

Functional Morphology of Extreme Jaw Protrusion in Neotropical Cichlids

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ABSTRACT The New World cichlids *Petenia splendida* and *Caquetaia* spp. possess extraordinarily protrusible jaws. We investigated the feeding behavior of extreme (here defined as greater than 30% head length) and modest jaw-protruding Neotropical cichlids by comparing feeding kinematics, cranial morphology, and feeding performance. Digital high-speed video (500 fps) of *P. splendida*, *C. spectabile*, and *Astronotus ocellatus* feeding on live guppy prey was analyzed to generate kinematic and performance variables. All three cichlid taxa utilized cranial elevation, lower jaw depression, and rotation of the suspensorium to protrude the jaws during feeding experiments. Extreme anterior jaw protrusion in *P. splendida* and *C. spectabile* resulted from augmented lower jaw depression and anterior rotation of the suspensorium. Morphological comparisons among eight cichlid species revealed novel anterior and posterior points of flexion within the suspensorium of *P. splendida* and *Caquetaia* spp. The combination of anterior and posterior loosening within the suspensorium in *P. splendida* and *Caquetaia* spp. permitted considerable anterior rotation of the suspensorium and contributed to protrusion of the jaws. *Petenia splendida* and *C. spectabile* exhibited greater ram distance and higher ram velocities than did *A. ocellatus*, resulting primarily from increased jaw protrusion. *Petenia splendida* and *C. spectabile* exhibited lower suction feeding performance than *A. ocellatus*, as indicated by lower suction-induced prey movements and velocities. Thus, extreme jaw protrusion in these cichlids may represent an adaptation for capturing elusive prey by enhancing the ram velocity of the predator but does not enhance suction feeding performance. *J. Morphol.* 257:96–106, 2003.

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KEY WORDS: jaw protrusion; premaxilla; ram; suction; prey capture; cichlids; feeding performance

Upper jaw protrusion is believed to be a major factor contributing to the success of teleost fishes (Schaeffer and Rosen, 1961; Alexander, 1967; Lauder and Liem, 1981; Lauder, 1982; Motta, 1984; Ferry-Graham et al., 2001a). Although numerous studies have explored the morphology and kinematics of upper jaw protrusion (reviewed in Motta, 1984), recent investigations continue to expand our knowledge of the mechanics of upper jaw protrusion in teleost fishes (Ferry-Graham et al., 2001a,b). Additionally, few studies have addressed how upper jaw protrusion enhances feeding performance (Motta, 1984). As measures of performance link or-

ganismal design (morphology) to resource use and fitness, any argument of the adaptive significance of upper jaw protrusion hinges on establishing feeding performance advantages.

During feeding all teleosts rotate the lower jaw around the hinge joint formed between the ventral-most bone of the suspensorium, the quadrate, and the articular of the lower jaw. The lower and upper jaws are either directly connected via ligaments or indirectly connected via ligamentous connections to the maxilla. Regardless of how the jaws are connected, depression of the lower jaw acts to pull the upper jaw into the protruded state. Although at least three other upper jaw protrusion mechanisms have been described, the “mandible depression model” is by far the most widely observed among teleosts (Motta, 1984).

At least three separate kinematic pathways allow the lower jaw to move anteriorly, resulting in the passive anterior protrusion of the upper jaws. In the “mandible depression model” depression of the lower jaw causes the anterior tip of the mandible to move anteriorly as it travels from an oblique closed position to a more horizontal open position. Lower jaw depression acts both to separate the upper and lower jaws, allowing space for prey, while at the same time facilitating the coordinated anterior movement of the jaws (Fig. 1A).

A second widespread kinematic pathway is cranial elevation, which when combined with lower jaw depression can result in substantial anterior movement of the lower jaw (Fig. 1B). *Luciocephalus pulcher*, a Southeast Asian anabantid that exhibits extreme anterior protrusion of the jaws, possesses a

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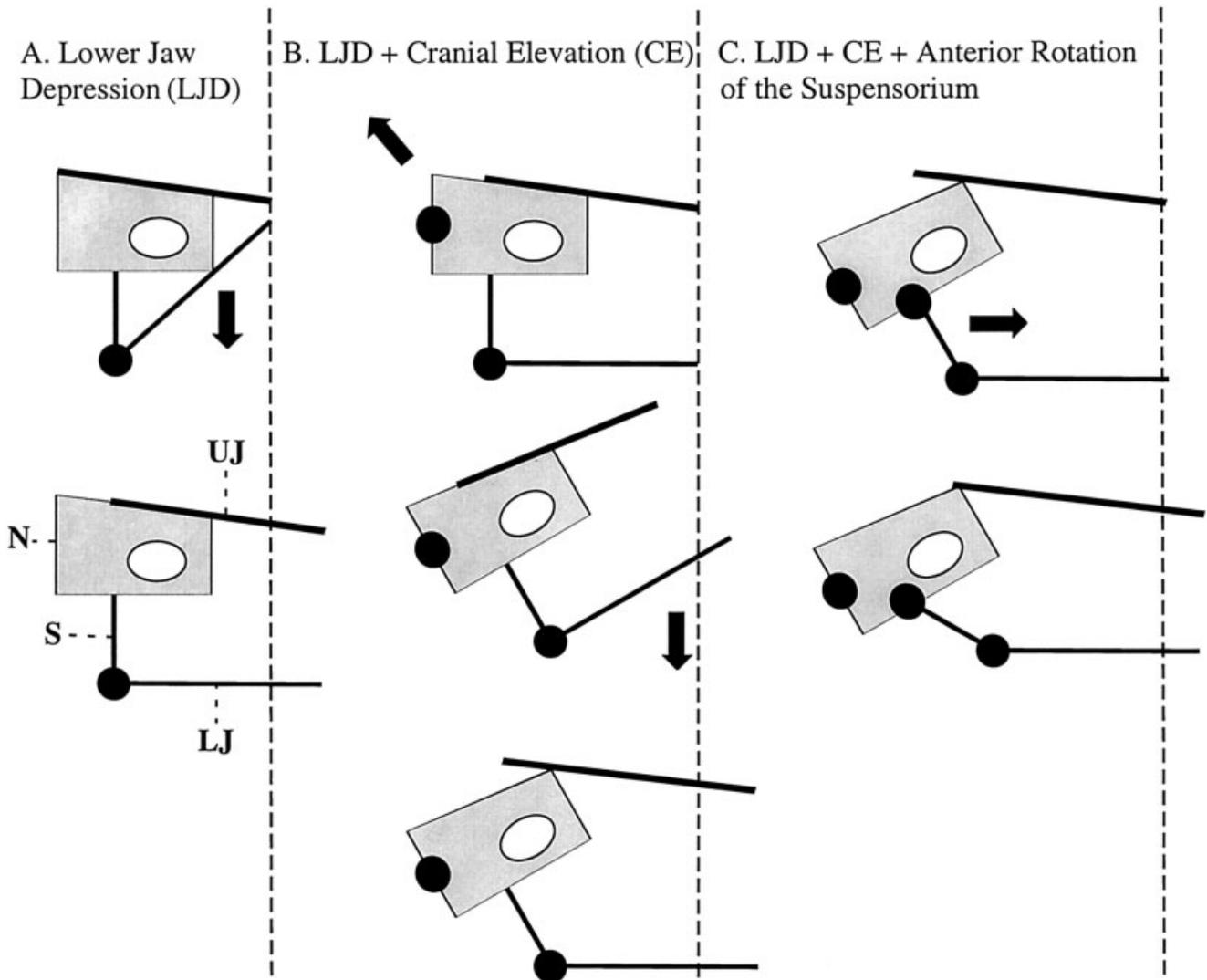


Fig. 1. Three motions that independently or together cause jaw protrusion. Solid circles represent points of flexion or joints permitting movement. **A:** Depression of the lower jaw at the quadromandibular joint. **B:** Both depression of the lower jaw and cranial elevation at the joint between the vertebral column and the neurocranium. **C:** Depression of the lower jaw, cranial elevation, and anterior rotation of the suspensorium at joints or points of flexion within the suspensorium. UJ, upper jaw; N, neurocranium; S, suspensorium; LJ, lower jaw.

lower jaw that when closed lies in a near horizontal position. During mouth opening the lower jaw rotates from a closed horizontal position to an open subhorizontal position, resulting in ventral protrusion of the jaws. However, as the lower jaw is depressed the neurocranium is rotated dorsally, which compensates for the ventral protrusion of the jaws ultimately acting to position the jaws in a near horizontal orientation. In *L. pulcher* the combination of lower jaw depression and cranial elevation resulted in upper jaw protrusion equaling 33% of the head length (Lauder and Liem, 1981).

A third kinematic pathway involves motion within the suspensorium that permits anterior movement of the lower jaw (Fig. 1C). Joints or points of flexion within the suspensorium allow portions of the suspensorium to swing forward independent of the neu-

rocranium. As the lower jaw is suspended by the suspensorium, rostral swinging of the suspensorium results in anterior movement of the lower jaw. The ligamentous connections between the lower and upper jaws results in synchronous anterior protrusion of the upper and lower jaws. Rotation of the suspensorium has been described in three chaetodontid species belonging to the genera *Chelmon* and *Forcipiger* (Ferry-Graham et al., 2001b) and in one labrid species, *Epibulus insidiator* (Westneat and Wainwright, 1989).

Several hypotheses have been proposed to explain how jaw protrusion enhances feeding performance, but the majority of these hypotheses have not been rigorously tested (Lauder and Liem, 1981; Motta, 1984). One hypothesis is the idea that jaw protrusion enhances ram velocity, since the ram velocity of

a fish exhibiting jaw protrusion is composed of a locomotor component plus a jaw protrusion component (Schaeffer and Rosen, 1961; Alexander, 1967; Nyberg, 1971; Lauder and Liem, 1981; Westneat and Wainwright, 1989; Ferry-Graham et al., 2001a).

A second hypothesis is that jaw protrusion enhances suction generation (Lauder and Liem, 1981; Motta, 1984). Suction is generated by rapid buccal expansion and acts to draw water and prey into the predator's mouth. While a general framework for evaluating suction feeding performance has remained elusive (Wainwright et al., 2001), it is generally expected that a better suction feeder will be able to draw prey into the mouth from a further distance and at a greater velocity (Van Leeuwen, 1984; Norton and Brainerd, 1993).

The exaggerated jaw protrusion exhibited by *Petenia splendida*, all three *Caquetaia* species, and other teleosts that results in the formation of an elongate tube through which prey pass has been argued to be a particularly effective suction apparatus (Pietsch, 1978; Konings, 1989; Conkel, 1993). Fish exhibiting jaw protrusion often have smaller and more circular mouth openings than fish not exhibiting jaw protrusion (Motta, 1984). Theoretical arguments based on fluid dynamics (Alexander, 1967) and experimental evidence (Lauder, 1979) suggest that a circular mouth opening increases the velocity of water entering the mouth. Similar theoretical arguments suggest that, all things being equal, a smaller mouth opening should increase the velocity of water entering the mouth (Alexander, 1967).

In this study feeding kinematics, cranial morphology, and feeding performance were compared between *Petenia splendida* and *Caquetaia spectabile*, which both exhibit extreme jaw protrusion, and *Astronotus ocellatus*, which does not exhibit extreme jaw protrusion. We were interested in determining whether *P. splendida* and *C. spectabile* used the same kinematic pathways during feeding as *A. ocellatus*. We also sought to reveal whether the extreme jaw-protruding taxa exhibited drastic structural change within the neurocranium. Finally, we explored feeding performance consequences of extreme jaw protrusion by quantifying differences among the three taxa in ram and suction variables. Using this comparative approach morphological features permitting novel kinematic pathways were linked to differences in feeding performance to better understand the adaptive significance of extreme jaw protrusion in Neotropical cichlids.

MATERIALS AND METHODS

Study Taxa: Phylogeny, Ecology, and Cranial Anatomy

The genus *Petenia* contains one species, *Petenia splendida*, which belongs to the heroine clade of Neotropical cichlids (Farias

et al., 1999, 2000). A second genus in this group, *Caquetia*, contains three species, *C. kraussii*, *C. myersi*, and *C. spectabile*. Using morphological data a fourth species, *C. umbiferum*, was tentatively placed in the genus *Caquetaia* (Kullander, 1983). Although both *P. splendida* and *C. spectabile* are members of the Neotropical heroine clade, the relationships between these taxa have thus far eluded investigators (Farias et al., 1999, 2000). The genus *Astronotus* contains two species. *Astronotus ocellatus* occurs in the upper Amazon and *A. crassipinis* occurs in the lower Amazon. Molecular and morphological data both strongly supported the basal position of *Astronotus* among Neotropical cichlids (Kullander, 1998; Farias et al., 1999, 2000).

Petenia splendida is one of the largest predaceous cichlids, growing to 60 cm, and it occurs in various riparian and lacustrine habitats along the Atlantic slope of southern Mexico, Guatemala, and Belize (Loiselle, 1980; Conkel, 1993; Staeck and Linke, 1995). *Petenia splendida* is a streamlined piscivore possessing enlarged recurved conical teeth in the upper and lower jaws and preying on small fishes such as characids and poeciliids (Hubbs, 1935; Konings, 1989; Conkel, 1993; Staeck and Linke, 1995; Kullander, 1996). This species possesses extraordinarily protrusible jaws (Gunther, 1869; Regan, 1924; Eaton, 1943). The mechanism of jaw protrusion in *P. splendida* was first described by Regan (1924) and then by Eaton (1943). Both authors state that the upper jaw is drawn out by depression of the mandible. Both *P. splendida* and *Caquetaia* spp. were found to possess unusually long upper (ascending process) and lower jaws, permitting extreme jaw protrusion (Regan, 1924; Eaton, 1943).

Caquetaia spp. are large predaceous South American cichlids growing to about 25 cm that are found in riparian and lacustrine habitats. Like *Astronotus* spp., *Caquetaia* spp. are laterally compressed as compared to the more fusiform *Petenia splendida*. *Caquetaia* spp. are piscivores possessing large recurved conical teeth in the upper and lower jaws (Kullander, 1996). *Caquetaia kraussii* ambushes small midwater characids from vegetation (Winemiller, 1989, 1990).

Astronotus ocellatus is a large predaceous cichlid growing to 30 cm and occurring in the upper Amazon River (Staeck and Linke, 1995). Winemiller (1990) found that *A. ocellatus* slowly inspect roots and floating vegetation to detect cryptic fishes, insects, and crustaceans. *Astronotus ocellatus* was found to consume relatively sedentary catfishes as compared to both *Petenia splendida* and *Caquetaia* spp. that capture small agile fish. *Astronotus ocellatus* possess small conical teeth on both the upper and lower jaws (Dutta, 1987). Unlike *P. splendida* and *Caquetaia* spp., *A. ocellatus* exhibits a relatively short ascending process of the premaxilla, maxilla, and lower jaw, permitting only modest upper jaw protrusion (Dutta, 1987). Anterior swinging of the maxilla resulting from lower jaw depression drives upper jaw protrusion in *A. ocellatus* (Dutta, 1987).

Husbandry, Kinematics, and Morphology

Specimens of eight Neotropical cichlid species were obtained commercially: *Petenia splendida*, *Caquetaia spectabile*, *C. kraussii*, *C. myersi*, *Acaronia nassa*, *Astronotus ocellatus*, *Cichla ocellaris*, and *Crenicichla geayi*. *Petenia splendida* (measuring 10.6, 10.3, 7.6 cm standard length), *C. spectabile* (9.4, 9.5, 9.7 cm), and *A. ocellatus* (7.7, 8.8, 9.8 cm) were maintained in separate 100-L aquaria with grid-marked backgrounds for at least 1 month before high-speed video recording experiments were conducted over a period of up to 2 weeks. Aquaria were kept at ~28°C and the three cichlid species were fed tetramin flake food and live guppies. Feeding sequences on live guppy prey were recorded at 500 frames s⁻¹ using a NAC Memrecam ci digital video system. During filming experiments two or three 600-W floodlights were used for illumination. Five feeding sequences for each of the three individuals per species were recorded in which the fish was in lateral view.

Feeding sequences were digitized frame by frame using Didge beta 6.0 for PC. Digitizing began with the onset of the strike, defined by the first frame of observable lower jaw depression, and

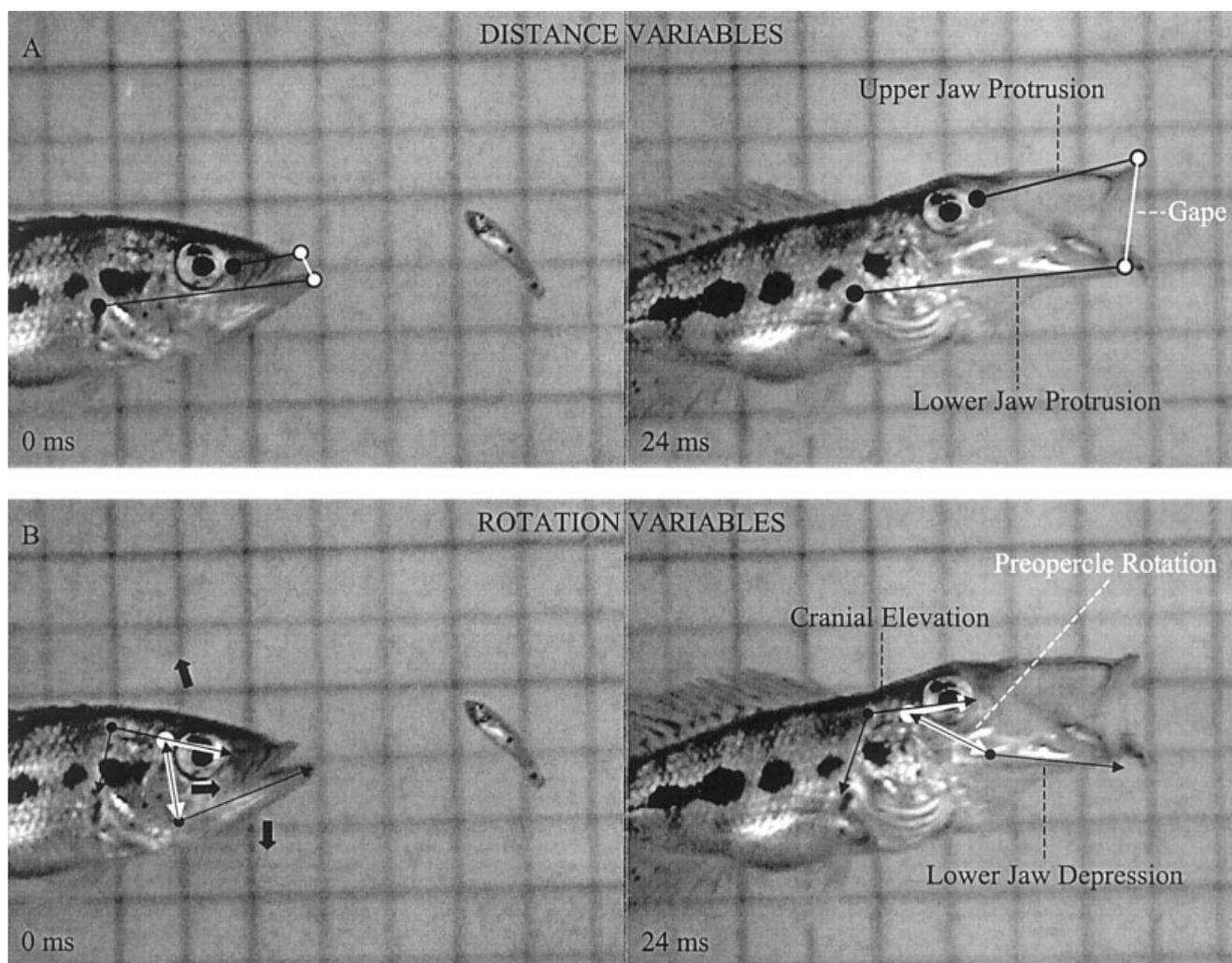


Fig. 2. Sample frames from a prey capture sequence of *Petenia splendida*. **A:** Maximum displacement was measured for upper jaw protrusion, lower jaw protrusion, and gape. Points digitized to measure upper jaw protrusion were the anterior tip of the upper jaw (UJ) and the anterior tip of the eye (EYE). Points digitized to measure lower jaw protrusion were the LJ and the most dorsal tip of the pectoral fin insertion (PF). **B:** Maximum angular rotation was measured for cranial elevation, preopercle rotation (rotation of the suspensorium), and lower jaw depression. Points digitized for cranial elevation were EYE, symphysis of the vertebral column with the neurocranium (VCN), and PF. Points digitized to measure preopercle rotation were EYE, most dorsal point of the preopercle, and the most ventral point of the preopercle. Points digitized to measure lower jaw depression were the most dorsal tip of the preopercle, the most ventral point of the preopercle, and the LJ. Arrows depict cranial elevation, rotation of the suspensorium (preopercle), and lower jaw depression.

ended after the strike with the frame in which the upper and lower jaws came back in contact. Cranial movements (displacement and rotation variables) were determined by tracking the X,Y coordinates of seven landmarks during the strike. The seven landmarks were: most anterior point of the premaxilla, most anterior point of lower jaw, most anterior point of the eye, most dorsal point of the preopercle, most ventral point of the preopercle, most dorsal point of the pectoral fin insertion, and the vertebral column/neurocranium symphysis (VCN). The lateral projection of the VCN was inferred from bone/cartilage cleared and stained specimens. Visualization of the VCN and the dorsal and ventralmost portions of the preopercle was made possible by injecting a small amount of Alcian blue stain just under the surface of the appropriately located scale (VCN) or bone (preopercle). Dye injection was performed on MS-222-anesthetized specimens. All other landmarks were readily visible without dye injection. From these landmark data four displacement variables were calculated: maximum upper jaw protrusion, maximum lower jaw protrusion, and maximum gape (Fig. 2A). Rotation

variables included: maximum lower jaw depression, maximum cranial elevation, and maximum preopercle rotation (a measure of rotation of the suspensorium) (Fig. 2B). Upper jaw protrusion was also expressed as percentage of head length for each of the three species in the single feeding sequence in which maximal upper jaw protrusion was the greatest. Excel macros were used to calculate the displacement and rotation variables.

At least three specimens of *Petenia splendida*, *Caquetaia spectabilis*, and *Astronotus ocellatus* were cleared using trypsin and double-stained using an Alcian-blue cartilage stain and alizarin-red bone stain (Dinkerhus and Uhler, 1977) to determine cranial differences between the extreme and modest jaw-protruding taxa. Specimens of *C. kraussii*, *C. myersi*, *Cichla ocellaris*, *Acaronia nassa*, and *Crenicichla geayi* were also cleared and stained for comparative purposes. Manipulations of anesthetized and cleared and stained specimens of all eight species were used to identify morphological changes permitting extreme jaw protrusion in *P. splendida* and *Caquetaia* spp.

Ram Performance

As an indication of ram performance, we measured the distance the predator moved toward the prey. Ram distance was measured as the distance the tip of the premaxilla moved toward the prey from the onset of the strike until the prey's center of mass passed the plane of the predator's mouth. Ram distance was broken down into the distance the predator moved due to axial locomotion (body ram) and the distance the predator moved due to protrusion of the upper jaws (jaw ram). The distance the premaxilla moved (ram) minus the distance the eye moved (body ram) was used to measure the distance the predator moved as a result of jaw protrusion (jaw ram). Ram, body ram, and jaw ram were also expressed as average velocities by dividing the relevant distance by the time between the onset of the strike to when the prey's center of mass passed the plane of the predator's mouth. The distance of the predator to the prey was also measured at the onset of the strike (PPD).

Suction Performance

As an indication of suction performance, we measured the distance the prey moved toward the predator as a result of suction. Suction distance was measured from the frame before the prey was first observed to move toward the predator until the frame before the center of mass of the prey passed the plane of the mouth. We measured suction distance from the beginning of suction-induced prey movement instead of from mouth opening to reduce the noise associated with prey movements not related to suction generation (e.g., prey locomotion, buoyancy, and drifting).

Suction-induced prey velocity was calculated from the last four frames before the center of mass of the prey entered the mouth. Three velocities were calculated as the prey item was drawn closer to the predator by suction. Velocity 1 was the velocity from frame 4 to 3, velocity 2 was the velocity from frame 3 to 2, and velocity 3 was the velocity from frame 2 to 1 with frame 1 being the frame before the prey's center of mass passed the predator's mouth. Feeding sequences in which the prey initiated an escape response were excluded from performance analyses.

Data Analysis

Using Systat 9.0, nested ANOVAS were performed. Individuals were nested within species. A Bonferroni-corrected post-hoc test was used to test for differences between *Petenia splendida*, *Caquetaia spectabile*, and *Astronotus ocellatus* in the kinematic and performance variables.

RESULTS

Kinematics

Following the introduction of guppy prey into experimental aquaria all predator species eagerly pursued and captured the prey. *Petenia splendida* and *Caquetaia spectabile* showed similar kinematic profiles that did not differ in any of the displacement or rotation variables. These species employed significantly more upper and lower jaw protrusion during prey capture than did *Astronotus ocellatus* (Fig. 3A; $F_{2,6} = 20.53$, $P = 0.002$ and $F_{2,6} = 8.61$, $P = 0.02$, respectively). *Petenia splendida*, *C. spectabile*, and *A. ocellatus* exhibited upper jaw protrusion as a percentage of head length equaling 55%, 52%, and 12%, respectively. On average, *A. ocellatus* exhibited less preopercle rotation (rotation of the suspensorium) at 10° than either *P. splendida* or *C. spectabile*, which exhibited 24° and 19°, respectively (Fig.

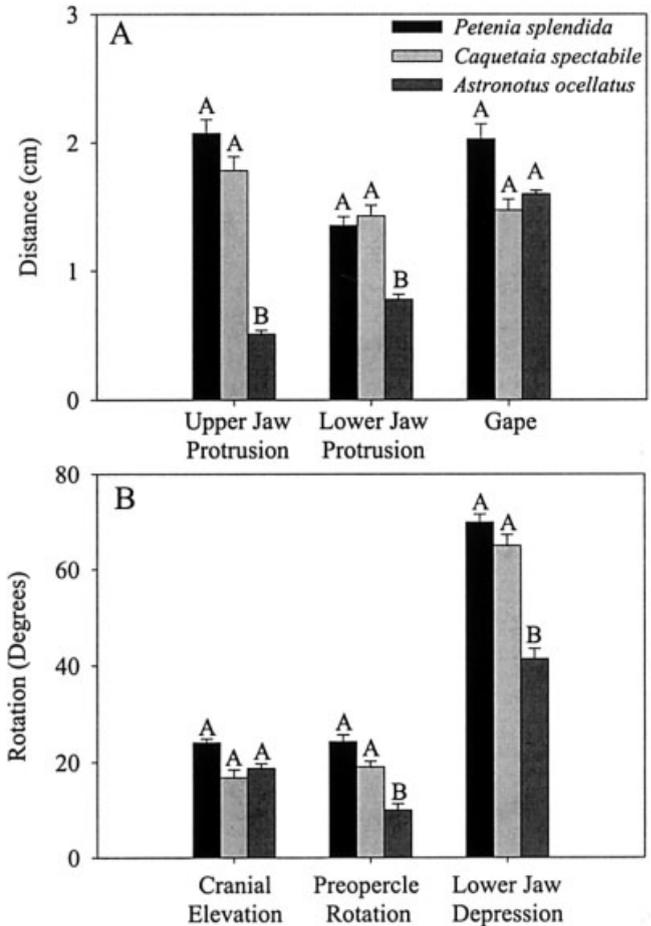


Fig. 3. Mean values and standard errors of maximum displacement and maximum rotation kinematic variables during feeding on live guppy prey. Each bar represents the mean of three individuals per species and five feeding events per individual (total = 15 feeding events per species). Indicated within the graphs are the results of the nested ANOVA tests to determine species differences ($P = 0.05$) in kinematics variables. **A:** Displacement variables were: upper jaw protrusion, lower jaw protrusion, and gape. **B:** Rotation variables were: cranial elevation, preopercle rotation, and lower jaw depression.

3B; $F_{2,6} = 12.82$, $P = 0.007$). *Astronotus ocellatus* exhibited less lower jaw depression, at 41°, than either *P. splendida* or *C. spectabile*, which exhibited 70° and 65°, respectively (Fig. 3B; $F_{2,6} = 13.35$, $P = 0.006$).

Jaw Morphology

Examination of cleared and stained specimens revealed longer upper jaws, longer lower jaws, and a longer maxilla in *Petenia splendida* and *Caquetaia spectabile* than in *Astronotus ocellatus* (Fig. 4). At rest, the extremely long ascending process of the premaxilla in *P. splendida* and *C. spectabile* extended almost to the occipital crest behind the eye, while in *A. ocellatus* the ascending process only reached the anterior margin of the eye (Fig. 4A,B).

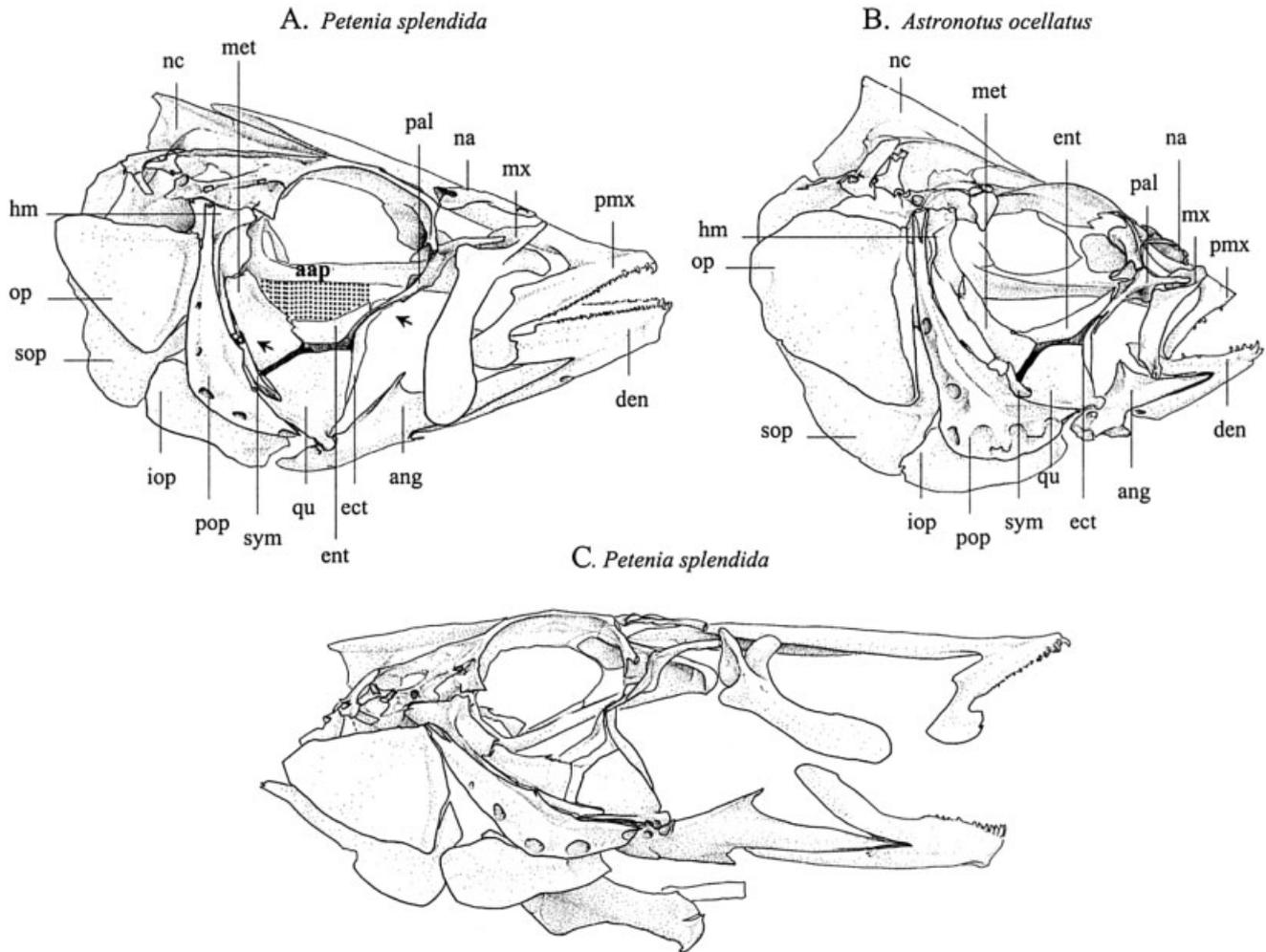


Fig 4. Anatomy of jaw protrusion: (A) the Neotropical cichlid, *Petenia splendida*, exhibiting extreme jaw protrusion and (B) *Astronotus ocellatus* exhibiting less jaw protrusion. (A) and (B) are shown in the relaxed position while (C) is shown in the protruded state. The arrows depicted in (A) reflect the anterior and posterior points of flexion within the suspensorium in both *P. splendida* and *Caquetaia spp.* Diagrams were prepared from cleared and stained specimens. aap, adductor arcus palatini; as, ascending process of premaxilla; av, alveolar process of premaxilla; pmx, premaxilla; mx, maxilla; nc, neurocranium; hm, hyomandibula; op, operculum; sop, suboperculum; iop, interoperculum; pop, preoperculum; sym, symplectic; qu, quadrate; ect, ectopterygoid; ang, angular; den, dentary.

The lower jaw in *P. splendida* and *C. spectabile* extended to the posterior margin of the eye. In *A. ocellatus* the lower jaw only reached the anterior-most margin of the eye. Additionally, manipulations of cleared and stained and anesthetized specimens revealed much greater jaw protrusion in *P. splendida* and *C. spectabile* than in *A. ocellatus*.

The ventralmost portion of the alveolar process of the premaxilla was tightly bound by ligaments to the ventralmost portion of the maxilla in *Astronotus ocellatus*. *Petenia splendida* and *Caquetaia spectabile* exhibited a loose ligamentous connection between these elements. This ligament has been referred to as the ligamentum maxillomandibulare anterius (MMA) (Kayser, 1962; Liem, 1970). In manipulated specimens of *P. splendida* and *C. spectabile* maximal jaw protrusion resulted in the alveolar process of the premaxilla extending far in front of

the ventralmost end of the fully rotated maxilla (Fig. 4C). Joining the ventral tips of these two separated bones, the MMA runs from the medial surface of the maxilla to the lateral surface of the alveolar process of the premaxilla. Extending anteriorly from the ventralmost portion of the alveolar process of the premaxilla, the MMA was found to join the lip tissue forming the corner of the mouth orifice. From their junction with the ventral end of the premaxilla, the lip tissue and MMA were found to extend ventrally, attaching to the anteriormost tip of the dentary. Thus, the ventrally extending lip tissue and MMA were found to directly connect the lower and upper jaws.

Suspensorium Morphology

Manipulations of anesthetized and cleared and stained specimens revealed greater anterior rota-

tion of the suspensorium in *Petenia splendida* and all three *Caquetaia* spp. as compared to *Astronotus ocellatus*, *Cichla ocellaris*, *Acaronia nassa*, and *Crenicichla geayi*. An anterior point of flexion was observed within the suspensorium of *P. splendida* and all three *Caquetaia* spp. *Astronotus ocellatus*, *C. ocellaris*, *A. nassa*, and *C. geayi* exhibited a rather firm connection between the pterygoids (ecto- and endopterygoid) and the palatine. However, in *P. splendida* and *Caquetaia* spp. the palatine articulated with the pterygoids by a thin flexible, cartilaginous strip (Fig. 4A).

A second point of flexion was observed between the hyomandibula and the symplectic in *Petenia splendida* and all three *Caquetaia* spp. (Fig. 4A). The loosening of the palatine from the pterygoids represents an anterior point of flexion within the suspensorium and the space between the hyomandibula and the symplectic represents a posterior point of flexion within the suspensorium. The presence of both an anterior and a posterior point of flexion within the suspensorium in *P. splendida* and all three *Caquetaia* spp. permits considerable dorsoanterior rotation of the distal portion of the suspensorium. In these species the suspensorium (composed of the symplectic, metapterygoid, ectopterygoid, endopterygoid, and quadrate) moved as a unit and was found to rotate dorsoanteriorly at the articulation with the hyomandibula. This dorsoanterior rotation of the suspensorium was made possible by the flexible connection between the palatine and the pterygoids. As is typical of teleosts, all other species examined in this study including *Astronotus ocellatus* exhibited a firm connection between the palatine and the rest of the suspensorium (pterygoids) and the neurocranium (Fig. 4B). No movement of the hyomandibula was observed in the anterior-to-posterior axis. The considerable rotation of the suspensorium in *P. splendida* and all three *Caquetaia* spp. increased lower jaw protrusion, which in turn augmented upper jaw protrusion.

The preopercle was located lateral to the suspensorium and was tightly connected by ligaments along its ventral ramous to the quadrate near the jaw joint. The connection to the quadrate resulted in the preopercle being functionally associated with the kinetic portion of the suspensorium rather than the hyomandibula. As reported by Kullander (1996), we found the bones of the suspensorium in *Petenia splendida* and all three *Caquetaia* spp. to be reduced in size as compared to *Astronotus ocellatus*, *Cichla ocellaris*, *Acaronia nassa*, and *Crenicichla geayi*.

Ram Performance

Petenia splendida exhibited greater ram distance than either of the other two species and *Caquetaia spectabile* was found to have greater ram than *Astronotus ocellatus* (Fig. 5A; $F_{2,6} = 11.71$, $P = 0.008$). *Petenia splendida* had a greater body ram than the

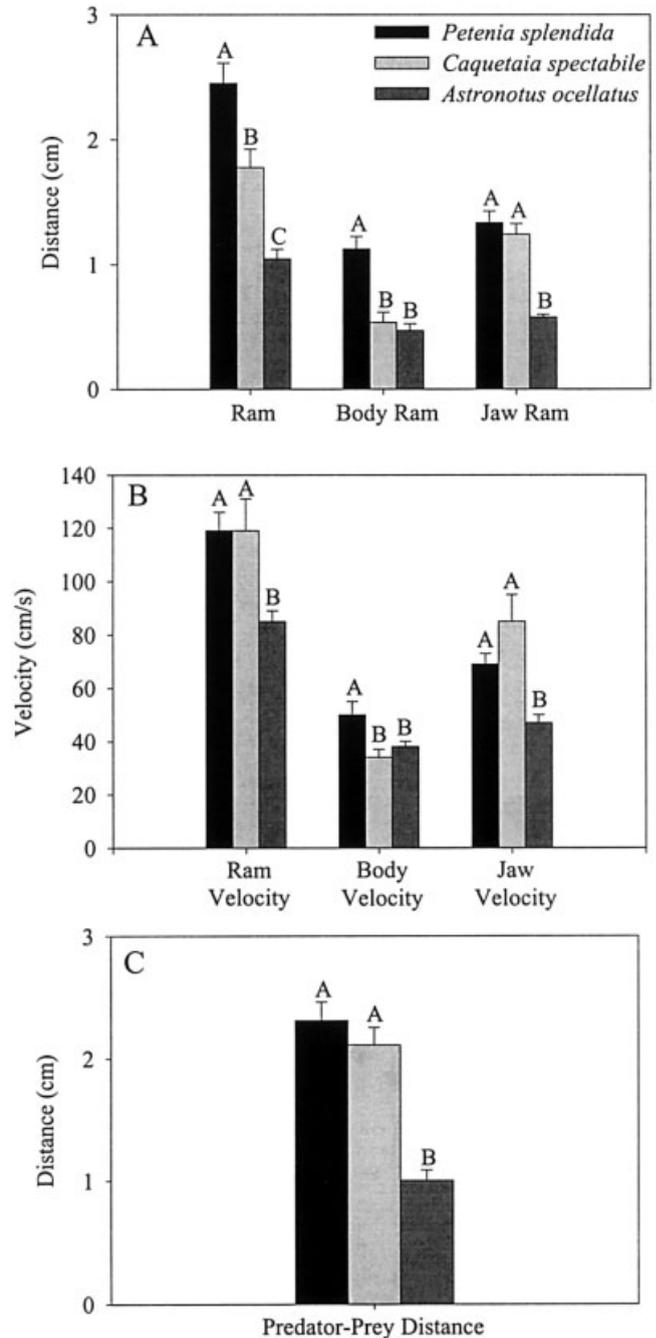


Fig. 5. Mean values and standard errors of ram performance variables during feeding on live guppy prey. **A:** Distance predator moved as a result of locomotion (body ram), upper jaw protrusion (jaw ram), and the combined total movement of the predator (ram). **B:** Predator body velocity, jaw velocity, and the combined ram velocity. **C:** Predator-prey distance at mouth opening. Each bar represents the mean of three individuals per species and five feeding events per individual (total = 15 feeding events per species). Indicated within the graphs are the results of the nested ANOVA tests to determine species differences ($P = 0.05$) in ram performance variables.

other two species, which were not statistically different from each other for this variable (Fig. 5A; $F_{2,6} = 7.41$, $P = 0.02$). *Petenia splendida* and *C.*

spectabile did not differ in jaw ram but both exhibited greater jaw ram than *A. ocellatus* (Fig. 5A; $F_{2,6} = 9.41$, $P = 0.01$). Ram performance using distance and velocity measures led to identical conclusions about species differences with one exception. *Petenia splendida* exhibited a statistically higher ram than *C. spectabile* in the distance analysis but the two species did not differ statistically in the velocity analysis (Fig. 5B). The distance at which *P. splendida* and *C. spectabile* initiated a strike, predator–prey distance, did not differ but both began their strikes at a distance greater than exhibited by *A. ocellatus* (Fig. 5C; $F_{2,6} = 9.89$, $P = 0.01$).

Suction Performance

Suction distance was significantly greater for *Astronotus ocellatus* than either *Petenia splendida* or *Caquetaia spectabile* (Fig. 6A; $F_{2,6} = 9.39$, $P = 0.01$). Average suction-induced prey velocity measures calculated from the last four frames before the prey's center of mass passed the mouth indicated higher suction generation in *A. ocellatus*. Although average prey velocity 1 did not differ among the species (Fig. 6B; $F_{2,6} = 0.53$, $P = 0.612$), average prey velocities 2 and 3 indicated that *A. ocellatus* moved guppy prey at significantly higher velocities than both *P. splendida* and *C. spectabile*, which did not differ (Fig. 6B; $F_{2,6} = 9.71$, $P = 0.01$ and $F_{2,42} = 9.32$, $P = 0.01$, respectively). All three species revealed a pattern of increased suction-induced prey velocity as the prey was drawn closer to the mouth.

DISCUSSION

All three of the Neotropical cichlids utilized lower jaw depression, cranial elevation, and rotation of the suspensorium to protrude the jaws anteriorly (Fig. 1C). Specimen manipulations and kinematic data revealed greater lower and upper jaw protrusion in *Petenia splendida* and *Caquetaia spectabile* as compared to the more generalized *Astronotus ocellatus*. Although cranial elevation acts to rotate the lower jaw into a more anterior position in these species, no significant difference in this contribution was found between the species. The greater anterior protrusion of the lower jaws exhibited by *P. splendida* and *C. spectabile* can be explained by a combination of increased lower jaw depression and increased prepercle rotation (rotation of the suspensorium). *Petenia splendida* and *Caquetaia spp.* exhibited anterior and posterior points of flexion within the suspensorium, permitting considerable dorsoanterior motion of the suspensorium augmenting lower jaw protrusion. Upper jaw protrusion results passively from movements of the lower jaw, so it was not surprising that the species exhibiting extreme lower jaw protrusion also exhibited extreme upper jaw protrusion.

This research has not directly addressed the problem of which muscles are the crucial actuators in the

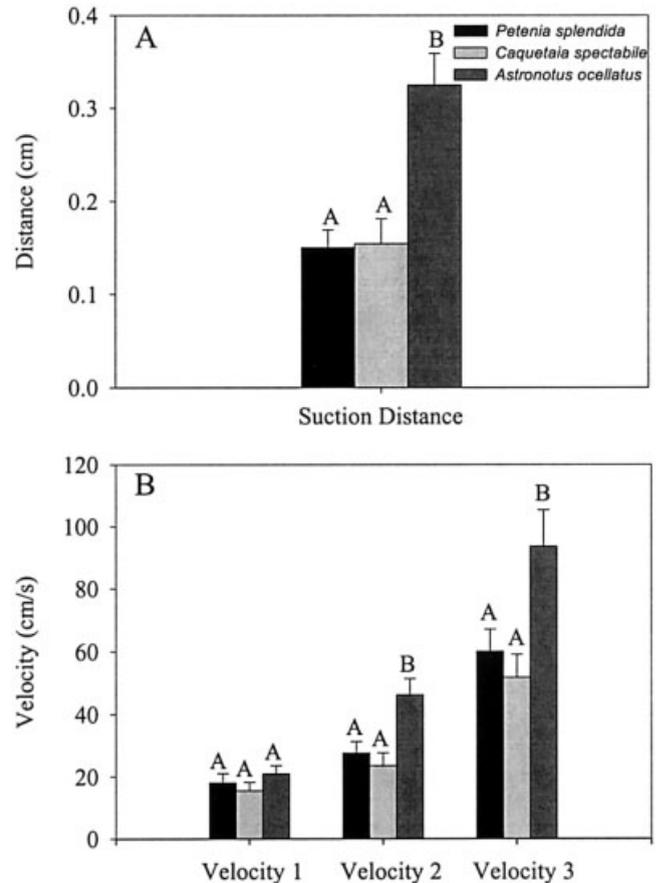


Fig. 6. Mean values and standard errors of suction performance variables during feeding on live guppy prey. **A:** Distance prey moved toward predator as a result of suction generation (suction distance). **B:** Average prey velocity calculated from the last four frames before the prey's center of mass entered the predator's mouth. Velocity 1 is the velocity from frames 4 to 3, velocity 2 is the velocity from frames 3 to 2, and velocity 3 is the velocity from frames 2 to 1 with frame 1 being the frame before the prey's center of mass passed the predator's mouth. Each bar represents the mean of three individuals per species and five feeding events per individual (total = 15 feeding events per species). Indicated within the graphs are the results of the nested ANOVA tests to determine species differences ($P = 0.05$) in suction performance variables.

novel jaw movements seen in *Petenia splendida* and *Caquetaia spp.*, but we offer the following inferences and predictions based on our observations of the anatomy and kinematics of feeding in these fishes. Most of the movements that we document during prey capture can be attributed to the traditional actions of cranial muscles. These include the role of the epaxialis in cranial elevation, the adductor mandibulae muscle in jaw adduction, and the sternohyoideus muscle in hyoid depression and rotation of the lower jaw during opening. But how is anterior rotation of the suspensorium on the neurocranium accomplished? We hypothesize that the adductor arcus palatini (aap) accomplishes this by drawing the suspensorium toward the origin of the muscle on the midline-positioned parasphenoid bone (Fig. 4A). As

in other described cichlids (Liem, 1979; Dutta, 1987), the aap muscle is parallel-fibered and inserts on the dorsomedial face of the suspensorium. If the suspensorium is initially oriented dorsoventrally, it appears that contraction of this muscle will rotate the suspensorium anteriorly while adducting it medially. It is interesting that our prediction for aap action during mouth opening and buccal expansion would involve a major change in the activity period of this muscle, which has been shown to be active during buccal compression in other cichlids (Liem, 1979). A similar role for the aap has been proposed to function in lower jaw-protruding chaetodontids (Ferry-Graham et al., 2001b).

Kinematic and Morphological Convergence Among Extreme Jaw-Protruding Teleosts

The labrid, *Epibulus insidiator*, exhibits the greatest amount of anterior jaw protrusion known (65% of its head length), relying almost exclusively on rotation of the suspensorium during jaw protrusion, rather than lower jaw depression or cranial elevation (Westneat and Wainwright, 1989). Feeding kinematics of *Luciocephalus pulcher* have revealed that it utilizes a combination of lower jaw depression and cranial elevation to protrude the jaws anteriorly as much as 33% of its head length (Lauder and Liem, 1981). Recent investigations have revealed that *Monocirrhus polyacanthus* is capable of anterior protrusion of 60% of the head length via lower jaw depression, extreme cranial elevation, and rotation of the suspensorium (Waltzek, unpubl. data). Thus, it appears that there are multiple kinematic pathways by which different lineages have evolved extreme jaw protrusion.

As lower jaw depression and cranial elevation are exhibited by nearly all teleosts, the morphological features that permit these kinematic events are well understood. However, prior to this study rigorous demonstration of rotation of the suspensorium had only been confirmed to have evolved once within labrids (Westneat and Wainwright, 1989), at least once within chaetodontids (Ferry-Graham et al., 2001b), and speculated to have evolved within nandids (Liem, 1970). While the aforementioned cichlids, chaetodontids, labrid, and nandid taxa differ in the location of the novel joints or points of flexion within the suspensorium, all taxa involved exhibit a marked reduction in some or all of the anterior bones of the suspensorium (e.g., ecto- and endopterygoids and palatine). This reduction provides room for the anterior rotation of the suspensorium. Reduction of the ecto- and endopterygoids often results in a loose cartilaginous connection (*Petenia splendida*, *Caquetaia spp.*, and *Monocirrhus polyacanthus*), ligamentous connection (*Chelmon rostratus*), joints (*Forcipiger longirostris*, *Forcipiger flavissimus*), or even a total disassociation (*Epibulus insidiator*) between these bones and the ventral end

of the palatine. As the palatine is ligamentously connected to the neurocranium, a loosening between the palatine and the rest of the suspensorium frees the rest of suspensorium from this rigid connection to the neurocranium. This anterior loosening combined with a posterior loosening within the suspensorium, as exemplified by a loose connection between the hyomandibula and the symplectic, permits anterior rotation of the suspensorium.

The disassociation of the palatine from the ecto- and endopterygoids has been noted in every fish known or suspected to exhibit extreme rotation of the suspensorium, including: the labrid *Epibulus insidiator* (Westneat and Wainwright, 1989), the chaetodontids *Forcipiger longirostris* and *F. flavissimus* (Ferry-Graham, 2001b), the nandid *Monocirrhus polyacanthus* (Liem, 1970; Waltzek, unpubl. data), and the cichlids *Petenia splendida* (this study) and *Caquetaia spp.* (this study). Thus, the evolution of a loose association between the palatine and the ecto- and endopterygoids via a reduction in these bones appears to represent a functional prerequisite to the development of extreme rotation of the suspensorium (Westneat, 1991). Interestingly, even *Astronotus ocellatus* exhibited modest rotation of the suspensorium, while exhibiting a rather firm connection between the palatine, ecto-, and endopterygoids. This modest rotation of the suspensorium may be the result of slight anterior rotation of the hyomandibula at its joint with the neurocranium or at its point of flexion with the symplectic, coupled with minor rocking movements of the palatine on the neurocranium.

Ram Performance

Petenia splendida and *Caquetaia spectabile* exhibited greater initial predator prey-distance (Fig. 5C) and ram velocity (Fig. 5B) than *Astronotus ocellatus*. These data are consistent with previous work on other cichlid species (Wainwright et al., 2001) that found that species that initiate strikes from further away exhibit higher ram velocities. Although ram was greater in *P. splendida* than in *C. spectabile* as a result of a significantly higher body ram, the ram velocity was not statistically different because *C. spectabile* performs its attack in less time than *P. splendida* (data not shown). The greater distances and velocities during the strike in *P. splendida* and *C. spectabile* as compared to *A. ocellatus* were primarily due to increased upper jaw protrusion (Fig. 5A,B). This supports the hypothesis that jaw protrusion increases the ram velocity of the predator (Schaeffer and Rosen, 1961; Alexander, 1967; Nyberg, 1971; Lauder and Liem, 1981; Westneat and Wainwright, 1989; Ferry-Graham et al., 2001a).

An elongate fusiform body, as exhibited by *Petenia splendida*, is often seen in predators capable of high ram velocities during prey capture (Videler, 1993). Lateral compression, as exhibited by *Caquetaia*

spectabile and *Astronotus ocellatus*, may increase maneuverability (Webb, 1976; Videler, 1993). As expected, *P. splendida* exhibits significantly greater body velocity than either *C. spectabile* or *A. ocellatus*, which primarily hunt fishes among structure such as the roots of trees and aquatic vegetation (Winemiller, 1990). *Petenia splendida* exhibited the highest ram velocity combining both high body velocity with substantial jaw velocity during prey capture. The ram velocity of *C. spectabile* is primarily composed of substantial jaw protrusion and moderate body locomotion. Finally, the ram velocity of the strike of *A. ocellatus* is best characterized as a nearly equal combination of moderate body locomotion and moderate jaw velocity.

Suction Performance

Astronotus ocellatus exhibited a higher suction distance than either *Petenia splendida* or *Caquetaia spectabile*. Suction-induced prey velocity was also higher in *A. ocellatus* than either *P. splendida* or *C. spectabile*. Thus, the extreme jaw-protruding taxa appear to generate less suction than *A. ocellatus*. Differences between species in suction distance may reflect differences in the flow that is generated during feeding. However, this interpretation is complicated by the fact that attack velocities were highest in *P. splendida* and *C. spectabile*, indicating that the suction-induced flow does not reach the prey until later in the strike, potentially constraining suction distance. Nevertheless, these data conflict with the hypothesis that increased jaw protrusion enhances suction generation.

Interestingly, in a previous study we found no significant difference in suction distance between *Astronotus ocellatus* and *Petenia splendida* (Wainwright et al., 2001). This discrepancy appears to result from a refinement in the method used to measure suction distance in the present study. Previously, we measured suction distance from the onset of fast mouth opening (Wainwright et al., 2001). Here we measured suction distance from the onset of movement of the prey toward the predator, an event that always occurred later in the strike sequence than the onset of fast opening. This difference in reference points for the onset of the measurement may limit error associated with prey motion that is not due to suction, such as an escape response or drifting. The previous values of mean suction distance (Wainwright et al., 2001; *P. splendida* = 0.15, *A. ocellatus* = 0.25) are similar to the present study (*P. splendida* = 0.15, *A. ocellatus* = 0.32). However, variance was dramatically reduced in the present study (compare *P. splendida* = 0.06, *A. ocellatus* = 0.07 and *P. splendida* = 0.01, *A. ocellatus* = 0.02, respectively).

A smaller, more circular mouth opening resulting from protrusion of the jaws has been suggested as a factor that could increase the velocity of water en-

tering the mouth. The diameter of the mouth from the tip of the upper jaw to the tip of the lower jaw at peak gape was not statistically different between the three species (Fig. 3A). Thus, these data cannot test the hypothesis that mouth size affects suction performance.

CONCLUSIONS

The Neotropical cichlids *Petenia splendida* and *Caquetaia spectabile* displayed extraordinarily protrusible jaws, equaling 55% and 52% of head length, respectively, as compared to the more modest 12% found in *Astronotus ocellatus*. Greater anterior jaw protrusion in *P. splendida* and *C. spectabile* resulted from increased lower jaw depression and anterior rotation of the suspensorium. Enhanced rostral motion of the suspensorium in *P. splendida* and *C. spectabile* was possible due to anterior and posterior points of flexion within the suspensorium. Extreme jaw protrusion in *P. splendida* and *C. spectabile* significantly increased ram performance but resulted in reduced suction performance.

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