

## LINKAGE BIOMECHANICS AND EVOLUTION OF THE UNIQUE FEEDING MECHANISM OF *EPIBULUS INSIDIATOR* (LABRIDAE: TELEOSTEI)

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### Summary

*Epibulus insidiator* (Pallas) possesses the most extreme jaw protrusion ever measured in fishes. Biomechanical models of the mechanisms of jaw protrusion and hyoid depression in *Epibulus* are proposed and tested. The models are designed using principles of four-bar linkages from engineering theory. The models calculate the geometry of the feeding mechanisms from morphometric data on cranial anatomy. Predictions made from the models about the feeding kinematics of *Epibulus* are tested by comparison with kinematic data. The model of the jaw mechanism is accurate in predicting the unique feeding mechanics of the jaws of *Epibulus* for most relationships between kinematic variables. A model of simultaneous cranial elevation and sternohyoideus muscle contraction is accurate in predicting hyoid depression during feeding. Biomechanical considerations limit the number of possible pathways of evolution of the jaw mechanism of *Epibulus* from that of its closest labrid relatives.

### Introduction

The use of biomechanical models in functional morphology enables the testing of hypotheses about structural design and behavioral mechanics in organisms. Models of functional morphology clarify the relationship between the geometric conformation and the function of musculoskeletal systems, and have been applied to the study of feeding mechanics in a diversity of fish taxa (e.g. Alexander, 1967; van Hasselt, 1978; Lauder, 1979; Liem, 1978; Otten, 1983). Several recent studies proposed that feeding mechanisms in teleosts may be modeled with a mechanical construction called a four-bar linkage (Fig. 1). The action of four-bar linkages in fishes has been examined during jaw protrusion (Aerts and Verraes, 1987; Anker, 1974; Barel *et al.* 1977; Westneat, 1990*a,b*), hyoid depression (Muller, 1987; Westneat, 1990*a,b*), head abduction (Muller, 1989) and respiration (Anker, 1978).

Recently I tested several linkage models of feeding in fishes of the family Labridae (Westneat, 1990*a,b*). I presented morphological and kinematic evidence for the existence of a previously undescribed four-bar mechanism for protrusion of the jaws in labrid fishes. In addition, the behavioral predictions of this new model

Key words: Labridae, feeding, biomechanics, *Epibulus insidiator*.

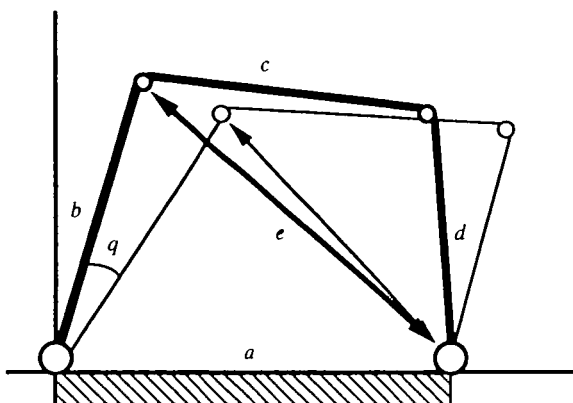


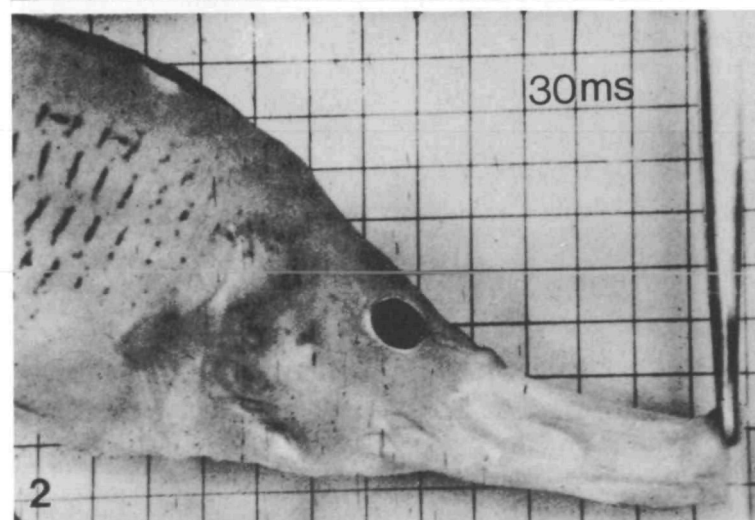
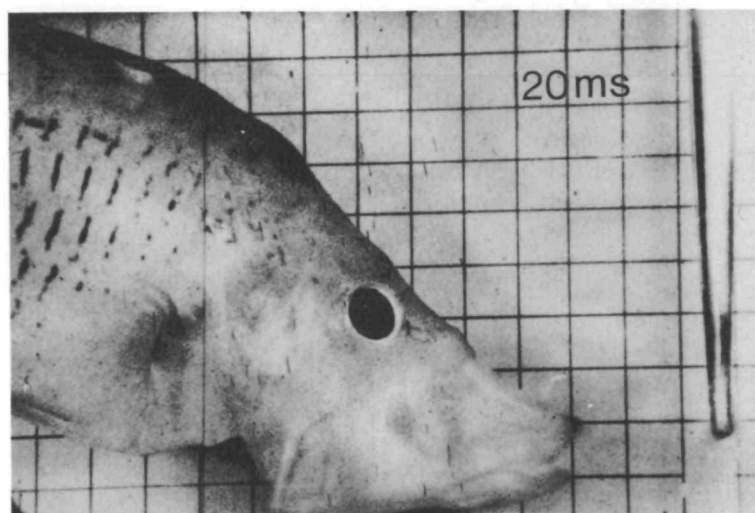
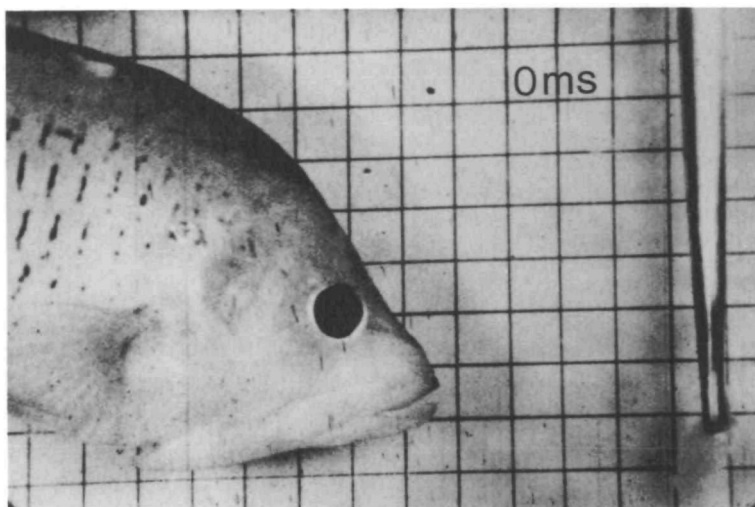
Fig. 1. A four-bar linkage undergoing movement. Heavy lines indicate initial positions of the fixed link (*a*), input link (*b*), coupler link (*c*), output link (*d*) and diagonal (*e*). The light lines indicate the position of the mechanism after link *b* has rotated through angle *q*.

and those of the two previous four-bar linkage models (Anker, 1974; Muller, 1987) were tested in fishes of the genus *Cheilinus* (Labridae).

*Epibulus insidiator* is a member of the phylogenetic sister group to *Cheilinus* (Westneat, 1991) that protrudes its jaws to an extreme degree (Fig. 2). The mechanism of jaw protrusion in *Epibulus* represents a major evolutionary change among the Labridae in cranial morphology and the kinematics of prey capture. Westneat and Wainwright (1989) proposed a mechanism by which *Epibulus* captures prey. The central conclusion of that study was that the extreme protrusive ability of this fish is due to a multitude of structural novelties occurring in the bones and ligaments of the head that produce a drastic reorganization of the linkage system of the jaws. Jaw protrusion is driven by the input motions of cranial elevation and opercular rotation. Cranial elevation caused by contraction of the epaxial musculature exerts an anterodorsal force along the length of the unique vomero-interopercular ligament (Fig. 3A). Opercular rotation pulls the dorsal tip of the interopercle posteriorly, and the vomero-interopercular ligament imparts an anteriorly directed force to the ventral portion of the interopercle. The interopercle rotates around its contact with the epihyal through an arc of nearly  $100^\circ$ , transferring an anterodorsally directed force to the lower jaw *via* the interoperculo-mandibular ligament (Fig. 3A). Forward movement of the lower jaw is guided by the rotation of the quadrate and maxilla, which also swing through large arcs.

The goal of this paper is to construct and test a quantitative kinematic model of the unusual kinematics of *Epibulus* feeding behavior using four-bar linkage theory. Additionally, the hyoid depression mechanism proposed by Muller (1987) is tested in *Epibulus*. It is shown that the linkage mechanisms described for *Cheilinus* (Westneat, 1990b) have been drastically altered in *Epibulus*, to produce

Fig. 2. Frames 1, 5 and 7 from a high-speed film ( $200\text{ frames s}^{-1}$ ) of the strike of *Epibulus insidiator*. Grid size  $1\text{ cm}^2$ .



a linkage system unique among fishes. The quantitative models of the jaw linkage and the hyoid linkage are good predictors of *Epibulus* feeding kinematics and provide insight into the evolution of this novel functional system.

### Materials and methods

#### *A model of the Epibulus feeding mechanism*

I translated the mechanism of jaw protrusion described above into a quantitative model. The model was constructed using four-bar linkage theory from mechanical engineering (Suh and Radcliffe, 1978). Four-bar linkage models for fishes have the objective of predicting feeding movements. A physical model was built from wood, metal and string to evaluate linkage mechanisms. A computer program was written to calculate linkage geometry from morphometric data on *Epibulus* cranial structure. The program runs in Think's Lightspeed Pascal (Symantec Corporation, Cupertino, CA) on a Macintosh computer. The program simulates an input motion (cranial elevation) and predicts the kinematics of the other links during feeding. The film results were then used to test these predictions. The general methods of calculation of linkage geometry were similar to those detailed in Westneat (1990b). Briefly, a four-bar crank chain (Fig. 1) is a mechanism composed of four co-planar links connected by joints to form a closed rhombohedron. This mechanism has one degree of freedom, because if the position of one element in the linkage is specified, then the positions of all other parts can be calculated. Fig. 1 shows the four links as the fixed (*a*), input (*b*), coupler (*c*) and output (*d*) links of the mechanism. In practice, the coupler and/or output links may deliver the desired output of the mechanism.

The mechanism of jaw protrusion of *Epibulus* is composed of two linkage systems (Fig. 3). The first linkage (Fig. 3B: links *A–D*) is a four-bar linkage formed by the neurocranium (link *A*), the opercle (link *B*), the interopercle (link *C*) and the vomero-interopercular ligament (link *D*). The input action of this linkage is elevation of the neurocranium, which causes dorsal rotation of link *A*. The opercle (link *B*) is modeled as the fixed link, although it is capable of motion due to contraction of the levator operculi muscle. An anteriorly directed force is transferred to the interopercle through the vomero-interopercular ligament (link *D*), causing anterior rotation of the interopercle (link *C*). Anterior rotation of the interopercle is the output motion of the linkage.

The second linkage in the feeding mechanism of *Epibulus* is a six-bar linkage (Fig. 3B: links 1–6). This six-bar linkage is composed of a four-bar linkage (links 1–4) with links 1 and 2 extended posteriorly where they attach to two additional links (5 and 6). Link 1 is the vomero-interopercular ligament, link 2 is the lower jaw, which is also extended anteriorly, link 3 is the maxilla, link 4 is the quadrate, link 5 is the interopercle and link 6 is the interoperculo-mandibular ligament. Two structures of this mechanism are shared by the two linkages. These are the vomero-interopercular ligament (link 1 and link *D*) and the interopercle (link 5 and link *C*).

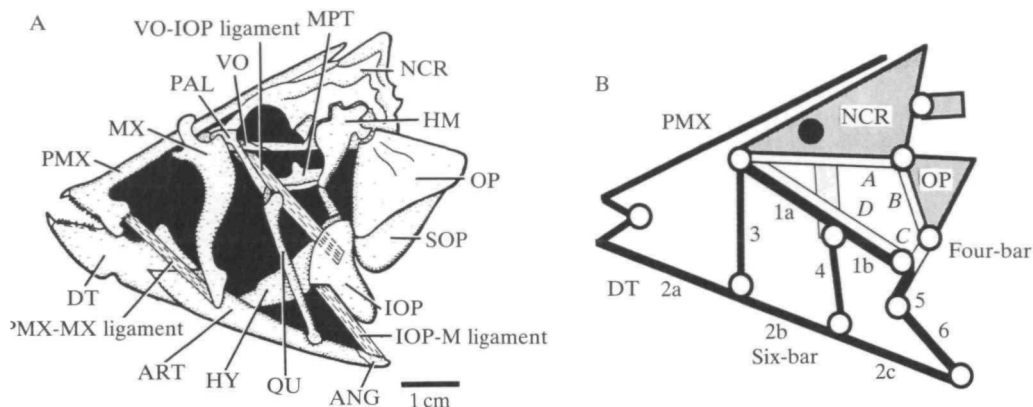


Fig. 3. (A) Cranial osteology of *Epibulus insidiator*, with preopercle and circumorbital bones removed. ANG, angular; ART, articular; DT, dentary; HM, hyomandibula; HY, hyoid; IOP, interopercle; IOP-M ligament, interoperculo-mandibular ligament; MX, maxilla; MPT, metapterygoid; NCR, neurocranium; OP, opercle; PAL, palatine; PMX, premaxilla; PMX-MX ligament, premaxillary-maxilla ligament; QU, quadrate; SOP, subopercle; VO, vomer; VO-IOP ligament, vomero-interopercular ligament. (B) The mechanical linkage model of *Epibulus*. A dorsal four-bar linkage is formed by a fixed link (B) the opercle, an input link (A) the neurocranium, an output link (C) the interopercle, and a coupler link (D) the vomero-interopercular ligament. A ventral six-bar linkage is formed by the input link (1) the vomero-interopercular ligament, and many output links (2) the lower jaw, (3) the maxilla, (4) the quadrate, (5) the interopercle and (6) the interoperculo-mandibular ligament.

Interopercular rotation is the input motion that drives the six-bar linkage. This action transfers anteriorly directed motion to the lower jaw through the interoperculo-mandibular ligament (link 6). The lower jaw is pulled forward, guided by the rotation of the quadrate (link 4) and maxilla (link 3). The quadrate and maxilla are both attached dorsally, so that the action of the four-bar portion of the lower linkage precisely determines the kinematics of the lower jaw, quadrate and maxilla. Premaxillary protrusion results when the lower jaw pulls the premaxilla anteriorly. The attachment between the dentary and premaxilla (Fig. 3B) transmits anteriorly directed motion to the premaxilla, causing it to slide forward along the neurocranium, as in a slider crank linkage (Suh and Radcliffe, 1978).

The hyoid model described for *Cheilinus* (Westneat, 1990b) was also tested in *Epibulus*. The hyoid linkage is a four-bar mechanism of hyoid depression (Fig. 4) involving the neurocranium and hyomandibula, hyoid, pectoral girdle and urohyal (Muller, 1987). The hyoid linkage has a fixed link (Fig. 4: link 1) formed by the pectoral girdle, from its ventral connection to the sternohyoideus muscle to the joint between post-temporal and neurocranium dorsally. The input link (Fig. 4: link 2) is composed of two elements, the neurocranium and hyomandibula. Input for the hyoid linkage is cranial elevation, effected by contraction of the epaxial musculature. A second input link of the hyoid mechanism (Fig. 4: link 4) is the

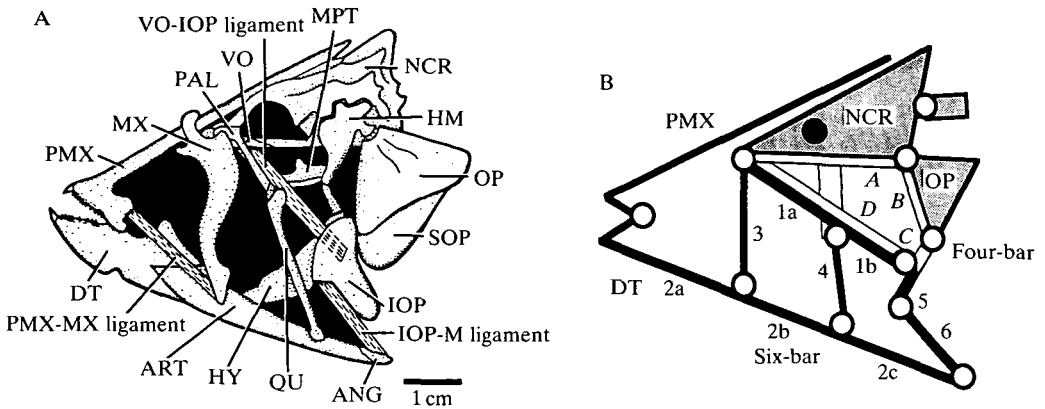


Fig. 3. (A) Cranial osteology of *Epibulus insidiator*, with preopercle and circumorbital bones removed. ANG, angular; ART, articular; DT, dentary; HM, hyomandibula; HY, hyoid; IOP, interopercle; IOP-M ligament, interoperculo-mandibular ligament; MX, maxilla; MPT, metapterygoid; NCR, neurocranium; OP, opercle; PAL, palatine; PMX, premaxilla; PMX-MX ligament, premaxillary-maxilla ligament; QU, quadrate; SOP, subopercle; VO, vomer; VO-IOP ligament, vomero-interopercular ligament. (B) The mechanical linkage model of *Epibulus*. A dorsal four-bar linkage is formed by a fixed link (B) the opercle, an input link (A) the neurocranium, an output link (C) the interopercle, and a coupler link (D) the vomero-interopercular ligament. A ventral six-bar linkage is formed by the input link (1) the vomero-interopercular ligament, and many output links (2) the lower jaw, (3) the maxilla, (4) the quadrate, (5) the interopercle and (6) the interoperculo-mandibular ligament.

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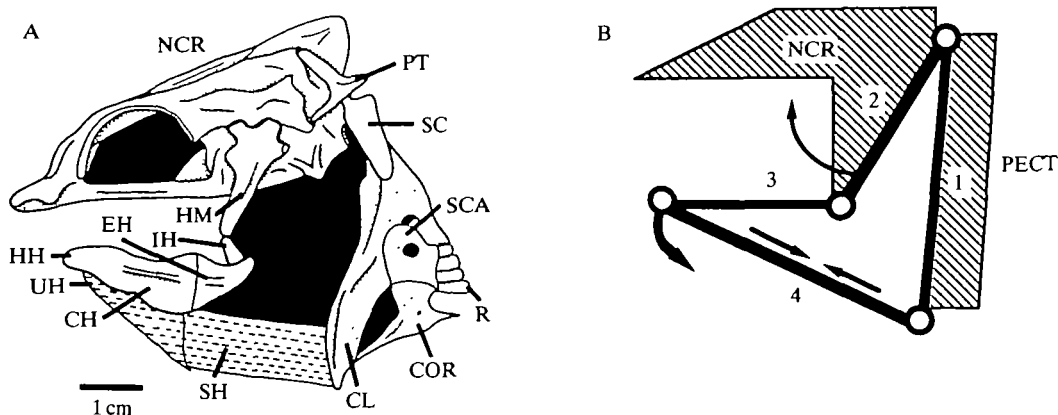


Fig. 4. (A) Morphology of *Epibulus insidiator* that forms the hyoid depression mechanism. (B) Mechanical diagram of the hyoid linkage (after Muller, 1987). Links 1–4 are the elements in a four-bar crank chain. CH, ceratohyal; CL, cleithrum; COR, coracoid; EH, epihyal; HH, hypohyal; HM, hyomandibula; IH, interhyal; NCR, neurocranium; PECT, pectoral girdle; PT, posttemporal; R, radials; SC, supracleithrum; SCA, scapula; UH, urohyal; SH, sternohyoideus muscle.

sternohyoideus (SH) muscle, which extends from the anterior tip of the hyoid to the ventral tip of the pectoral girdle. This link is capable of shortening, and the computer model allows shortening of the sternohyoideus as input to the mechanism. The coupler link in this mechanism (Fig. 4: link 3) is the hyoid, from the epihyal-hyomandibula joint to the joint between the hypohyal and the urohyal. The functional output of the hyoid four-bar linkage is rotation and depression of the hyoid.

#### Kinematic analysis

The kinematic data of Westneat and Wainwright (1989) were used to test predictions of the four-bar models. Briefly, living *Epibulus* were trained to feed upon shrimp pieces held by forceps. Feedings were filmed with a Redlake LOCAM model 51–0008 intermittent high-speed motion picture camera using 16 mm Kodak 7277 (400 ASA) black and white 4X reversal film. Camera settings were 1/2000 s shutter speed, aperture 4.0 and 200 frames  $s^{-1}$ .

Four feeding events for each of four *Epibulus* were selected from many films for kinematic analysis. Film analysis involved measurement of angles and distances between moving structures during feeding. Eight kinematic variables were measured, including five angles (1) cranial elevation, (2) opercular rotation, (3) interopercular rotation, (4) quadrate rotation and (5) maxillary rotation, and three distances (1) gape, (2) protrusion distance and (3) hyoid depression (see Fig. 1 of Westneat and Wainwright, 1989, for measurement landmarks).

#### Testing the models

Comparisons were made between model predictions and the feeding kinematics

of living *Epibulus*. The specimens used in the films were killed by an overdose of anesthetic (methane tricaine sulfonate), and the lengths of the bones in the jaw mechanism of each fish were measured using Helios dial calipers (accuracy  $\pm 0.05$  mm). These measurements were used as input for the computer model. Each individual fish ( $N=4$ ) was modeled independently, so that model predictions show variance that reflects morphometric variation. Thus, the model has a correlation of 1.0 for an individual but, because lines are fitted to the model predictions for four individuals, the pooled, within-group correlations are often less than 1.0.

The predictions of the two linkage models were generated in the following way. Cranial elevation angles ( $1-10^\circ$ ) were used as input for the jaw-protrusion mechanism. This range was chosen as input for the model because a  $10^\circ$  cranial elevation is typical of an *Epibulus* feeding event (Westneat and Wainwright, 1989). These simulations yielded kinematic predictions for interopercular rotation, maxillary rotation, quadrate rotation and premaxillary protrusion. Input for the hyoid linkage is cranial elevation and/or sternohyoideus (SH) contraction. A range of values for cranial elevation ( $1-10^\circ$ ) and SH contraction ( $1-10\%$  shortening) were simulated as input. A  $10\%$  muscle shortening was used because muscle contractions of  $6-15\%$  are typical of striated muscles in fishes (Bone *et al.* 1986; Curtin and Woledge, 1988). The hyoid model simulated two types of input (1) cranial elevation alone and (2) cranial elevation with simultaneous shortening of the SH muscle (see Table 1). The predicted output variable for the hyoid linkage is hyoid depression.

The accuracy of each linkage model was evaluated based on the linear relationships between kinematic variables of the strike. Least-squares regression lines were fitted to the relationship between the input (independent) variable and the output (dependent) variable. The regression lines for pairs of variables from model predictions and film kinematics were compared by analyses of covariance that tested for differences between the slopes and y-intercepts of the regression lines for model predictions and films. If the correlations between input motion and output motion were high ( $0.80-1.0$ ) for both model and films, and if the model was found not to be statistically different from the films, then it was concluded that the model was accurate in predicting feeding behavior. Because seven tests of significance were performed using data from the same feeding events, a conservative probability of  $P < 0.01$  was used, rather than  $P < 0.05$ . This lessened the chances of finding significant differences simply because so many tests were performed. This conservative probability value also offset the fact that the predictions of the geometric models often had a correlation close to 1.0. Statistics were performed using SYSTAT (Wilkinson, 1989) on a Macintosh IICX computer.

## Results

### *Feeding kinematics*

The most striking features of the feeding kinematics of *Epibulus* (Fig. 2) are



extreme protrusion of both the upper and lower jaws, rotation of the neurocranium, opercle, interopercle, quadrate and maxilla, and increase in gape (Westneat and Wainwright, 1989). The output movements of interopercular rotation, quadrate rotation, maxillary rotation, protrusion and gape are all virtually synchronous with cranial elevation (an input movement). The highly synchronous pattern of movement among many of the kinematic variables was followed by peak hyoid depression 10–15 ms later.

*Test of the sling-jaw linkage model*

Table 1 presents morphometric data from both the jaw protrusion and hyoid mechanisms of *Epibulus insidiator* that were used as input to the computer model. Table 2 presents the regression equations for films and model results. Coefficients of determination ( $r^2$ ) between input and output variables for film data were high ( $>0.93$  for most variables). The input motion of cranial elevation was used by the model to predict interopercular rotation, maxillary rotation and jaw protrusion (Fig. 5). The results of analysis of covariance (ANCOVA) tests show that there is no significant difference between the slopes of model and film data (Table 3).

Table 1. *Epibulus linkage morphometrics*

Variable	Mean (mm)	S.D.	Repeatability (%)
Jaw linkage			
A. Neurocranium length	23.03	4.48	1.0
B. Opercle length	12.18	2.70	2.0
C. Interopercle (1) length	1.98	0.39	6.3
D. VO-IOP ligament length (1a+1b)			
1a. VO-IOP ligament (1) length	15.43	2.84	1.2
1b. VO-IOP ligament (2) length	6.90	1.64	4.3
2a. Lower jaw (1) length	22.65	5.51	1.1
2b. Lower jaw (2) length	16.33	2.70	2.1
2c. Lower jaw (3) length	8.15	1.87	2.0
3. Maxilla length	18.95	4.71	1.6
4. Quadrate length	19.83	4.67	1.0
5. Interopercle (2) length	9.73	2.32	3.1
6. IOP-M ligament length	15.63	3.62	2.3
Hyoid linkage			
1. Pectoral girdle height	35.56	6.56	1.2
2. Cranium and hyomandibular	15.15	3.38	2.1
3. Hyoid length	20.65	5.13	2.3
4. Sternohyoideus muscle length	28.55	5.84	1.4

Mean and standard deviation ( $N=4$ ) of the cranial dimensions that were used as input to the jaws linkage model and the hyoid depression model.

Repeatability is the standard deviation of three repeated measures expressed as a percentage of the mean of those measures.

Lettering and numbering coincide with those of Figs 3B and 4B.

VO-IOP, vomero-interopercular; IOP-M, interoperculo-mandibular.

Table 2. *Epibulus linkage regressions*

	Films		Model	
Cranial elevation				
Interopercular rotation	$y=7.54x-1.6$	$r^2=0.97$	$y=7.30x-3.3$	$r^2=0.98$
Cranial elevation				
Maxillary rotation	$y=7.95x-3.1$	$r^2=0.96$	$y=7.10x-0.85$	$r^2=0.97$
Cranial elevation				
Premaxillary protrusion	$y=0.29x-0.18$	$r^2=0.93$	$y=0.20x+0.11$	$r^2=0.78$
Interopercular rotation				
Quadrato rotation	$y=1.23x-6.0$	$r^2=0.97$	$y=0.93x+3.7$	$r^2=0.99$
Interopercular rotation				
Maxillary rotation	$y=1.02x+0.40$	$r^2=0.97$	$y=0.97x+3.1$	$r^2=0.98$
Quadrato rotation				
Maxillary rotation	$y=1.00x-0.52$	$r^2=0.99$	$y=1.04x-0.81$	$r^2=0.99$
Maxillary rotation				
Premaxillary protrusion	$y=0.03x+0.24$	$r^2=0.94$	$y=0.03x+0.08$	$r^2=0.86$

Least-squares regression equations of the relationship between input and output variables from film kinematics and model predictions. The first variable listed is the input (independent) variable.

The means of four feedings for each of four individuals were used for film regressions.

However, there is a significant difference between the y-intercepts for the film and model data for the output variable of interopercular rotation, and there are relatively low correlations between cranial elevation and premaxillary protrusion (Fig. 5C, Table 2). These low correlations are due to variation in absolute size, causing two individuals to have a lower protrusion distance than the others (Fig. 5C).

The comparison of film and model results for several other input and output variables are presented in Fig. 6. These graphs illustrate the transfer of motion from the interopercle to the quadrato, maxilla and jaws. Interopercular rotation is the input variable that predicts quadrato rotation (Fig. 6A) and maxillary rotation (Fig. 6B). The relationships between interopercular rotation and quadrato rotation are significantly different for films and model, but interopercular rotation is an accurate predictor of maxillary rotation (Table 3). Quadrato rotation predicts maxillary rotation accurately (Fig. 6C, Table 3), and maxillary rotation predicts jaw protrusion accurately (Fig. 6D, Table 3).

#### *Hyoid model*

The results of testing the hyoid linkage model in *Epibulus* (Fig. 7) were similar to those for *Cheilinus* (Westneat, 1990b). A model using cranial elevation only was inaccurate in predicting hyoid depression, but the model that simulated a simultaneous cranial elevation and sternohyoideus muscle contraction was a good

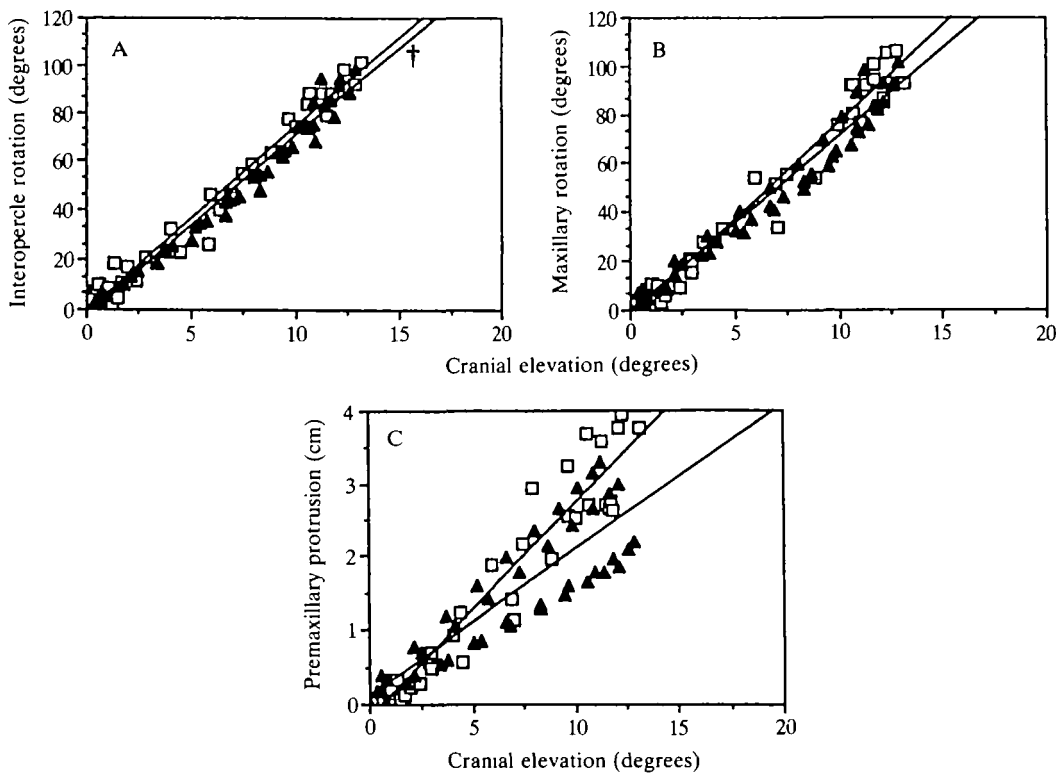


Fig. 5. Regression lines comparing predictions of the linkage model of the jaws (▲) with film results (□) for *Epibulus insidiator*. Each graph plots the input motion of cranial elevation against an output variable. † indicates a significant difference between the y-intercepts of the film and the model. See Table 3 for ANCOVA results.

predictor of hyoid depression (Fig. 7, Table 4). The extent of hyoid depression in *Epibulus* (0.4–0.6 cm) is similar to that of *Cheilinus* (0.3–0.6 cm).

Discussion

Structural modifications of the bones and ligaments of the jaws of *Epibulus insidiator* have produced a unique geometric configuration of elements that is the basis for the most extreme jaw protrusion ever measured in fishes. In contrast, the mechanism of hyoid depression during feeding is similar to the ancestral condition. A major conclusion of this study is that the unique feeding mechanics of the jaws of *Epibulus* and the mechanics of the hyoid are accurately modeled by using four-bar linkage theory from engineering. The reorganization of the jaw mechanism is discussed with respect to the mechanisms found in fishes closely related to *Epibulus*. Consideration of linkage structure shows that biomechanical constraints limit the number of possible pathways of evolution of the jaw mechanism of *Epibulus* from that of its closest labrid relatives.

Table 3. *Epibulus linkage ANCOVA results*

	Slope	y-intercept
Cranial elevation Interopercular rotation	0.42	0.01*
Cranial elevation Maxillary rotation	0.02	0.06
Cranial elevation Premaxillary protrusion	0.10	0.16
Interopercular rotation Quadrate rotation	0.001*	
Interopercular rotation Maxillary rotation	0.10	0.79
Quadrate rotation Maxillary rotation	0.16	0.02
Maxillary rotation Premaxillary protrusion	0.91	0.46

*P*-values from analyses of covariance testing for differences between film kinematics and model predictions.

The first variable listed is the input (independent) variable in all tests.

Significant differences (\* $P < 0.01$ ) indicate that the model fails to predict well for that pair of variables.

Slopes and y-intercepts were tested except when slopes were significantly different.

#### *Accuracy of the linkage models*

The linkage model of the jaws of *Epibulus insidiator* (Fig. 3) predicted a relationship between input and output kinematics that is not statistically different from real feeding behavior (Table 3). Cranial elevation accurately predicted output kinematics throughout the entire linkage system (Fig. 5, Table 3). Interopercular rotation is directly connected to cranial elevation through a four-bar linkage (Fig. 3) that is unique among fishes and is due to the presence of the vomero-interopercular ligament. The four-bar model had a statistically different y-intercept from that for the films for the relationship between input (cranial elevation) and output (interopercular rotation). However, the model accurately predicted the slope of the relationship between cranial elevation and interopercular rotation of this linkage.

The linear relationships between cranial elevation and the output motions of maxillary rotation and jaw protrusion (Fig. 5) were also accurately predicted by the linkage model involving the six-bar chain (Fig. 3). The graphs of Fig. 6 further illustrate a pattern of kinematics in which the relationship between bone movements is rigidly defined (note the high correlations between input and output: Table 2). Only the relationship between interopercular rotation and quadrate rotation was found to differ between the model and the film results

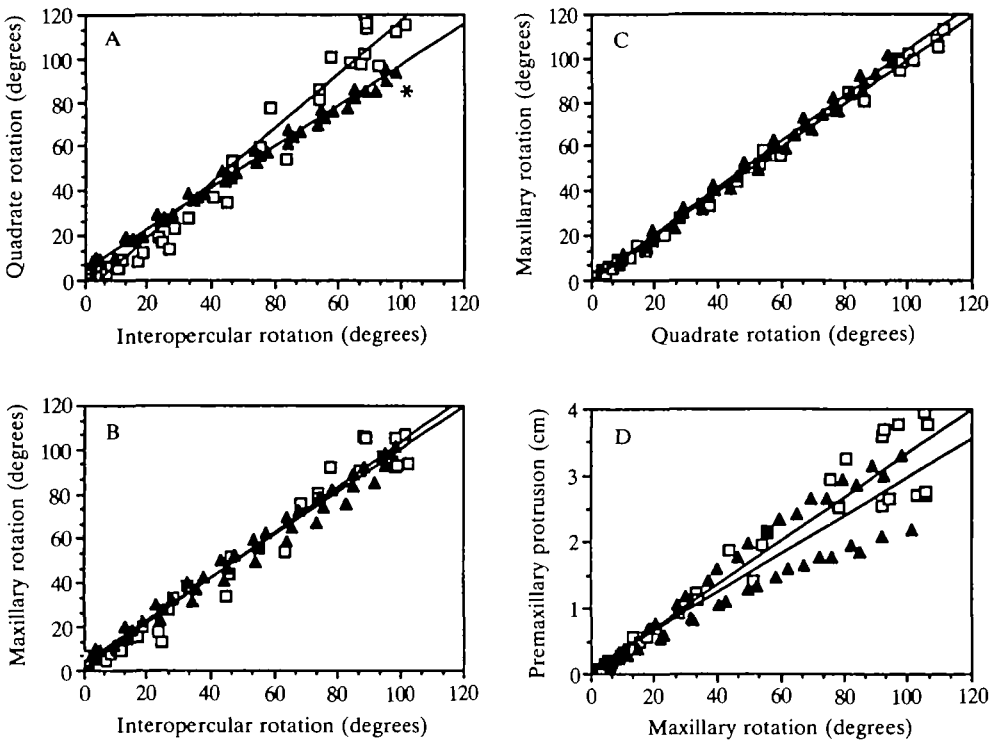


Fig. 6. Regression lines comparing predictions of the linkage model of the jaws (▲) with film results (□) for *Epibulus insidiator*. Each graph plots an input (independent, abscissa) variable against an output (dependent, ordinate) variable. \* indicates a significant difference between the slopes of the films and the model. See Table 3 for ANCOVA results.

(Table 3, Fig. 6). Despite a slightly lower correlation, the accuracy of the model in the case of cranial elevation as a predictor of jaw protrusion is noteworthy, because the transfer of motion was accurately predicted through seven structures: from the neurocranium to vomero-interopercular ligament, to interopercle, to interoperculo-mandibular ligament, to lower jaw, quadrate and maxilla.

In vertebrate musculoskeletal systems, it is usual for joints between movable parts to be cushioned with connective tissues and fluids. Consequently, the transfer of force and motion between elements is imperfect, owing to the elasticity of muscle and connective tissue or to friction between moving parts (Alexander, 1988; Wainwright *et al.* 1976). The assumptions of the linkage model constructed for the jaws of *Epibulus* do not allow for imperfect transmission of force and motion, and one might predict that error in the predictions of the model would accumulate over a series of joints in the mechanism. Instead, the model maintains the accuracy of kinematic prediction through a long series of angle and distance calculations, from the input of cranial elevation to the final output of jaw protrusion. This suggests that the joints of the *Epibulus* jaw mechanism, between

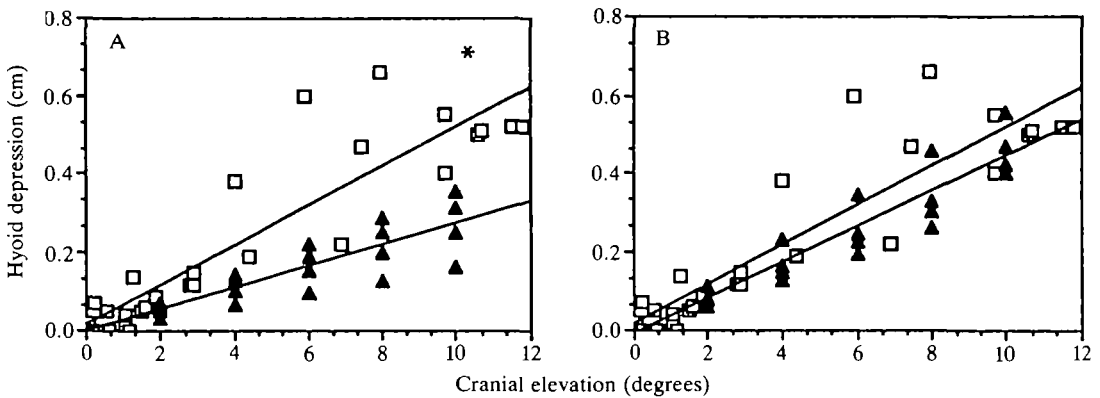


Fig. 7. Regression lines comparing predictions of the hyoid depression model ( $\blacktriangle$ ) with film results ( $\square$ ) in *Epibulus insidiator*. Two models are tested: one with 10% contraction of the sternohyoideus (SH) muscle (B) and one without (A). Each graph plots the input motion of cranial elevation against the output of hyoid depression. \* indicates a significant difference between the slopes of the films and model. See Table 4 for ANCOVA results.

bones and between bones and connective tissues, are efficient at transferring force and motion during feeding.

The accuracy of the quantitative models of the feeding mechanics of *Epibulus* illustrate the potentially wide applicability of linkage models to fish feeding systems. The linkage system of the trophic apparatus in *Epibulus* has been extensively reorganized compared with that in *Cheilinus*. The versatility of the modeling techniques used in this study and in the study of *Cheilinus* feeding (Westneat, 1990b) suggests that these methods may be applicable to a wide range of forms with very different cranial anatomy. Continuing research projects include testing of the generality of four-bar linkage models in perciform fishes other than labrids.

#### Hyoid linkage

The hyoid linkage model of *Epibulus* was an accurate predictor of hyoid depression when simultaneous cranial elevation and sternohyoideus contraction were simulated (Fig. 7, Table 4). This model predicted a relationship between input and output kinematics that is not statistically different from real feeding behavior (Table 4). These results are similar to those described for *Cheilinus* (Westneat, 1990b). The pattern of timing of hyoid depression and the extent of hyoid depression in *Epibulus* are also comparable to those in *Cheilinus*. Previous kinematic data (e.g. Lauder, 1980; Liem, 1978; Muller, 1987; Muller and Osse, 1984; Osse, 1969; Westneat and Wainwright, 1989) show that peak hyoid depression occurs approximately 10 ms after peak cranial elevation in most species.

The mechanism of hyoid depression in *Epibulus* has not undergone a drastic reorganization similar to the morphological and functional changes seen in the jaws. The extensive modifications of the jaws and the relative lack of evolutionary

Table 4. Epibulus hyoid linkage results

	Films	Model
A Regression results:		
Model 1: CE→HD	$y=0.05x+0.02, r^2=0.80$	$y=0.03x+0.0007, r^2=0.81$
Model 2: CE+SH→HD	$y=0.05x+0.02, r^2=0.80$	$y=0.05x-0.008, r^2=0.91$
B ANCOVA results:		
	Slope	y-intercept
Model 1: CE→HD	0.001*	—
Model 2: CE+SH→HD	0.45	0.05

(A) Equations from least-squares regressions performed on input and output variables from film kinematics and model predictions.

(B) *P*-values from analyses of covariance testing for differences between film kinematics and model predictions.

The means of four feedings for each of four individuals were used for film regressions. Significant differences (\**P*<0.01) indicate that the model fails to predict well for that pair of variables. Slopes and y-intercepts were tested except when slopes were significantly different. CE, cranial elevation. HD, hyoid depression. SH, sternohyoideus muscle contraction.

change in the hyoid mechanism suggest that these feeding mechanisms may be functionally independent of one another. Observations of rapid evolutionary change in functional systems have often led to hypotheses of ‘decoupling’ as a factor in structural and functional evolution (Lauder, 1981; Liem, 1980; Lauder and Liem, 1989). Decoupling hypotheses propose that an evolutionary change that allows multiple functional systems to be independent of one another may permit previously constrained mechanisms to increase their phenotypic and behavioral ranges.

The degree of coupling between the jaw and hyoid systems in fishes has been discussed by Muller and Osse (1984) and van Leeuwen and Muller (1984). The relative contributions of suction and jaw protrusion to the feeding strikes of fishes with different body shapes and swimming modes were analyzed in these studies. Lauder (1980) demonstrated that the phylogenetically primitive mechanism of lower jaw depression includes a mandibulo-hyoid coupling. In this mechanism, found in *Lepisosteus*, *Polypterus*, *Amia* and primitive euteleosts, sternohyoideus contraction against the pectoral girdle causes retraction of the hyoid apparatus. This exerts a posterodorsal force on the mandible *via* the mandibulo-hyoid ligament. Lauder (1983) points out the phylogenetic level at which the mandibulo-hyoid ligament shifts insertion from the mandible to the interopercle. Future research should examine evolutionary changes in the mechanisms of the oral jaws, pharyngeal jaws and hyoid mechanisms of perciform fishes within a phylogenetic framework to establish the degree of phylogenetic congruence between these feeding mechanisms.

*Evolution of the Epibulus feeding mechanism*

There are no described fish species with a feeding mechanism that might be

considered intermediate between that of *Epibulus* and other labrids. The sister taxa to *Epibulus* are the two species of *Wetmorella* (Westneat, 1991) each of which has a feeding mechanism more similar to *Cheilinus* (Fig. 8A) than to *Epibulus*. It is difficult to construct scenarios for the transition from the mechanism of *Cheilinus* or *Wetmorella* to that of *Epibulus* because of the large number of modifications involved. The evolution of the *Epibulus* jaw mechanism involves the derivation of a unique ligament (Fig. 3A, the vomero-interopercular ligament) and the change of structure and activity of the quadrate, the palatine, the interopercle, the lower jaw, the pterygoid elements and the interoperculo-mandibular ligament. Further derived characteristics have evolved in the premaxilla, maxilla, neurocranium and other ligaments, each of which plays a role during jaw protrusion.

Because four-bar models are accurate in predicting feeding kinematics, evolutionary changes in the links of the four-bar mechanisms of the jaws are likely to be the most critical for the biomechanics of feeding. Fig. 8 illustrates the four primary linkage changes that have occurred in *Epibulus*. In what order did the changes occur? Which intermediate linkages are functionally viable? These questions can be addressed by considering the biomechanical results of any given change.

The initial assumption is that the four major linkage changes (Fig. 8) are independent evolutionary events. Fig. 8A presents the morphology and linkage system of *Cheilinus diagrammus* (Westneat, 1990a,b). In this system, the posterior opercular linkage (links A–D) acts to drop the lower jaw (after Anker, 1974). Lower jaw depression operates the anterior four-bar linkage of the jaws (links 1–4) and involves the palatine as a movable link (link 4). However, the *Epibulus* linkage has lost the palatine link (Fig. 8B) because the anterior head of the palatine is shortened. The mechanism shown in Fig. 8B is not functional, because a three-bar linkage is formed by links 1–3. This mechanism has zero degrees of freedom, and is unlikely to have been an intermediate form.

The movable quadrate in *Epibulus* is one of the most unusual linkage changes (link 5, E in Fig. 8C). A movable quadrate, as a single first step, would also render the *Cheilinus* mechanism inoperative, because the fulcrum for lower jaw rotation would be removed if the quadrate was no longer stationary. Additionally, both the anterior and posterior linkages are five-bar mechanisms (Fig. 8C, links 1–5 and A–E), with two degrees of freedom each. Motion is only defined and predictable for five-bar mechanisms if the positions of two links are known. Thus, muscular control would be required to operate directly or indirectly two of the five links in each mechanism. The only links under direct muscular control in either *Epibulus* or *Cheilinus* are the opercle (levator operculi muscle) and the maxilla (adductor mandibulae muscle).

Fig. 8D illustrates the linkage produced from addition of the vomero-interopercular ligament to the *Cheilinus* linkage system. This mechanism is also non-functional because it changes the structure of the posterior linkage so that it is immovable. If the interopercle (link C) is stiff and the vomero-interopercle ligament (link E) is inextensible, then posterior rotation of the opercle (link B) is



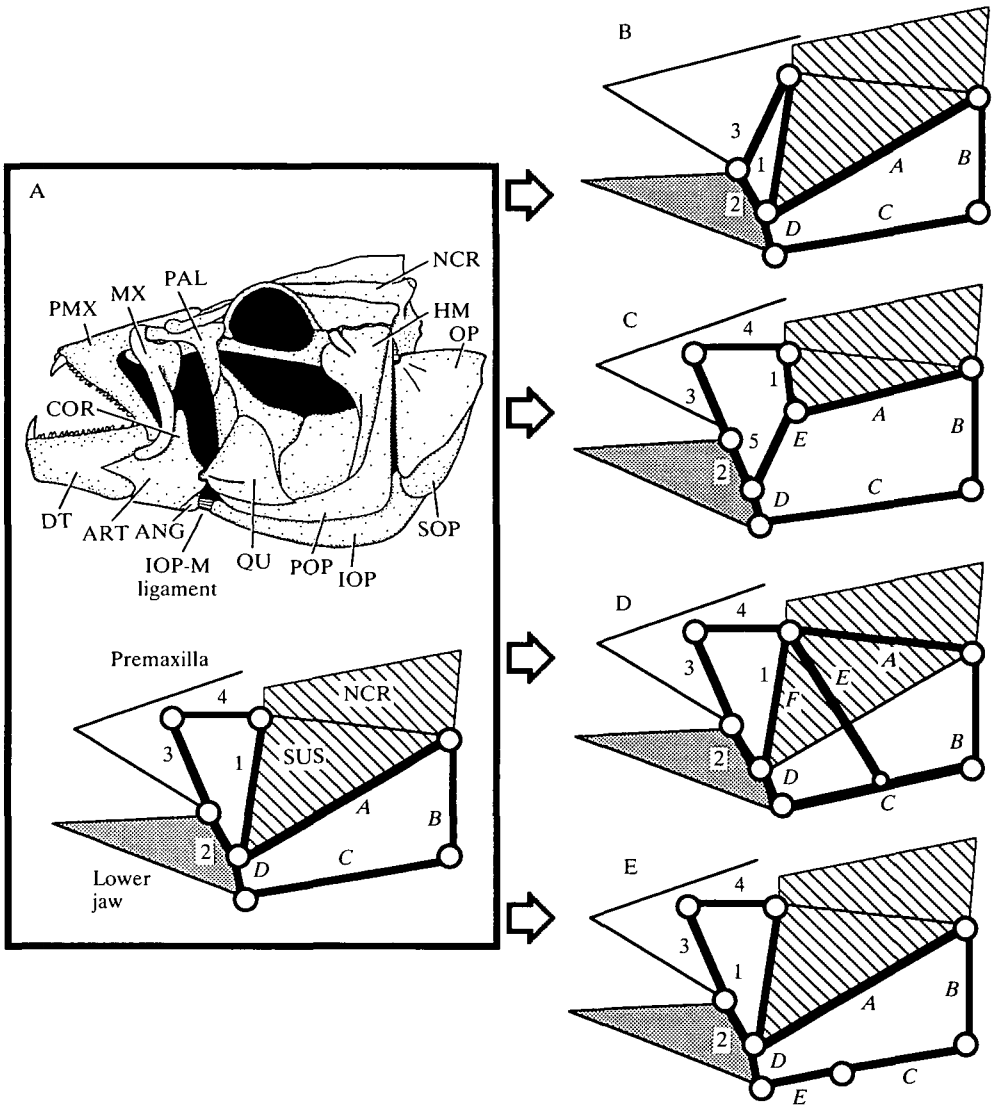


Fig. 8. (A) Cranial osteology of *Cheilinus diagrammus* (above) and a mechanical diagram of the anterior jaws and opercular linkage mechanisms (below). Links 1–4 are the anterior linkage mechanism of jaw protrusion. Links A–D are the opercular linkage of lower jaw depression. (From Westneat, 1990b.) (B–D) Four structural changes in the evolution of the *Epibulus* jaw mechanism from that of a related labrid, *Cheilinus*. Only E is biomechanically functional. (B) Loss of the palatine link. (C) Gain of a movable quadrate link. (D) Gain of a vomero-interopercular ligament link. (E) Gain of an elongated interoperculo-mandibular ligament link. ANG, angular; ART, articular; COR, coronoid process; DT, dentary; HM, hyomandibula; IOP, interopercle; IOP-M ligament, interoperculo-mandibular ligament; MX, maxilla; NCR, neurocranium; OP, opercle; PAL, palatine; PMX, premaxilla; POP, preopercle; QU, quadrate; SOP, subopercle; SUS, suspensorium.

impossible. The linkage is functional only if the fixed link *F* is made movable (i.e. via the movable quadrate) before the advent of the vomero-interopercular ligament.

Fig. 8E presents the linkage system resulting from elongation of the interoperculo-mandibular ligament to form a new link (link *E*), as it does in *Epibulus*. This mechanism is a functional linkage system if the new ligament is positioned parallel to the direction of motion of the interopercle (link *C*). Although this system contains a five-bar linkage (Fig. 8E, links *A–E*), the linkage behaves as a four-bar linkage when links *C* and *E* are pulled posteriorly. This system is the only viable mechanism that can be produced from the addition of a single structural novelty found in *Epibulus*.

If the evolution of the *Epibulus* linkage system began with the advent of the elongated interoperculo-mandibular ligament, then what was the likely pattern of subsequent changes? Fig. 9 presents the first intermediate linkage (Fig. 9A, same as Fig. 8E) and a possible sequence of structural changes that arrives at the *Epibulus* geometry through biomechanically feasible intermediates. Fig. 9B presents the linkage system occurring after the addition of the vomero-interopercular ligament to form a new link (link *F*). This evolutionary event is critical to the *Epibulus* jaw mechanism because the vomero-interopercular ligament acts as the coupler link in the four-bar mechanism and the input link of the six-bar linkage (Fig. 3B). The new ligament represents a potential new source of input to the posterior linkage, that of cranial elevation and force transfer to the interopercle. The linkage of Fig. 9B is a posterior six-bar linkage (*A–F*) and the remaining anterior four-bar linkage (1–4).

Fig. 9C illustrates the final linkage change, the simultaneous loss of the palatine link (link 4 of 9A) and gain of the movable quadrate link (new link 4 of Fig. 9C). These two evolutionary events must have occurred simultaneously, because the linkage resulting from either one occurring alone at any point results in a non-functional anterior jaw linkage (Figs 8B,C). The anterior linkage in Fig. 9C is a true six-bar linkage (links 1–6), a biomechanically feasible mechanism with a new input motion source, from cranial elevation and interopercular rotation. This mechanism is identical to the posterior four-bar (*A–D*) and anterior six-bar (1–6) linkages that are found in *Epibulus*, except that the dimensions have been kept proportional to *Cheilinus* morphology. Two links are shared, link 1/*D* and link *C*/5. This is the first appearance of a jaw mechanism in which both the lower jaw and the upper jaw are protrusive.

A reorganization of the linear dimensions of the links (Fig. 9D) completes the transition to the feeding mechanism of *Epibulus*. The specific dimensional changes at each stage are uncertain, but are likely to have occurred during all stages. Physical models indicate that these systems are sensitive to small changes in the relative dimensions of the links. For example, increasing the relative length of the quadrate bar by as little as 10% renders the *Epibulus* system inoperative. Evolutionary changes in the geometry of the linkage must therefore have taken place within a limited range of biomechanically feasible dimensions.

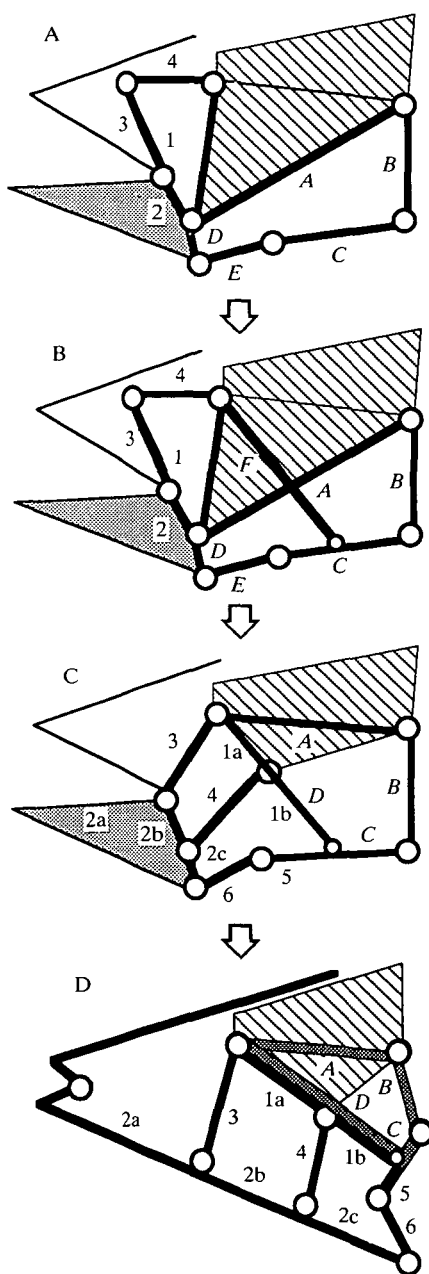


Fig. 9. One possible evolutionary sequence of events leading to the *Epibulus* jaw mechanism from (A) the primitive mechanism with the interoperculo-mandibular ligament added (*E* from Fig. 8E). (B) Gain of the elongated vomero-interopercular ligament link. (C) Loss of the palatine link and simultaneous gain of the movable quadrate link. This is the basic linkage system of *Epibulus* with the proportions of the elements unchanged. (D) The mechanism with the linkage geometry similar to that of *Epibulus*.

Alternative sequences of events to explain the feeding mechanism of *Epibulus insidiator* could be constructed, but the sequence presented above is to be favored for two reasons. First, each intermediate form (Fig. 9) is biomechanically feasible, with a linkage system that should theoretically work to open the jaws. Second, the hypothesis presented above is the most parsimonious explanation of the changes observed in cranial structure. The initial assumption was that the four major linkage changes (Fig. 8) are independent evolutionary events. However, it was shown that loss of the palatine link and gain of the quadrate link must have been simultaneous, for reasons of functional continuity.

Thus, the simplest hypothesis is that three events took place in the evolution of the *Epibulus* linkage system. (1) For biomechanical reasons, the advent of the interoperculo-mandibular ligament (Figs 8E, 9A) is the only single event that could have started the transition. (2) The evolution of the vomer-interopercular ligament is likely to have been the second step. (3) Simultaneous loss of the palatine link and gain of the quadrate link was probably the final event. Therefore, unless we invoke hypotheses of a 'hopeful monster' that evolved all changes in linkage structure and geometric dimensions at once, the most parsimonious hypothesis is one that combines the fewest number of evolutionary events into a biomechanically feasible series of intermediate forms.

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