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Modeling the Jaw Mechanism of *Pleuronichthys verticalis*: The Morphological Basis of Asymmetrical Jaw Movements in a Flatfish

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ABSTRACT   Several flatfish species exhibit the unusual feature of bilateral asymmetry in prey capture kinematics. One species, *Pleuronichthys verticalis,* produces lateral flexion of the jaws during prey capture. This raises two questions: 1) How are asymmetrical movements generated, and 2) How could this unusual jaw mechanism have evolved? In this study, specimens were dissected to determine which cephalic structures might produce asymmetrical jaw movements, hypotheses were formulated about the specific function of these structures, physical models were built to test these hypotheses, and models were compared with prey capture kinematics to assess their accuracy. The results suggest that when the neurocranium rotates dorsally the premaxillae slide off the smooth, rounded surface of the vomer (which is angled toward the blind, or eyeless, side) and are "launched" anteriorly and laterally. The bilaterally asymmetrical trajectory of the upper jaw is determined by the orientation of the "launch pad," the vomer. During lower jaw depression, the mandibles rotate about their articulations with the quadrate bones of the suspensoria. The quadrato-mandibular joint is positioned farther anteriorly on the eye side than on the blind side, and this asymmetry deflects the lower jaw toward the blind side. Asymmetry in the articular surfaces of the lower jaw augments this effect. Thus, it appears that fish with intermediate forms of this asymmetrical movement could have evolved from symmetrical ancestors via a few key morphological changes. In addition, similar morphological modifications have been observed in other fish taxa that also produce jaw flexion during feeding, which suggests that there may be convergence in the basic mechanism of asymmetry. J. Morphol. 256:1–12, 2003.   © 2003 Wiley-Liss, Inc.

KEY WORDS: flatfish; feeding; asymmetry; modeling

All flatfish (Pleuronectiformes) are descended from a common ancestor that was pelagic (i.e., living in the water column) and morphologically bilaterally symmetrical (Carroll, 1988; Chapleau, 1993). However, extant flatfish are benthic (spending most of their time on the bottom) and are morphologically asymmetrical as adults. Much of this morphological asymmetry appears to be a consequence of an unusual modification for their benthic habit: all adult flatfish have both eyes on one side of the head. This modification allows flatfish to lie on the bottom on their eyeless (or blind) side while looking into the water column for potential predators or prey. However, the presence of both eyes on the same side of the head (i.e., the eyed side) also causes morphological asymmetry of the skull and jaws (Yazdani, 1969).

Morphological asymmetry of the feeding apparatus creates the potential for another unusual vertebrate trait: asymmetry in jaw movements during prey capture. Two species of flatfish are known to exhibit asymmetrical jaw movements during prey capture (Gibb, 1995, 1996), although the type of asymmetrical movement (i.e., kinematic asymmetry) is different in the two species examined. One species, *Xystreurys liolepis*, produces limited kinematic asymmetry during prey capture. In this species, the maxilla (a bone of the upper jaw) is longer on the eyed side than on the blind side. The additional length of the eyed-side maxilla allows it to rotate farther anteriorly than the blind side maxilla and obscure the "V" created by lower jaw depression during prey capture. This is the only kinematic asymmetry present in the feeding behavior of *X. liolepis* (Gibb, 1996).

The second species of flatfish, *Pleuronichthys verticalis,* exhibits more extreme kinematic asymmetry. In this species, the jaws deflect toward the blind side during prey capture. This deflection involves a suite of asymmetrical movements: the bones of the lower jaw and the upper jaw deviate from the anatomical midline of the fish (i.e., the midsagittal plane), and gape is smaller on the blind side. Deviation of the jaws out of the midsagittal plane is unusual among vertebrates; natural selection is thought to maintain symmetry in most vertebrate jaws because any deviation from symmetry could negatively affect the ability to acquire food (Neville, 1976). Thus, the jaw mechanism of *P. verticalis* presents two interesting questions, one biomechanical

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and one evolutionary. First, how is asymmetrical movement generated? Second, how could this unusual jaw mechanism have evolved?

To address these questions, I will: 1) describe the morphology of the feeding apparatus in *Pleuronichthys verticalis* to determine which structures may produce asymmetrical movements, 2) formulate hypotheses about the function of these structures, 3) use three-dimensional physical models to test the hypotheses, and 4) compare the mechanical models with *P. verticalis* prey capture kinematics to assess the models. In addition, I compare the jaw mechanisms of this species with those previously described for: 1) symmetrical teleosts (i.e., derived bony fishes), 2) *Perissodus eccentricus*, a cichlid known to have asymmetrical jaw movements (Liem and Stewart, 1976), and 3) *Pleuronectes platessa*, a related species of flatfish. Finally, I propose a pathway by which this unusual prey capture mechanism may have evolved.

MATERIALS AND METHODS
Species Used

Pleuronichthys verticalis (Jordon and Gilbert) were chosen for this study because of their asymmetrical morphology and prey capture kinematics (Gibb, 1995). Specimens of *P. verticalis* were collected at 30-m depths in the coastal waters of Orange County, California, using an otter trawl. Specimens collected in good condition were kept alive in saltwater aquaria and used for high-speed video analysis of prey capture. Details of methods used for the videotaping and kinematic analysis can be found in Gibb (1995). Other specimens were euthanized, preserved, and used for anatomical preparations.

Anatomical Description

Anatomical drawings of the head and jaws *Pleuronichthys verticalis* were made using preserved specimens, a Zeiss microscope with a camera lucida attachment, a graphics tablet, and a Macintosh personal computer. Some specimens were chemically preserved by immersion in buffered formalin for several days, then transferred to a 70% ethanol solution. These specimens were cleared and stained following methods described in Taylor (1967) to examine the cephalic bones and cartilage of intact individuals. Drawings of the intact skull and jaws were made directly from cleared and stained individuals using the camera lucida and the graphics tablet.

Other specimens were preserved by freezing, then thawed and dissected. Drawings of individual bones from one specimen were made using a microscope, camera lucida, and computer as described above. Images of bones taken from another specimen were recorded using a video camera with a macro lens, uploaded to a computer, and measured using custom digitizing software. Angles of skull bones relative to the midsagittal plane were determined using the base of the skull as a surface perpendicular to the anatomical midline (a frontal plane), and assuming the midsagittal plane would transect the foramen magnum; this region shows little morphological asymmetry in this species (pers. obs.).

Models of Jaw Mechanisms

A physical model was constructed in the BioDesign Laboratory at Duke University in three steps. First, frozen specimens were thawed, manipulated, and dissected to assess the contributions that different structures of the cephalic region make to passive asymmetrical jaw movements. Second, detailed notes and drawings were made of the cephalic structures and passive movements of the jaws and skull. Third, the information gathered in the first two steps was used to create a physical model based on the cephalic morphology of *Pleuronichthys verticalis*. One of the main criteria used in building the model was that it be as simple as possible. Thus, only information believed to be relevant to the jaw movements was incorporated into the model.

The model was built out of a variety of materials. In general, materials were selected to imitate the property of the structures they represented. Thus, wood (stiff and inflexible) was used to represent bone, string (compressible and somewhat compliant) was used for ligaments and tendons, and elastic (compliant and resilient) was used to represent antagonistic muscles. The articulation between the neurocranium (the vomer region) and the upper jaw was represented by a sliding joint that allowed movement in only one plane. However, this plane was not parallel to any of the three anatomical planes (sagittal, frontal, or transverse) of the fish, but instead allowed the upper jaw to move both anteriorly and ventrally during mouth opening. The articulations between the suspensoria and the mandibles of the lower jaw (the quadrato-mandibular or QM joints) were represented by two ball-and-socket joints that allowed both dorsal-ventral and medial-lateral rotation of the jaw about the fulcra. Movement was produced by pulling on strings attached to the posterior region of the neurocranium (representing the epaxial musculature) and the posterior end of the lower jaw (representing the ligaments attaching the mandibles to the opercular series).

The model was built in two stages. The initial model did not incorporate asymmetrical morphology and did not produce asymmetrical jaw movements when manipulated. However, the second version of the model did incorporate asymmetrical morphology and did produce asymmetrical movements. This approach was used to determine the minimum changes necessary in the skull and jaws of *Pleuronichthys verticalis* to produce asymmetrical jaw movements (i.e., the number of differences between the two versions of the model). After the asymmetrical version of the model was constructed, it was manipulated to determine if it emulated the jaw movements of *P. verticalis*. At this point, the model was evaluated qualitatively on its ability to emulate the jaw movements of the flatfish and design features of the model were modified to improve the emulation.

Computer-generated graphical representations of the physical model were made using the program Ray Dream Studio for the Macintosh. Length, width, and depth parameters were entered into the computer for bones of the upper jaw, lower jaw, suspensoria, and neurocranium. These parameters were used to generate schematic, three-dimensional models of the jaw mechanisms. The primary goal of the computer models was to create 3D animations that represent the physical model. QuickTime movies based on these animations are posted on the World Wide Web (http://jan.ucc.nau.edu/~acg/models/).

RESULTS
Cephalic Anatomy and Asymmetry

Individuals of *Pleuronichthys verticalis* possess asymmetry in the neurocranium, the suspensoria, the palatine bones, and the upper and lower jaws. The opercular series and the hyoid region show little asymmetry (Fig. 1). The neurocranium is twisted toward the eyed side of the head and the upper and lower jaws point slightly toward the blind side of the head.

Individual bones used in the morphological analysis were taken from a representative specimen of 172 mm standard length (a different individual of a similar size was used for the camera lucida drawings of individual bones, see Materials and Meth-
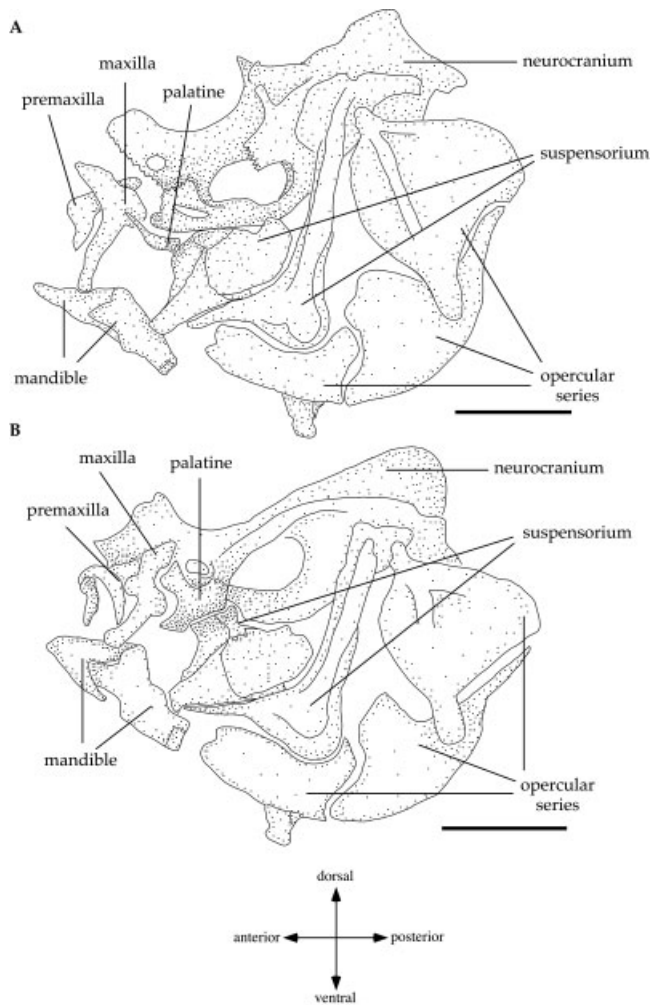
Fig. 1. Camera lucida drawings of lateral views of a cleared and stained skull of *Pleuronichthys verticalis*: (**A**) blind side and (**B**) eyed side. The bony ridge between the orbits (part of the right frontal and prefrontal bones) has been removed to expose the jaw structure beneath. Note that the eyed side has been flipped horizontally to facilitate comparisons with the blind side. Scale bar = 1 cm.

ods); individuals used for kinematic analyses ranged from 159–183 mm standard length (Gibb, 1995). Examination of the bones reveals that the palatine has a different shape on the two sides of the head (Fig. 2A). The blind side palatine is 5.2 mm long and 0.5 mm deep at its tip and is slender and delicate in shape. In contrast, the eyed side palatine bone is 6.3 mm long and 0.29 mm deep at its tip and is large and robust overall. The palatine of the blind side articulates with the left prefrontal bone of the neurocranium and abuts the posterior surface of the head of the maxilla (Fig. 1). The palatine on the eyed side does not abut the neurocranium or the maxilla (in Fig. 1 it is lateral to the maxilla).

The maxilla is the most asymmetrical bone in the cephalic region (Fig. 2B). On both sides, the maxilla has a shape that is very different from the maxillae

previously described for other species of teleost fishes (see Gregory, 1932). On the blind side, it is possible to identify the "head" and the ventral process of the maxilla (Fig. 2B). However, on the eyed side, this bone is almost unrecognizable as a maxilla. The anterior process protruding from the "head" of the maxilla (Fig. 2B) and the rounded surface of the posterior region of the "head" are particularly unusual. In the intact organism, the anterior process abuts the medial ethmoid region of the neurocranium (Fig. 1) and the posterior rounded surface is dorsal to the vomer.

For *Pleuronichthys verticalis*, it is useful to consider the bones of the head and jaws as functional units. In an intact specimen, the premaxillae and maxillae are tightly bound together by connective tissue. Thus, these four bones and the associated cartilage and connective tissue comprise a single functional unit (Fig. 3) of the upper jaw: the
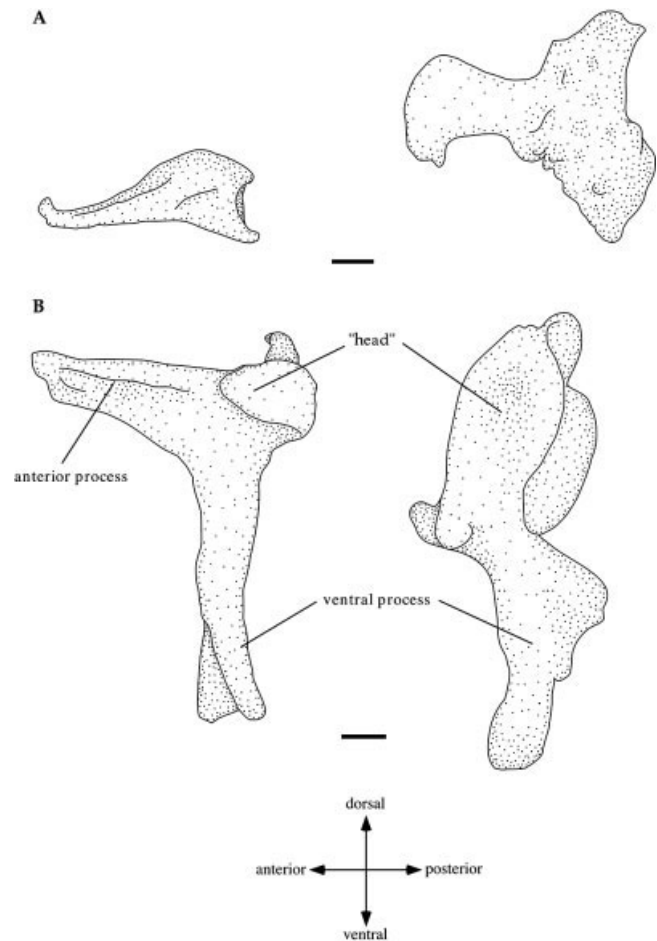

Fig. 2. Camera lucida drawings of lateral views of isolated bones from *Pleuronichthys verticalis*: (**A**) the palatine bones; (**B**) the maxillae. Bones from the eyed side of the head are on the left; bones from the blind side of the head are on the right. Palatine bones and maxillae are drawn from a lateral view. Bones from the eyed side have been reversed horizontally to facilitate comparisons with the blind side. Scale bar = 1 mm.
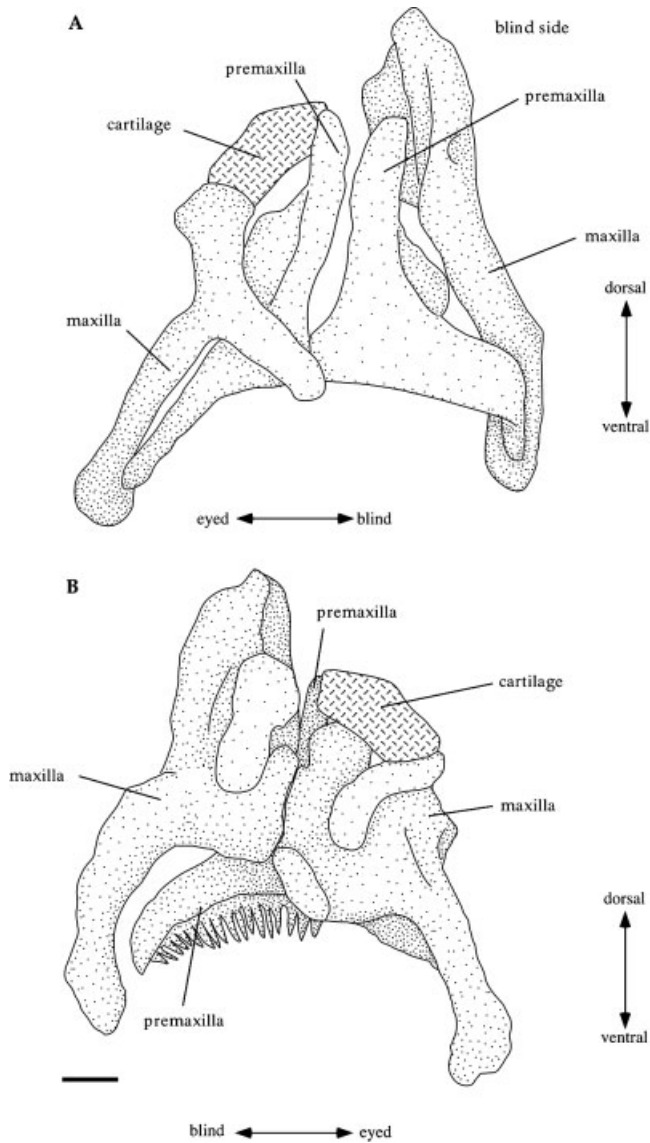
Fig. 3. Camera lucida drawings of the maxillae–premaxilla complex (MPC) of *Pleuronichthys verticalis*: (**A**) a dorsal view (looking down on the upper jaw) and (**B**) a posterior view (looking out through the mouth). The maxillae and premaxillae are held together with connective tissue. Scale bar = 1 mm.

maxillae–premaxillae complex (MPC). The MPC is curved at the articulation of the four bones and the descending processes of the two maxillae protrude laterally and ventrally (Fig. 3A). In a MPC from a fresh specimen, there are several small circular pads of cartilage loosely attached to the medial surface of the complex. Teeth are only present on the blind side premaxilla (Fig. 3B).

The portion of the neurocranium immediately medial to the MPC is the vomer (Fig. 4). In *Pleuronichthys verticalis* the vomer is not parallel to the midsagittal plane (Fig. 4C) and the parasphenoid, which supports the vomer, is also tilted relative to the sagittal plane (Fig. 4A,C). The dorsal surface of the

vomer has a steep dorsal-ventral slope of approximately 54° (Fig. 4A).

The dentary, angular, and articular bones form a complex commonly referred to as the mandible. The two mandibles in *Pleuronichthys verticalis* are asymmetrical and form a lower jaw complex that is more robust on the blind side than on the eyed side. Teeth are only present on the blind side dentary (Fig. 5). The dentary bones are particularly asymmetrical; at the anterior tip the eyed-side dentary bone is approximately 2.8 mm wide and the blind side dentary bone is 4.5 mm wide (Fig. 5). The entire mandible is longer on the blind side than on the eyed side; however, the articular groove (which abuts the suspensorium) is located more anteriorly on the
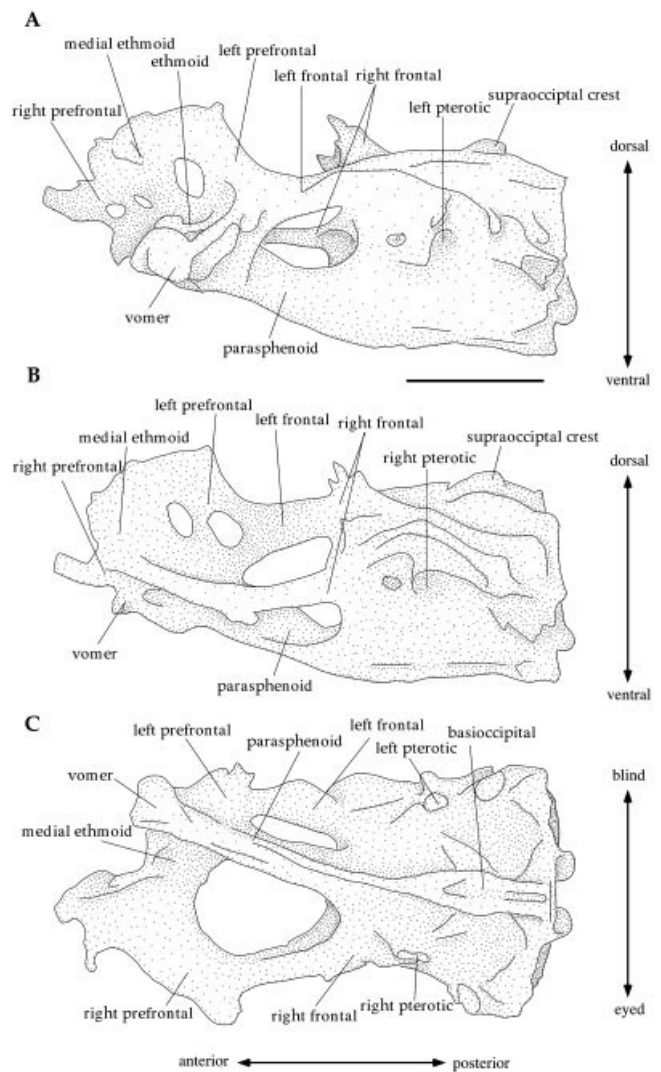

Fig. 4. Camera lucida drawings of the skull of *Pleuronichthys verticalis* from three views: (**A**) a lateral view of the blind side, (**B**) a lateral view of the eyed side, and (**C**) a medial view of the ventral aspect of the skull. Note that the eyed-side image of the skull has been reversed horizontally to facilitate comparisons with images of the blind side and ventral aspect of the skull. Scale bar = 1 cm.

long (anteroposteriorly) on the eyed side and 17 mm long on the blind side and the hyomandibula and preopercle are 24 mm high (dorsoventrally) on the eyed side and 23 mm high on the blind side. In addition, the articulation of the hyomandibula with
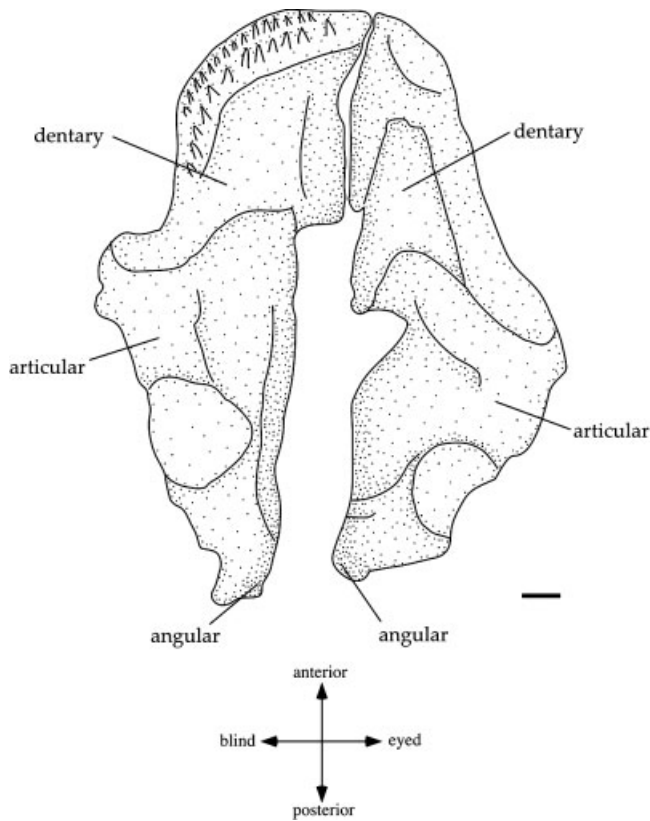

Fig. 5. Camera lucida drawings of a medial view of the lower jaw of *Pleuronichthys verticalis*. The two mandibles are composed of the dentary, articular, and angular bones. Scale bar = 1 mm.

blind side (Fig. 5). Due to this asymmetry, the distance from the articular groove to the jaw symphysis is actually longer on the eyed side than on the blind side. Thus, the two halves of the mandible are distinct when compared to one another.

The suspensorium is involved in movements of both the upper and the lower jaw. At the anteroventral end of the suspensorium the quadrate bones form articular surfaces (Fig. 6). These surfaces serve as fulcra about which the mandibles (Fig. 5) rotate during lower jaw depression (this joint is termed the quadrato-mandibular or QM joint). The dorsal region of the suspensorium is composed of the hyomandibula, which suspends the entire apparatus from the pterotic region of the neurocranium (Figs. 1, 6). The anterodorsal region of the suspensorium is attached to the palatine bone (Figs. 1, 4, 6). The palatine bone, in turn, is connected by the maxilla-palatine ligament to the maxilla (Yazdani, 1969; Gibb, 1995). On the blind side, the palatine bone physically abuts the maxilla in addition to being connected by a ligament (Fig. 1); on the eyed side, the palatine bone is only connected to the maxilla by the maxilla-palatine ligament. In addition, the suspensorium is asymmetrical in length, height, and position of attachment to the skull (Figs. 4, 6). The preopercle, quadrate, and symplectic are 19 mm
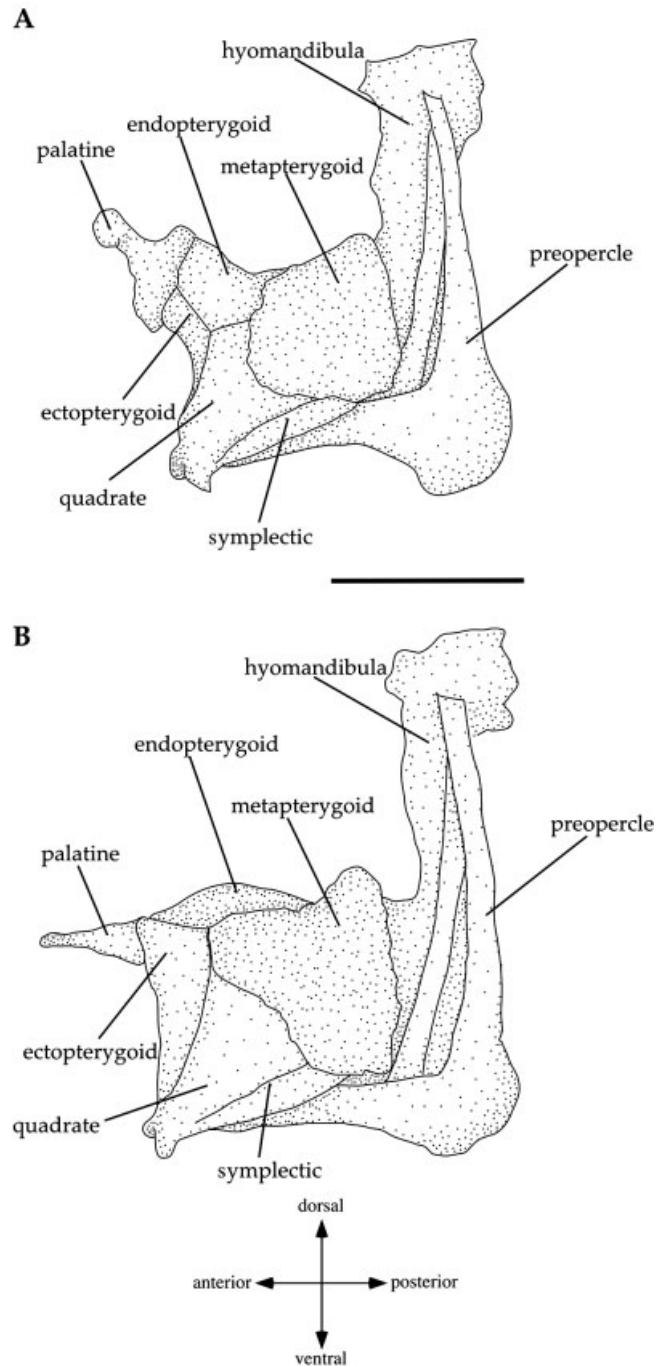

Fig. 6. Camera lucida drawings of the suspensoria (comprised of the preopercles, hyomandibulae, pterygoid processes, and the quadrate, symplectic, and palatine bones) of *Pleuronichthys verticalis:* (A) blind side and (B) eyed side. The eyed side suspensorium has been reversed horizontally to facilitate comparisons with the blind side. Scale bar = 1 cm.
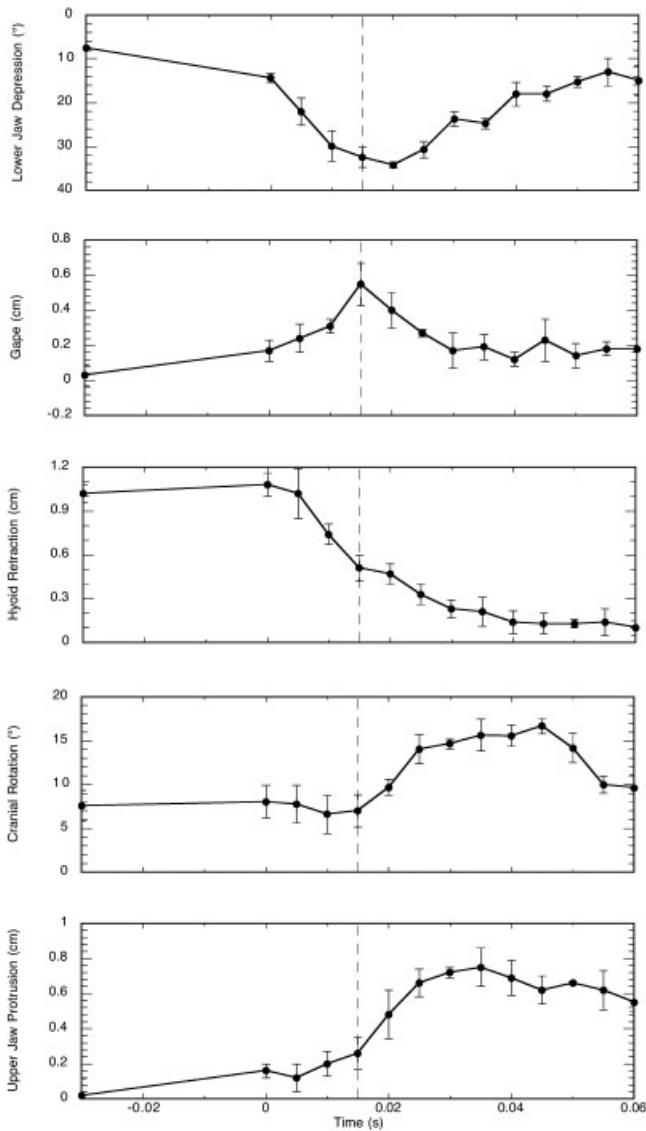
Fig. 7. Kinematic summary of four feeding sequences for one individual *Pleuronichthys verticalis*. Points represent mean values and the error bars represent one standard error of the mean. All variables are given in cm, with the exception of cranial rotation and lower jaw depression, which are given in degrees. Time 0 is the start of rapid mouth opening and the dashed line indicates maximum gape. The elements of the skull and jaws do not return to their original positions until well after the mouth closes.

the neurocranium is positioned farther anteriorly on the eyed side (13.1 mm from the skull base) than on the blind side (12.6 mm from the skull base).

Kinematic Patterns

A brief description of prey capture kinematics in *Pleuronichthys verticalis* is given here; a more detailed analysis is given in Gibb (1995). Figure 7 is a summary kinematic profile of four separate prey capture events for one individual. Figure 8 is a car-

toon based on video frames from a representative prey capture sequence for one individual.

Lower jaw depression begins slightly before mouth opening (Fig. 7) and maximum jaw depression occurs just after maximum gape. The lower jaw remains slightly depressed at an angle of approximately 20° for some time after the mouth has closed (Fig. 7). Rapid hyoid retraction begins shortly after mouth opening (Fig. 7) and this posterior movement continues throughout the gape cycle (i.e., the period of time during which the mouth is open).

The neurocranium is held in a position of slight dorsal rotation as the fish approaches the prey. Rapid dorsal cranial rotation begins after the mouth has opened and the neurocranium is maximally rotated during mouth closing (Fig. 7). After the mouth closes, the neurocranium begins to rotate ventrally
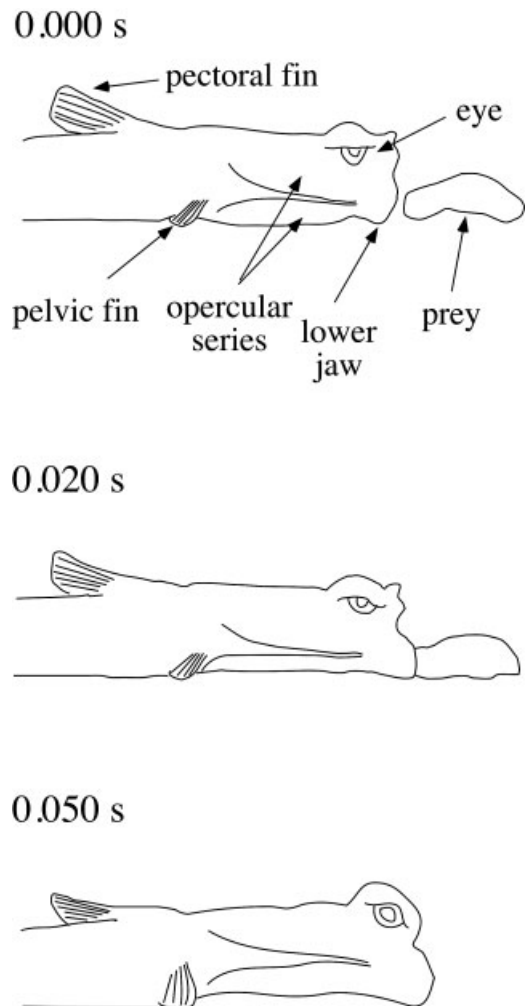

Fig. 8. Cartoon representing a feeding event in *Pleuronichthys verticalis* as seen from a ventral view. At the beginning of prey capture (**A**), the lower jaw appears to be parallel to the midsagittal plane of the head. However, as the jaw is depressed (**B**) it appears to flex toward the blind side and remains flexed (**C**) until after the jaws have been retracted. Time during the feeding event is given in the upper left corner of each panel.

(Fig. 7) and reaches minimum cranial rotation after the feeding event. Rapid protrusion of the upper jaw occurs simultaneously with cranial rotation (Fig. 7).

When observed from a ventral view, the jaws appear to be parallel to the midsagittal plane before *Pleuronichthys verticalis* begins the gape cycle (Fig. 8A). However, during the gape cycle the jaws appear to deflect laterally toward the blind side of the head (Fig. 8B). The apparent angle of the jaws relative to the head increases until it reaches a maximum value of approximately 28° (Gibb, 1995). The jaws return to their original positions as the upper jaw is retracted and the lower jaw elevated, well after the gape cycle is complete.

Models of Jaw Mechanisms

A preliminary model of the jaws was built to emulate the mechanisms that produce lower jaw depression and cranial rotation in *Pleuronichthys verticalis*; no attempt was made to incorporate asymmetrical morphology into this version of the model. To emulate cranial rotation, the posterior region of the neurocranium was rotated ventrally against the fulcrum (the "spine"), which produced dorsal movement in the anterior region. To emulate lower jaw depression, the posterior regions of the two mandibles were rotated dorsally about their articulations with the quadrate bones, which produced a corresponding ventral rotation of the anterior regions.

The model was then modified to emulate asymmetrical movements in *Pleuronichthys verticalis* by adding asymmetry to the model structure. Asymmetrical movement of the upper jaw was emulated by repositioning the elements representing the parasphenoid and ethmo-vomerine regions of the neurocranium (Figs. 4, 9). When these bones are positioned out of the midsagittal plane (i.e., angled toward the blind side), the element representing the upper jaw (i.e., the maxilla-premaxilla complex, or MPC) is obliged to slide off the vomer, out of the midline, and toward the blind side (Fig. 9).

Iterative experimentation with the asymmetrical model indicated that the simplest way to create asymmetry during lower jaw depression was to modify the position of the quadrato-mandibular (QM) joint. When the QM joint is positioned farther anteriorly on the eyed side than on the blind side, the jaw is tilted slightly toward the blind side. This slight tilting is almost impossible to detect when the jaw is elevated but becomes obvious when the jaw is depressed (Figs. 8, 10). This asymmetry is generated even when: 1) the two mandibles used in the model are symmetrical, 2) the joints between the mandibles and the quadrate bones are identical, and 3) the same force is applied to both sides of the lower jaw. This modification corresponds with the asymmetrical location of the suspensoria on the skull of *Pleuronichthys verticalis* and the asymmetrical lengths of the preopercle, symplectic and quadrate bones (Figs. 4, 6).

Comparison of the Model and the Kinematics

The predictive value of the model can be evaluated by examining the asymmetry of the shape of the vomer and the position of the suspensoria in the osteological specimens. Mean jaw flexion, as measured during the kinematic analysis, was 27.7° (Gibb, 1995). Morphological analysis of the parasphenoid indicates that it is tipped 22° out of the midsagittal plane of the head (Fig. 11). The vomer is additionally tilted out of the midsagittal plane and the angle that results from these two asymmetries is approximately 27° (Fig. 11). Thus, during prey capture, the MPC will be launched from the vomer at approximately a 27° angle relative to the midsagittal plane (Fig 9).

Additionally, most of the flexion of the lower jaw is due to the asymmetrical position of the QM joints. Figure 12 illustrates that, using measurements from the anatomical specimens and an entirely symmetrical lower jaw, the asymmetry of the QM joints alone creates approximately 20° of jaw flexion (Figs. 10, 12). This is over two-thirds of the observed 27.7° of jaw flexion. However, this change does not account for all of the observed kinematic asymmetry; apparently, the lower jaw of the model must be more complex to accurately predict the extent of jaw flexion.

In fact, the bones that comprise the two mandibles are asymmetrical in depth and width and the articular grooves for the quadrate are in different positions. If the asymmetry of these bones is included in the model it augments the lower jaw deflection caused by the asymmetrical QM joint (Fig. 13). In Figure 13, the articular surfaces of the mandible have been lined up along a transverse plane (Fig. 13B) and then that plane has been tipped (by moving the eyed-side joint anteriorly 2.5 cm) to represent the asymmetrical QM joint position (Fig. 13C). The resulting angle of the lower jaw is approximately 28°, which is very similar to the value calculated in the kinematic analysis (27.7°).

DISCUSSION
Mechanisms of Jaw Protrusion and Depression in *Pleuronichthys verticalis*

Pleuronichthys verticalis individuals appear to employ a modified version of Liem's (1979) "decoupled" model for upper jaw protrusion (for details, see Gibb, 1995). In the decoupled model, dorsal rotation of the neurocranium allows the premaxilla to slide anteriorly, opposite to the direction of movement of the neurocranium. Thus, movements of the upper jaw are decoupled from movements of the lower jaw. According to Liem, the premaxillae slide
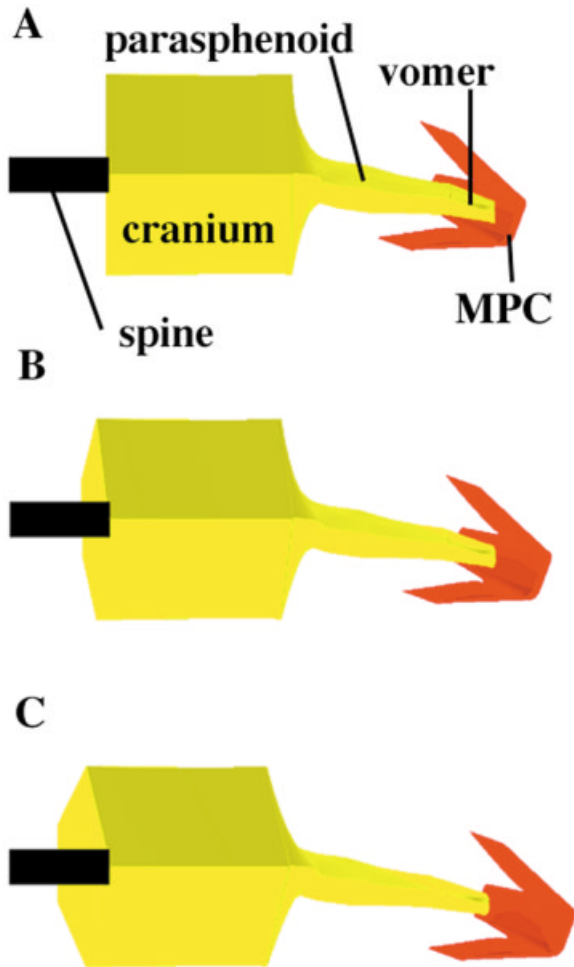
Fig. 9. Rendered images of the asymmetrical upper jaw model for *Pleuronichthys verticalis* from a ventral view. Only the parasphenoid, ethmoid, and vomer regions of the neurocranium are shown for simplicity; the frontal and prefrontal bones are not depicted. Dorsal rotation of the neurocranium causes the premaxilla and the attached maxilla (the MPC) to slide anteriorly. The asymmetrical position of the parasphenoid and vomer creates bilateral asymmetry in the movement of the premaxilla during cranial rotation; as the neurocranium moves dorsally (**A–C**) the premaxilla is "launched" anteriorly and to the right (blind side). QuickTime movies based on this animation are posted on the World Wide Web at http://jan.ucc.nau.edu/~acg/models/.

over a "steep ethmo-vomerine slope" and are assisted in sliding by the "rostral cartilage" (which is located between the premaxillae and the vomer). As predicted by this model, upper jaw protrusion in *Pleuronichthys verticalis* is decoupled from lower jaw protrusion and coupled with movements of the neurocranium. Kinematic data (Fig. 7) support this conclusion in two ways: 1) the onset and maximum protrusion of the upper jaw consistently lag movements of the lower jaw, and 2) upper jaw protrusion occurs simultaneously with cranial rotation (Gibb, 1995). The presence of a steep slope on the vomer (Fig. 4C) and the success of the physical model (which employs an analogous mechanism to emulate

upper jaw protrusion) provide additional support for this model.

Lower jaw movements are produced by the rotation of the mandible (dentary, angular, and retroarticular bones) about its articulation with the suspensorium at the QM (quadrato-mandibular) joint. This movement may be produced by either the sternohyoideus muscle or the levator arcus palatini muscle via two different bone–ligament linkages (Liem, 1970). Previous analysis of the kinematic patterns suggested that the levator arcus palatini rotates the mandible via the opercular series in *Pleuronichthys verticalis* (Gibb, 1995). However, the model used in
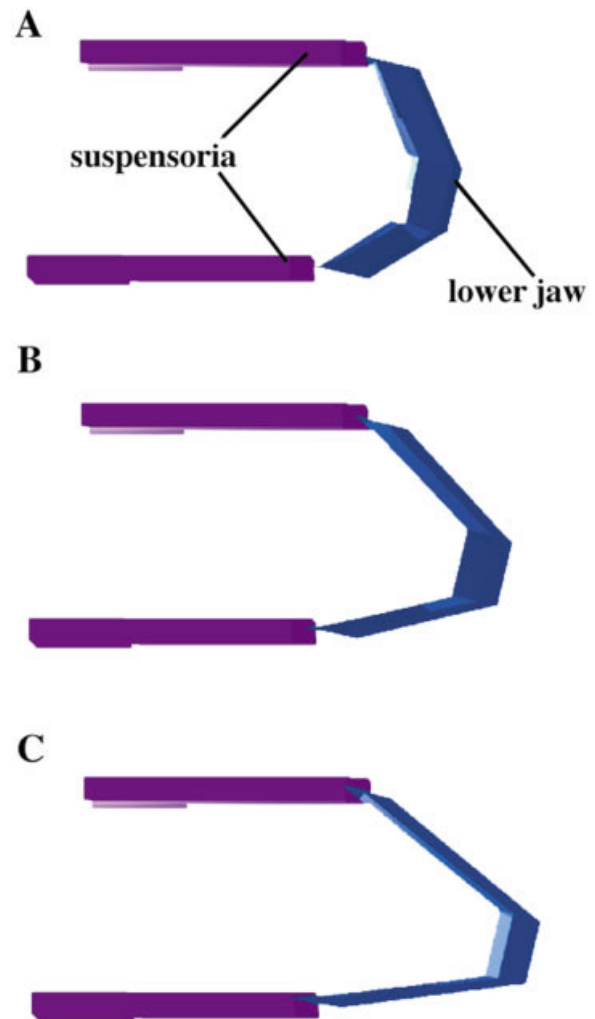

Fig. 10. Rendered images of the asymmetrical lower jaw model for *Pleuronichthys verticalis* from a ventral view. The eyed-side suspensorium is positioned farther anterior than the blind side suspensorium. The lower jaw (i.e., both mandibles together) is symmetrical but pivoted laterally to accommodate the asymmetrical position of the suspensorium. During lower jaw depression, the lower jaw rotates about its articulations with the quadrate (QM joints). Positions shown in **A, B,** and **C** in this figure correspond with **A, B,** and **C** in Figure 8. QuickTime movies based on this animation are posted on the World Wide Web at http://jan.ucc.nau.edu/~acg/models/.
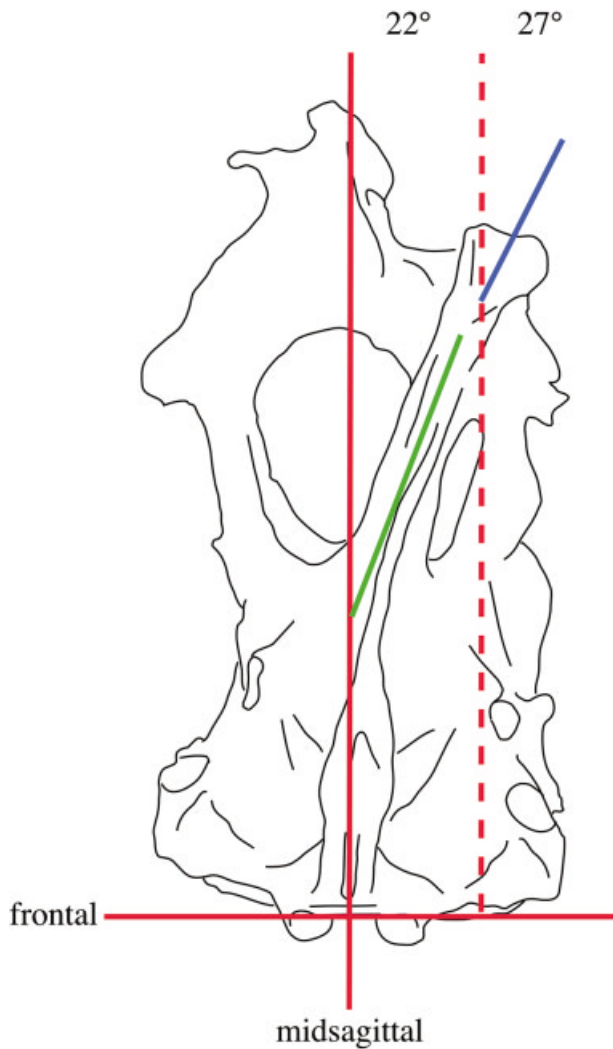
Fig. 11. View of the medial surface of the neurocranium of *Pleuronichthys verticalis*. The parasphenoid bone is tipped approximately 22° out of the sagittal plane and the vomer is tipped an additional 5°.
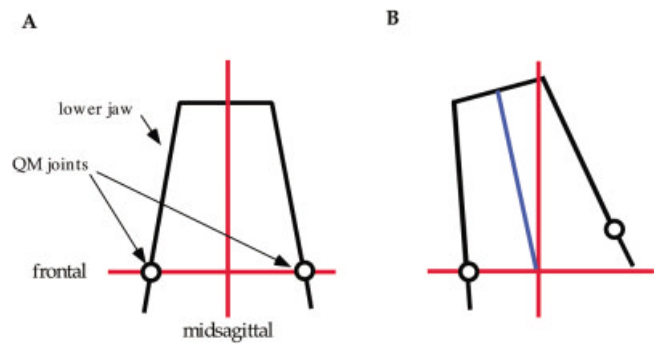

Fig. 12. Schematic drawing representing lower jaw flexion with asymmetrical QM joints but a symmetrical lower jaw (from medial view). In **A** the QM joints are symmetrical and the jaw is parallel with the sagittal plane. In **B** the QM joints are asymmetrical and the jaw is tipped approximately 20° out of the sagittal plane (angle calculations made using measurements from anatomical specimens).

(Fig. 9). This simple model appears to explain the observed asymmetry in upper jaw movements.

A model that generated asymmetrical lower jaw movements could only be produced using asymmetrically located QM joints. Other authors (see below) have suggested that bilateral asymmetry in the magnitude of angular rotation in the two mandibles creates lateral deflection of the lower jaw, or that a small degree of medial movement about the blind side fulcrum will translate into a large lateral deflection of the anterior lower jaw. However, all attempts to create an asymmetrical movement about symmetrically placed QM joints with the physical model failed.

These attempts appeared to be unsuccessful for two reasons. First, the two mandibles are firmly attached to one another at the jaw symphysis and the rotation of one mandible is transmitted to the other via this attachment. Second, the bilaterally symmetrical position of the quadrate bones creates an impediment to asymmetrical movement of the

this study did not require emulation of either of these specific linkages; only dorsoventral rotation of the mandible about the QM joint was required to produce jaw depression.

Asymmetrical Jaw Movements in *Pleuronichthys verticalis*

In *Pleuronichthys verticalis*, asymmetry in upper jaw movements appears to occur because the parasphenoid, ethmoid, and vomer regions of the skull are oriented toward the blind side of the head (Fig. 4C). During upper jaw protrusion in *P. verticalis*, the maxilla–premaxilla complex (MPC) is launched off the vomer (the "launch pad" for the upper jaw in the decoupled mechanism of jaw protrusion) and out of the midline when the neurocranium rotates dorsally
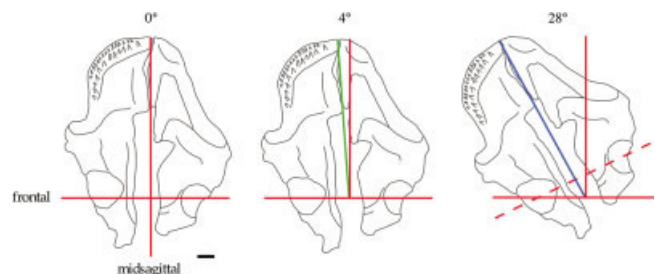

Fig. 13. View of the medial surface of the lower jaw of *Pleuronichthys verticalis*. In **A** the tip of the lower jaw is placed parallel to a frontal plane. In **B** the lower jaw is reoriented to align the articular grooves along a frontal plane. In **C** the lower jaw is repositioned (one side has been moved anteriorly 2.5 cm) to mimic the asymmetrical position of the QM joints. The combination of these two adjustments produces approximately 28° of deviation from the midsagittal plane.

lower jaw. Symmetrically placed QM joints effectively oppose any asymmetrical movement of the mandibles because the lower jaw is forced to rotate about the same location on both sides of the head.

In addition, the QM joint asymmetry incorporated into the model built for this study is also present in the skull and jaws of *Pleuronichthys verticalis*. The suspensorium is asymmetrical in length and position on the skull in this species (Figs. 4, 6). Thus, this appears to be the primary mechanism that creates lower jaw asymmetry. Additional asymmetry in the articular surfaces of the lower jaw (Figs. 5, 13) enhances this effect.

Asymmetrical Jaw Movements in *Pleuronectes platessa*

Yazdani (1969) conducted extensive work on asymmetrical jaw movements in several flatfish species; his work on *Pleuronectes platessa* is of particular interest because of its close taxonomic relationship with *Pleuronichthys verticalis*. Yazdani observed that when the mouth is opened passively in *P. platessa* the upper jaw is deflected toward the blind side of the head. He also reported that in *P. platessa* the skull is "strongly twisted" in the "ethmoidal region" and this causes the upper jaw to be "deflected" toward the blind side. Unfortunately, Yazdani did not measure the angle between the ethmoid-vomer region and the sagittal plane of the neurocranium. Flüchter (1963) also shows asymmetry in the ethmoid region of the skull in his detailed drawings of *P. platessa*. (Neither of these articles includes a ventral view of the complete neurocranium, so I was unable to make measurements from their figures.)

However, the maxillae and the premaxillae in *Pleuronectes platessa* do not form a tightly bound complex, as they do in *Pleuronichthys verticalis*. The maxillae are more plesiomorphic (i.e., similar in shape to those found in less specialized perciform fishes and more symmetrical) in appearance in *P. platessa* than in *P. verticalis* and the premaxillae are not firmly bound to the maxillae by connective tissue (Flüchter, 1963; Yazdani, 1969). Thus, asymmetry of the parasphenoid, ethmoid and vomer are involved in producing asymmetry in *P. platessa*, but the bones of the upper jaw are not as modified as they are in *P. verticalis*.

Yazdani (1969) also noted that, during passive manipulation, the "angle of the gape with the midplane" in *Pleuronectes platessa* is approximately 35°, a value that is similar to the 28° lateral jaw flexion measured for *Pleuronichthys verticalis* during prey capture (Gibb, 1995). He observed that the interoperculum on the blind side is "somewhat median" to the lower jaw and speculated that when the interoperculum pulls the posterior end of the mandible dorsally, it also pulls it medially. Yazdani predicted that this movement would cause the anterior end of the mandible to pivot laterally, out away from the midline of the head and toward the blind side. In addition, he noted that the articular cavity is "bigger" on the blind side than on the eyed side, which causes the blind side mandible to slide "backwards" (posteriorly) during passive mouth opening (Yazdani, 1969).

Asymmetrical Jaw Movements in the Cichlidae

Asymmetry in jaw movements during prey capture has been described only for one family of non-pleuronectiform fish, the Cichlidae (Liem and Stewart, 1976; Mboko et al., 1998). At least one species of cichlid shows asymmetrical feeding on encrusting algae (Mboko et al., 1998), although the function of asymmetrical feeding in this situation is not clear. However, the majority of the cichlids that demonstrate asymmetrical feeding eat the scales of other fishes (i.e., they are lepidophagous). In this situation, the jaws deflect to one side of the predator to scrape scales off the adjacent prey (Liem and Stewart, 1976). The only lepidophagous cichlid for which jaw asymmetry is well described is *Perissodus eccentricus*.

The jaws of *Perissodus eccentricus* deflect out of the midline when the lower jaw is passively depressed (Liem and Stewart, 1976). This species of fish also possesses asymmetrical dentition, although the asymmetry is less extreme than that seen in most flatfish species (Yazdani, 1969). According to Liem and Stewart, there are no modifications of the upper jaw in *Perissodus eccentricus* for asymmetrical feeding behavior. Instead, they suggest that the upper jaw bones are pulled out of the midline by asymmetrical movement of the lower jaw.

Liem and Stewart (1976) propose that asymmetrical lower jaw movements occur because of two asymmetries of the lower jaw and suspensorium. (In their analysis of the jaws they use as an example a dextral individual, one which flexes its jaws toward the right.) First, on the side of the head toward which the jaw deflects (the right side), the articulation of the quadrate bone with the mandible is "deeper." According to Liem and Stewart (1976), this allows the mandible a "wider abduction angle" during jaw opening. Second, "the distance between the quadratomandibular joint and the place where the interoperculum attaches to the suboperculum is larger" on the left side than on the right side. (Note: Liem and Stewart actually report that the distance is larger on the *right* side, but this is apparently a mistake. I have measured the original specimens to confirm that it is consistently longer on the left side in dextral specimens.) The result of this asymmetry is that the articulation between the QM joint and the mandible is further anterior on the left side than on the right (see fig. 15 in Liem and Stewart, 1976).

Liem and Stewart (1976) suggest that this asymmetry gives the right side greater "kinematic efficiency" (Anker, 1974). Simply put, a lower jaw with greater kinematic efficiency has a smaller opening in-lever, which will result in a more effective transmission of displacement to the lower jaw (Anker, 1974; Westneat, 1994). Thus, the same muscle input on both sides of the head could yield a greater angular movement of the mandible on the right side of the head than on the left side of the head in a dextral *Perissodus eccentricus*. Liem and Stewart propose that the greater angular movement of the mandible on the right side of the head will cause the entire lower jaw to swing toward that side.

Comparisons Among Taxa

The mechanism that generates upper jaw asymmetry appears similar among flatfish species, but may be different in cichlids. In *Pleuronectes platessa* (Yazdani, 1969) and *Pleuronichthys verticalis*, twisting in the ethmoid region of the skull causes the upper jaw to be deflected toward the blind side. Yazdani (1969) and Bürgin (1986) also report a deviation of the ethmoid region from the anatomical midline in four other species of flatfish (representing several different families). However, Liem and Stewart (1976) did not report this asymmetry for the lepidophagous cichlid. It is possible that the similarities between the various flatfish species are due, at least in part, to their shared ancestry. It is also possible that the relatively small degree of asymmetry produced by the cichlid during feeding does not require this modification of the neurocranium.

More similarities are apparent in a comparison of the mechanisms of lower jaw asymmetry. Yazdani (1969) observed that the eyed side suspensorium is "bigger" than the blind side in *Pleuronectes platessa* and Bürgin (1986) noted the same pattern in another flatfish species, *Microchirus theophila*. Liem and Stewart (1976) also noted asymmetry in the suspensorium of *Perissodus eccentricus*. Thus, asymmetry of the QM joint, similar to that found in *Pleuronichthys verticalis*, may produce asymmetrical jaw movements in *all* of these species. In fact, the physical model suggests that this is the primary mechanism of lower jaw asymmetry and that the other methods proposed by previous authors (medial-lateral pivoting or asymmetrical rotation at the two QM joints) cannot produce lower jaw asymmetry (see above).

In addition, Yazdani (1969) and Liem and Stewart (1976) observed that the articular groove on the mandible is bilaterally asymmetrical for both *Pleuronectes platessa* and *Perissodus eccentricus*; the groove is consistently larger on the side toward which the jaw deflects. Yazdani also observed that the blind-side mandible slides posteriorly when the lower jaw is passively opened. This movement would effectively change the length of the blind-side mandible (i.e., make it shorter). A similar mechanism may be found in another flatfish species, *Microchirus theophila* (Bürgin, 1986). *Pleuronichthys verticalis* shows bilateral asymmetry in the size and position of the articular groove of the mandible; the blind-side groove is positioned farther anteriorly than the eyed-side groove (Fig. 5). Thus, in all of these species the mandible on one side is functionally longer than the mandible on the other side. This would augment the asymmetry created by the asymmetrical position of the QM joints (Fig. 13).

Evolution of Asymmetrical Jaw Movements

The distinctive feature of the jaw movement of *Pleuronichthys verticalis* is obligate lateral flexion. The models produced for this study demonstrated that two modifications of the jaw apparatus are sufficient to allow asymmetry to occur: 1) the twisting of the ethmoid, vomer, and parasphenoid region of the skull toward the blind side, and 2) repositioning of the QM joints. Asymmetry is augmented by a third modification: asymmetry of the articular surfaces on the mandible. This finding implies that other modifications of the structure of the cephalic region of *P. verticalis* are either further refinements to facilitate asymmetrical movements (e.g., the formation of an asymmetrical MPC), or modifications of structures for other purposes (e.g., the bony ridge between the eyes). Therefore, the evolution of the asymmetrical jaw movements could occur by two developmental changes: 1) a change in the orientation of the parasphenoid or vomer, and 2) a change in the position of the QM joints. Even small morphological changes in these locations would allow the jaws to deflect during prey capture. In fact, *Perissodus eccentricus*, the lepidophagous cichlid, can produce some asymmetry in jaw movements without any modification of the upper jaw mechanism. This implies that the first stage in the evolution of asymmetrical jaw movements is modification of the lower jaw, without concomitant modification of the upper jaw.

Finally, similarities between the lower jaw bones of the cichlid and the flatfishes provide strong evidence for convergent evolution of an asymmetrical jaw mechanism. In all of these taxa the QM joint is asymmetrical in location and the lower jaw is functionally asymmetrical in length due to the position and shape of the articular surfaces of the mandible. These similarities suggest that there is a common pathway by which lateral flexion of the jaws can be produced via key modifications of the cephalic bones.

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