly, 2000). However, Wilkinson and Nussbaum (1997) suggest that a habitat shift, from burrow-dwelling sit and wait predators to a free-swimming active predatory lifestyle, may be involved in the evolution of the unusually kinetic skull of *Atretochoana*.

The jaw adductors of caecilians are constrained in size by the maxillopalatine and squamosal bones that close over the entire 'cheek' area, restricting the adductors to rather narrow channels medial to these two bones (Bemis et al., 1983; Nussbaum, 1983; Straub, 1985; O'Reilly, 2000; Wake, 2003). Small jaw closing muscles are at odds with the strong sharp teeth and robust jaws of these active predators (Fig. 1). However, caecilians have an alternative method of exerting closing force that involves two unique characters – an unusually pronounced retroarticular process (RA) of the lower jaw, and a hypaxial muscle, the interhyoideus posterior (IHP), that exerts a ventro-posteriorly directed force

on the RA (Bemis et al., 1983; Nussbaum, 1983). The lower jaw is composed of two compound elements, the pseudoangular, bearing the articular facet and the retroarticular process, and the pseudodentary, the dentigerous component. Force exerted by the IHP on the RA, which forms a significant rearward projection of the pseudoangular bone of the lower jaw (compared to that of reptiles, including fossil taxa – see Gans, 1966), acts to close the jaws by rotating the lower jaw about the quadrate–articular joint. The RA is variable in both its length and its angle relative to the body of the pseudoangular and the pseudodentary (see Wake, 2003). Thus, variation in RA will likely have consequences for the biomechanics of jaw closure.

The force of jaw closure is an important biomechanical determinant of trophic niche, limiting a predator to prey that it can reduce between its jaws (Hernandez and Motta, 1997; Wainwright, 1987). Variation in bite force can be so closely tied to dietary niche that it has been used to explain the small divergences in diet within a single lizard species with a sexually dimorphic head shape (Herrel et al., 1996, 1999, 2001). There are no published bite forces for caecilians, but in spite of data from some species suggesting that they eat small prey (Gaborieau and Measey, 2004; Measey et al., 2004), caecilians are opportunistic, and larger species can and will consume mammals and lizards. The lack of dietary analyses for the vast majority of species makes it difficult to guess the importance of a strong bite; but in some cases difficult prey is consumed (e.g. *Dermophis* eating lizards; Moll and Smith, 1967). The unique morphology of the caecilian head allows some insight to be gained by simple biomechanical modeling of the jaw closure forces. The aims of this paper are three-fold: (1) to model the effect of changing RA angle and length on the jaw closure force exerted by the IHP; (2) to model the effect of a mobile quadrate (streptostyly) on jaw closure force; and (3) to determine whether there is appreciable variation in expected force output for a variety of actual caecilian morphologies.

Materials and methods

Modeling

Jaw closure force was modeled using the MatLab mathematical analysis environment. The simplest model assumed: (1) closure forces due to the IHP muscle were directed purely posteriorly (any inclination of this muscle would be equivalent to a change in the angle of the RA); (2) no contribution to closure force from the jaw adductor muscles; (3) IHP muscle force did not vary with gape; and (4) no rotational freedom at the quadrate–articular joint. Closure force was calculated

for gape angles between 0° and 90° in 1° increments. The RA angle was also varied between 0° and 90° in 1° increments, and the ratio of RA length to pseudodentary + pseudoangular length (PD) was varied from 0.10 to 0.50 in 0.05 increments. The range of gape angles we tested (0 – 90°) is far greater than has been observed during feeding in *Dermophis mexicanus* (Bemis et al., 1983). However, there are scant comparative data available, so we extended the model well beyond values from the literature and our own observations. The closure force for this preliminary model was calculated as

$$F_{\text{closure}} = F_{\text{IHP}} \frac{\text{RA}}{\text{PD}} \sin(x + y), \quad (1)$$

where x is the gape angle and y is the angle between the RA and PD (Fig. 2).

We also constructed a more complicated model that made assumptions 1–3 above, and also incorporated streptostyly. This freedom of rotational movement of the quadrate relative to the skull is complex and variable in caecilians (M.H. Wake, pers. obs.). Quadrate movement at its joints with the stapes and the os basale, and in the quadrate–squamosal ‘package’ required adding a further variable to the equation – the angle of the quadrate. Jaw closure force in the streptostyly model was calculated as

$$F_{\text{closure}} = \left(F_{\text{IHP}} \frac{\text{RA}}{\text{PD}} \sin(x + y) \right) + (F_{\text{IHP}} \cos(x + z) \sin(z)), \quad (2)$$

where z is the angle of the quadrate with respect to the horizontal (Fig. 3).

When computing maximum and minimum bite force we restricted the model to gapes from 0° to 60° to more closely approximate the range seen in life.

Morphology

To assess the degree to which our model inputs varied among caecilian species we measured jaws and quadrates from dried skeletons or cleared and stained specimens from the Museum of Vertebrate Zoology and MHW’s personal collection. In some cases jaws were drawn with a *camera lucida* and the ratio of the RA length to the length of the lower jaw anterior to the quadrate articulation was determined from the drawings. The angle and length of the retroarticular process, the length of the lower jaw, and the angle of the

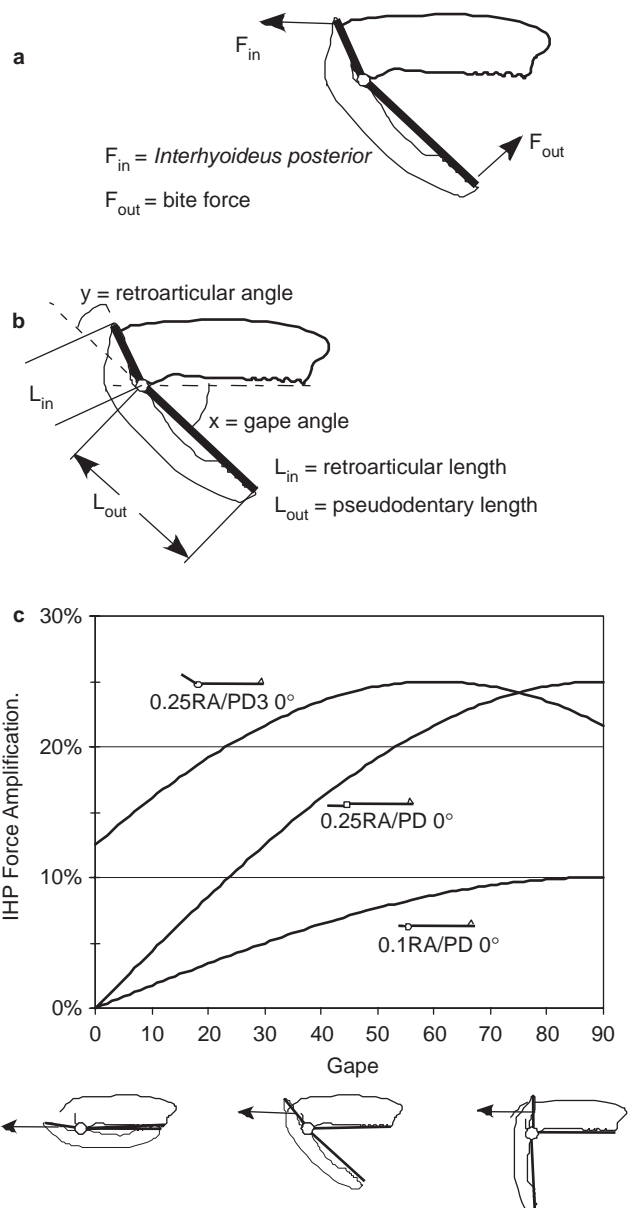


Fig. 2. A two-dimensional analysis of the mechanics of the jaws of a generalized caecilian. (a) The force exerted by the major jaw closing muscle, the *interhyoideus posterior*, is assumed to be exerted at the distal end of the retroarticular process. The additional jaw closing force due to the *adductor mandibularis* complex is ignored for simplicity. The force of the *interhyoideus* is assumed to act purely posteriorly. (b) The lever arms and angles of the jaw closing model. Gape angle is the angle between the upper and lower jaws. For clarity the upper jaw is aligned with the horizontal, though during actual feeding events this angle is variable. (c) A graph of the jaw closing force as a function of the gape angle for three hypothetical morphologies. In two cases the retroarticular process (RA) is in line with the lower jaw ($y = 0$), but the length of the RA relative to the length of the rest of the lower jaw varies from 10% to 25%. In both cases the jaw closing force goes to 0 as the jaw closes, the length of the RA has a profound affect on the magnitude of the maximum closing force. In the third hypothetical case the relative length of the RA is 0.25 and the angle of the RA to the lower jaw is 30° . The force with the jaws fully closed is no longer zero and the maximal closing force has been shifted to a smaller gape angle.

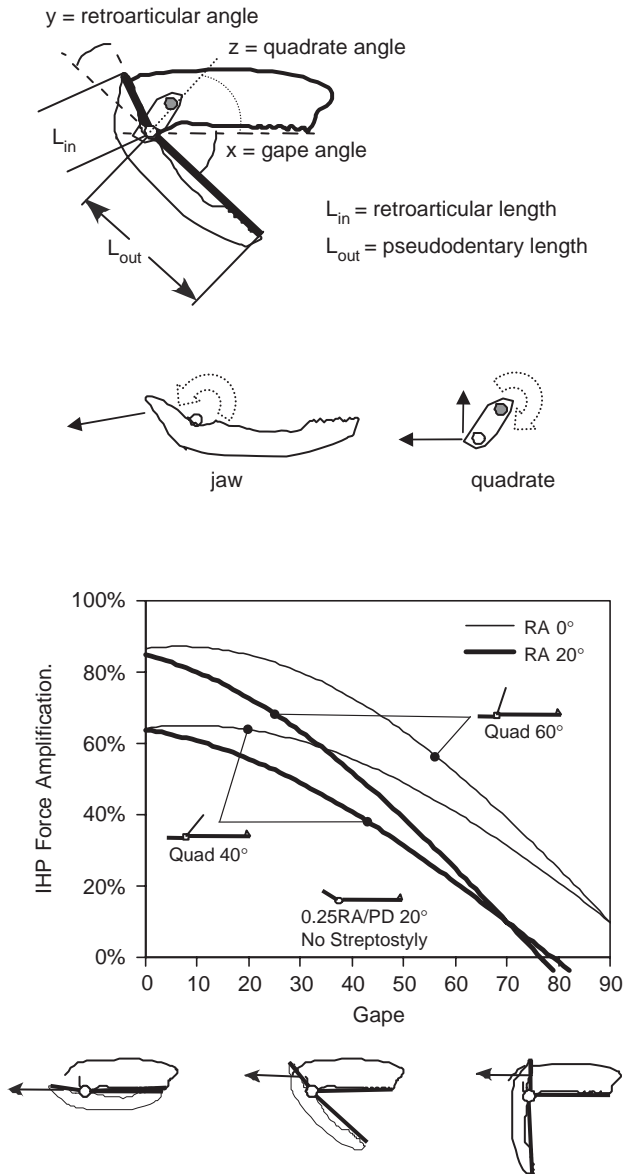


Fig. 3. A two-dimensional analysis of the mechanics of the jaws of a generalized caecilian assuming streptostyly allows rotation of the quadrate. (a) For the purposes of this model the major jaw closing muscle, the *interhyoideus posterior*, acts at the distal end of the retroarticular process (RA) and exerts force purely posteriorly. The additional jaw closing force due to the *adductor mandibularis* is ignored for clarity. (b) The forces can be decomposed into the same closing force exerted by the lower jaw as in the model in Fig. 2 plus an added component due to the rotational freedom of the squamosal quadrate complex. (c) A graph of the jaw closing force as a function of the gape angle for five hypothetical morphologies. In all cases the RA is 25% of the length of the lower jaw. The dotted line assumes no streptostyly and an RA angle of 0. The other four lines represent data from the streptostyly model for two quadrate angles (40° and 60°) and two RA angles (0° and 20°).

quadrate with respect to the antero-posterior axis of the skull were measured with an ocular micrometer/goniometer on a Wild dissecting microscope (Fig. 4). We

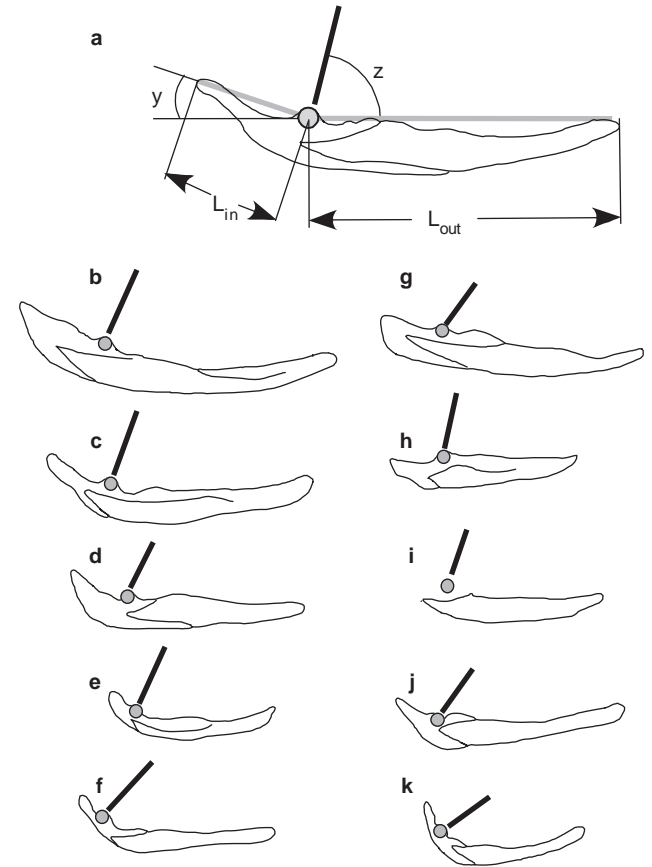


Fig. 4. The lower jaw of several species of caecilians seen in lateral view. The articulation between the quadrate and the articular is indicated with a gray filled circle. The input lever is measured to the tip of the pseudodentary, and the output lever arm is measured to the tip of the RA process. The heavy line from the filled circle indicates the angle of the quadrate when the jaw is closed. (a) *Dermophis mexicanus* (adult), (b) *Typhlonectes natans*, (c) *Geotrypetes seraphini*, (d) *Ichthyophis acuminatus*, (e) *Scolecomorphus kirki*, (f) *S. vittatus*, (g) *Caecilia occidentalis*, (h) *D. mexicanus* (juvenile), (i) *Hypogeophis rostratus*, (j) *T. compressicauda* (juvenile), (k) *S. uluguruensis*.

collected data from 11 species of caecilians representing four of the six extant families, as well as adult and juvenile individuals of *D. mexicanus*.

Results

Simple model (no streptostyly)

With the RA angle held at 0° (in line with the PD) the force at the tip of the jaws (output force) is maximized when the jaws are open to 90° and decreases to 0° as the jaws close (Fig. 2c). Output force scales with RA/PD, a larger RA relative to PD leads to increased output force.

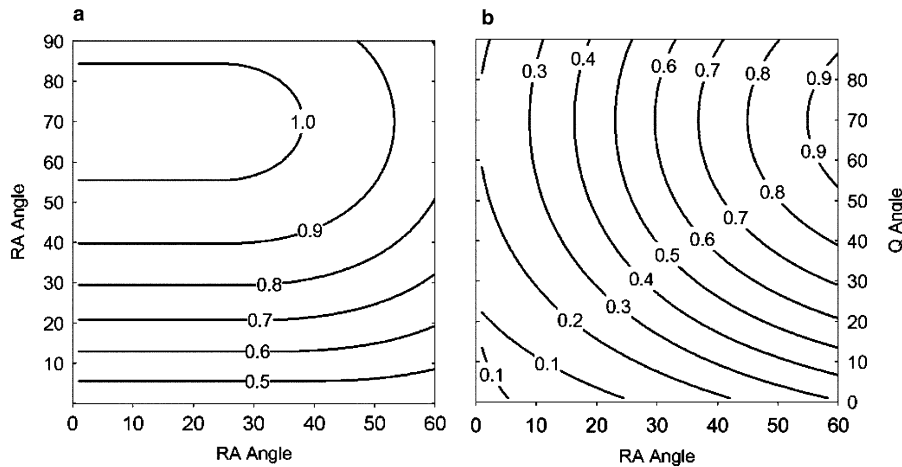


Fig. 5. These graphs show the effect of changing morphology on the jaw closing force as a function of gape angle. The isolines represent closing force expressed as a fraction of the force generated by the *interhyoideus posterior* muscle. (a) The effect of the retroarticular angle (RA angle) on jaw closing force for the streptostyly model with a quadrate angle (Q angle) of 20° . The maximum force is not sensitive to RA angle, but the gape at which maximum force occurs is inversely proportional to RA angle. The force isolines for different Q angles have different values but the same arrangement. (b) The effect of changing Q angle on closing force with an RA angle of 20° . Variation in quadrate angle has a large effect on maximum force when compared to varying RA angle.

Changing the angle of the RA decreases the gape angle of maximum output force to a 90° -RA angle. Peak output force is input force multiplied by RA/PD, and so it never exceeds 50% of the force generated by the IHP muscle (Fig. 2c).

Model with streptostyly

With the addition of rotational freedom in the quadrate (Fig. 3a), the output force increases with

decreasing gape angle peaking at or near jaw closure (Fig. 3b). Changing the RA length relative to the PD length has the same multiplicative effect on output force as in the simpler model. The output of the model, jaw closing force expressed as a percentage of IHP force, is shown for two RA angles and two quadrate angles, with the ratio RA/PD held at 0.25 (Fig. 3b).

Bite force varies with gape in both models; however, there are complex tradeoffs between maximal force generation and even force generation throughout the gape cycle in the model with streptostyly (Figs. 5 and 6).

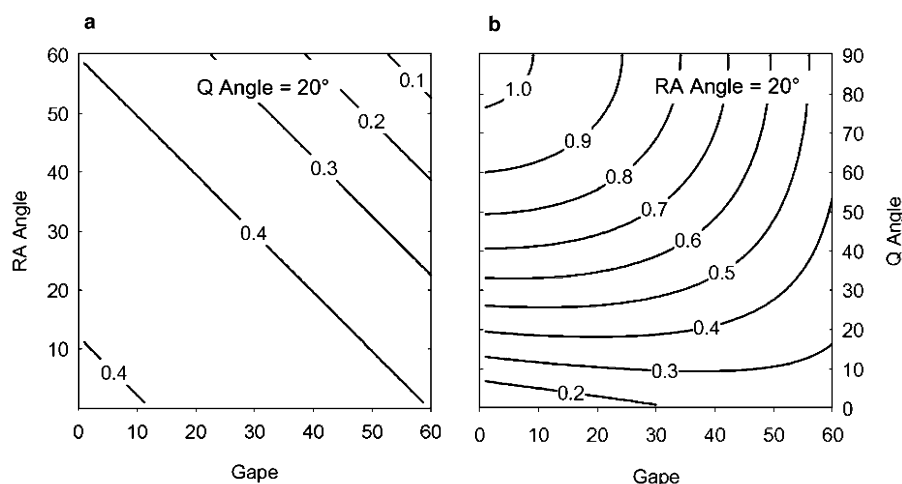


Fig. 6. Two parameters of potential ecological import are the maximum closing force over the range of possible gape angles and the difference between the largest and smallest force as the mouth closes. These graphs show isolines representing the fraction of force generated by the *interhyoideus posterior* muscle. (a) The maximum force as a function of both RA angle and Q angle. Maximum force is calculated over a gape from 0° to 60° . For a given Q angle the RA angle has little effect on maximum force. (b) The difference between maximum and minimum force over a gape of 0 – 60° as a function of Q angle and RA angle. The steeper the angle of the quadrate the more heterogeneous the jaw closing force.

Changes in RA angle, with quadrate angle constant, have little effect on the peak force generation, but can have a profound effect on the difference between maximum and minimum bite force over the gape (Fig. 6).

Morphology

The length and angle of the RA relative to the PD and the angle of the quadrate relative to the long axis of the body varied among species and among developmental stages (Table 1).

When the morphological measurements of 11 individual caecilians from 10 species were used as inputs to the streptostyly model, the peak output force was within 10% of the IHP input force in all but three species (Table 1). In *Scolecormorphus kirki* and *Scolecormorphus uluguruensis* the bite force was less than the IHP force and in *Hypogeophis rostratus* the maximum bite force was higher than IHP force. The difference between maximum bite force and the minimum bite force over a 60° gape cycle is a measure of the functional flexibility of the system. A large differential indicates that the animal can exert high force over only a narrow range of its gape. The force heterogeneity varied from 0.20 in *H. rostratus* to 0.60 in *S. kirki* (Table 1).

Discussion

Our models of jaw function imply new interpretations of the functional significance of the RA and the streptostylic jaw joint of caecilians. The RA is thought to have been the site of insertion for a jaw opening muscle that originated on the posterior of the skull in extinct amphibian and reptilian lineages including nectrideans, captorhinomorphs and goniorhynchids (Carroll, 1988). In caecilians the RA has a nearly opposite function, serving as an insertion for a hypaxial jaw closing muscle (Bemis et al., 1983; Nussbaum, 1983). Previous models of RA function proposed that the length and angle of the process was driven by a need to open the jaws rapidly (Gans, 1966), or to increase the gape (Parrington, 1955). In caecilians an elongate RA increases bite force through providing a longer input lever, at all gape angles, for the IHP. The angle of the RA relative to the long axis of the lower jaw prevents the jaw closing force from dropping to zero when the mouth is closed.

There are at least two reasons why it is important to be able to generate force with the mouth nearly, or completely, closed. Though caecilians do not have a dentition that suggests they can shear their prey to

Table 1. Measurements and calculations of functionally important parameters from the jaws of several species and ontogenetic stages of caecilians

Species	PD length (mm)	RA length (mm)	RA angle (deg)	Quadrate angle	Computed RA/JL (%)	Max. bite/IHP	Bite force difference
<i>Epicrionops bicolor</i> (larva)	50	15	0	NA	30		
<i>Epicrionops bicolor</i> (adult)	42	16	−8	NA	38		
<i>Ichthyophis</i> sp. (adult)	50	18	10	NA	36		
<i>Ichthyophis</i> sp. (larva)	47	18	12	NA	38		
<i>Ichthyophis acuminatus</i>	52	20	18	82	38	1.06	0.48
<i>Scolecormorphus kirki</i>	37	7	25	59	19	0.87	0.60
<i>Scolecormorphus uluguruensis</i>	30	8	52	33	27	0.57	0.54
<i>Scolecormorphus uluguruensis</i>	37	14	40	NA	38		
<i>Scolecormorphus vittatus</i>	43	15	0	68	35	1.01	0.23
<i>Caecilia occidentalis</i>	39	14	16	72	36	1.04	0.45
<i>Dermophis mexicanus</i> (117 mm TL)	30	12	−6	79	40	1.07	0.16
<i>Dermophis mexicanus</i> (150 mm TL)	45	17	12	70	38	1.04	0.38
<i>Dermophis mexicanus</i> (189 mm TL)	26	15	−9	NA	58		
<i>Dermophis mexicanus</i> (370 mm TL)	50	20	0	NA	40		
<i>Geotrypetes seraphini</i>	40	10	21	53	25	0.90	0.52
<i>Hypogeophis rostratus</i>	34	20	5	78	59	1.15	0.20
<i>Uraeotyphlus narayani</i>	43	15	23	NA	35		
<i>Idiocranium russelli</i>	43	22	5	NA	51		
<i>Schistometopum gregorii</i>	30	7	19	70	23	1.00	0.59
<i>Schistometopum thomense</i>	36	16	19	NA	44		
<i>Boulengerula boulengeri</i>	39	16	0	NA	41		
<i>Boulengerula taitanus</i>	32	15	15	NA	47		
<i>Typhlonectes compressicauda</i>	45	15	19	70	33	1.04	0.52
<i>Typhlonectes compressicauda</i>	37	15	21	NA	41		
<i>Typhlonectes natans</i>	42	12	15	NA	29		

NA = value not available.

reduce it in size, after grasping a large prey item a caecilian will perform a typical amphibian and reptile behavior of scraping that part of the prey item hanging out of the mouth against the substrate. Using the ground or the sides of the burrow to reduce prey in this way requires a firm grip. The interlocking upper and lower teeth certainly help maintain hold, but there must also be closure force holding the upper and lower jaws together. The lack of occlusal surfaces on caecilian teeth also means that as prey is bitten, the softest tissues, such as muscle or gut, are cut first, leaving the tougher connective tissues until the mouth is nearly closed. In other words, a prey item reduced by a blunt closure mechanism increases in toughness as the gape closes.

Our models assume that the IHP is aligned with the skull and the long axis of the body. There is reason to believe that this is not necessarily the case during feeding. Bemis et al. (1983) found that the head was flexed ventrally when *D. mexicanus* was closing its jaws on a worm. This ventral flexion would serve to increase the effective angle of the RA by rotating the jaws relative to the central axis of the IHP. Even in those species with a relatively straight RA the jaw closure force need not go to zero as the mouth closes if the head is ventrally rotated. The generality of these feeding kinematics is not known, but we suppose that even for species that feed in burrows of compacted soil there would be sufficient room to flex the head downwards and increase the effective RA angle.

The amplification of force generated by the IHP by the streptostylic connection of the quadrate to the skull resolves biomechanical issues related to feeding. In burrowing animals extra material must be excavated to allow protrusions, such as hypertrophied jaw muscles, to move through the tunnel. By enclosing the adductors in bone, and maintaining a streamlined head shape, caecilians reduce the cost of pushing their head through the soil (Bemis et al., 1983). This comes at a cost, as only limited adductor muscle will fit in the bony enclosures. The IHP jaw closing mechanism gets around this constraint by moving jaw closing muscles into the trunk of the animal. The attachment site of the IHP and the length of the RA conspire to limit the force at the tips of the jaws to no more than 50% of the force generated by the muscle (Fig. 5). In most species it is even less than that (Table 1). The additional force that results from a rotating quadrate is a significant contribution to the total jaw closing force. Of equal concern is the severe drop in force with jaw closure in the non-streptostylic model. The force drops because the effective length of the input lever decreases with decreasing gape. In the streptostylic model, though the force does drop with decreasing gape, the drop is far less severe and the minimum closing force, at zero gape, is higher than in the fixed quadrate model.

The rotational freedom of the quadrate and the squamosal need not be high for the streptostylic model to transmit force; however, there must be some free rotation of both when the jaw makes contact with the prey. In our dissections of freshly dead caecilians we have observed some freedom of the quadrate to move, as has been reported elsewhere (Wake, 2003; Wake and Hanken, 1982). Even a few degrees of rotation are sufficient to require that the balancing forces for the quadrate come from the tips of the jaws rather than the connective tissue that binds the quadrate to the squamosal. This is important because it has been suggested that the elements in some species have very limited or no mobility (summarized by Wake, 2003).

The highly variable angle of the quadrate (Fig. 4) as well as the variation in both the quadrate–pseudoarticular joint and the Q–S apparatus imply wide variation in jaw closure forces. This variation is evident between species, but is even clearly seen within a developmental series of a single species – *D. mexicanus* (Table 1; Wake and Hanken, 1982). Little is known of the feeding mechanics of caecilians, but diets include small and large arthropods, fishes, and even small mammals (Exbrayat, 2000; Gaborieau and Measey, 2004; Himstedt, 1999; Measey et al., 2004; O'Reilly, 2000; Presswell et al., 2002; Taylor, 1968; Wake, 1980, 1983). This variation in diet may be correlated with variation in the force generated during jaw closure. An examination of diet in light of calculated jaw closing force would provide an interesting insight into the factors that govern the distribution and abundance of these seldom encountered animals.

The two jaw adductor systems in caecilians are functionally well separated. The adductor mandibuli lie anterior to the jaw joint and insert on the pseudoarticular, while the IHP lies posterior to the skull and inserts on the RA. This separation allows functional specialization that is impossible in simpler systems. There is a fundamental constraint on mechanical leverage systems: either the system amplifies the input force (long input lever and short output lever) or the input speed (short input lever and long output lever). There is a one-to-one tradeoff such that increasing force transmission decreases speed transmission. This tradeoff is an important one and is thought to have played a pivotal role in the evolution of the feeding mechanism of fishes (Wainwright et al., 2004; Westneat, 2004).

Caecilians have the luxury of one jaw closure system that provides a forceful closure (IHP) and another that closes the mouth quickly (adductor) (Fig. 1). The IHP jaw closing system transmits force well. Few biological leverage systems come close to a multiplier of 1; however, over 80% of the species we examined have transmission efficiencies of 90% or higher (with a streptostylic suspension). Inspection of the adductor system reveals traits that suggest high kinematic

advantage. The adductor inserts very close to the jaw joint, often within 10% of the length of the PD (Wake, 2003). In addition, the adductor muscle is parallel fibered and surprisingly long, extending from fossae in the skull to the lower jaw. Long, parallel fibered muscles shorten more quickly than a shorter, pinnate fibered muscle of the same type. Rapid jaw closure would be an advantage in capturing elusive prey, and relative to the usually slow movements of caecilians most arthropods and all vertebrates are elusive. We offer our models as means of facilitating analysis of structure–function relationships involved in the evolution of jaw closing mechanisms.

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References

- Bemis, W.E., Schwenk, K., Wake, M.H., 1983. Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia: Gymnophiona). *Zool. J. Linn. Soc.* 77, 75–96.
- Carroll, R.L., 1988. *Vertebrate Paleontology and Evolution*. W.H. Freeman and Co., New York.
- Exbrayat, J.-M., 2000. Les Gymnophiones, ces curieux Amphibiens. Ed. Boubée, Paris, p. 443.
- Gaborieau, O., Measey, G.J., 2004. Termitivore or detritivore? A quantitative investigation into the diet of the East African caecilian *Boulengerula taitanus* (Amphibia: Gymnophiona: Caeciliidae). *Anim. Biol.* 54, 45–56.
- Gans, C., 1961. The feeding mechanism of snakes and its possible evolution. *Am. Zool.* 1 (N2), 217–227.
- Gans, C., 1966. The functional basis of the retroarticular process in some fossil reptiles. *J. Zool. London* 150, 273–277.
- Hernandez, L.P., Motta, P.J., 1997. Trophic consequences of differential performance: ontogeny of oral jaw-crushing performance in the sheepshead, *Archosargus probatocephalus* (Teleostei, Sparidae). *J. Zool. London* 243, 737–756.
- Herrel, A., Van Damme, R., De Vree, F., 1996. Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. *Neth. J. Zool.* 46, 253–262.
- Herrel, A., Spithoven, L., Van Damme, R., De Vree, F., 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* 13, 289–297.
- Herrel, A., Aerts, P., Vree, F.D., 2000. Cranial kinesis in geckos: functional implications. *J. Exp. Biol.* 203, 1415–1423.
- Herrel, A., Van Damme, R., Vanhooydonck, B., De Vree, F., 2001. The implications of bite performance for diet in two species of lacertid lizards. *Can. J. Zool.* 79, 662–670.
- Himstedt, W., 1999. Die Blindwühlen. Die Neue Brehm-Bücherei No. 630. Westarp Wissenschaften, Magdeburg, p. 160.
- Marcus, H., Winsauer, O., Huber, A., 1933. Beitrag zur Kenntnis der Gymnophionen XVIII. Der kinetische Schädel von *Hypogeophis* und die Gehörknöchelchen. *Z. Anat. Entw.* 100, 149–193.
- Measey, G.J., Gower, D.J., Oommen, O.M., Wilkinson, M., 2004. A subterranean generalist predator: diet of the soil-dwelling caecilian *Gegeneophis ramaswami* (Amphibia; Gymnophiona; Caeciliidae) in southern India. *C.R. Biologies* 327, 65–76.
- Moll, E.O., Smith, H.M., 1967. Lizards in the diet of an American caecilian. *Nat. Hist. Misc. Chic. Acad. Sci.* 187, 1–2.
- Nussbaum, R.A., 1983. The evolution of a unique dual jaw-closing mechanism in caecilians (Amphibia: Gymnophiona). *J. Zool. London* 199, 545–554.
- O'Reilly, J.C., 2000. Feeding in caecilians. In: Schwenk, K. (Ed.), *Evolution of Feeding in Tetrapods*. Academic Press, San Diego, pp. 149–166.
- Parrington, F.R., 1955. On the cranial anatomy of some gorgonopsids and the synapsid middle ear. *Proc. Zool. Soc. London* 125, 1–40.
- Presswell, B., Gower, D.J., Oomen, O.V., Measey, G.J., Wilkinson, M., 2002. Scolecophidian snakes in the diets of South Asian caecilian amphibians. *Herpetol. J.* 12, 123–126.
- Straub, J.O., 1985. Contributions to the Cranial Anatomy of the Genus *Grandisonia* Taylor 1968 (Amphibia: Gymnophiona). Basler Schnelldruck Bernhard Schlattmann, Basel.
- Taylor, E.H., 1968. *The Caecilians of the World*. University of Kansas Press, Lawrence.
- Wainwright, P.C., 1987. Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool. London* 213, 283–297.
- Wainwright, P.C., Bellwood, D.R., Westneat, M.W., Grubich, J.R., Hoey, A.S., 2004. A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.* 82, 1–25.
- Wake, M.H., 1980. Reproduction, growth and population structure of the Central American caecilian *Dermophis mexicanus*. *Herpetology* 36, 244–256.
- Wake, M.H., 1983. *Gymnopsis multiplicata*, *Dermophis mexicanus*, and *Dermophis parviceps*. In: Janzen, D.H. (Ed.), *Costa Rican Natural History*. University of Chicago Press, Chicago, pp. 400–401.
- Wake, M.H., 1993. The skull as a locomotor organ. In: Hanken, J., Hall, B.K. (Eds.), *The Skull*. University of Chicago Press, Chicago, pp. 197–240.

- Wake, M.H., 2003. The osteology of caecilians. In: Heatwole, H., Davies, M. (Eds.), *Osteology*. Surrey Beatty and Sons, Chipping Norton, NSW, p. 2019.
- Wake, M.H., Hanken, J., 1982. Development of the skull of *Dermophis mexicanus* (Amphibia: Gymnophiona), with comments on skull kinesis and amphibian relationships. *J. Morphol.* 173, 203–223.
- Westneat, M.W., 2004. Evolution of levers and linkages in the feeding mechanisms of fishes. *Integr. Comp. Biol.* 44, 378–389.
- Wilkinson, M., Nussbaum, R.A., 1997. Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). *Biol. J. Linn. Soc.* 62, 39–109.