

# Trophic Apparatus in Cyprinodontiform Fishes: Functional Specializations for Picking and Scraping Behaviors

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**ABSTRACT** Cyprinodontiforms are a diverse and speciose order that includes topminnows, pupfishes, swordtails, mosquitofishes, guppies, and mollies. Sister group to the Beloniformes and Atheriniformes, Cyprinodontiformes contains approximately twice the number of species of these other two orders combined. Recent studies suggest that this group is well suited to capturing prey by “picking” small items from the water surface, water column, and the substrate. Because picking places unusual performance demands on the feeding apparatus, this mode of prey capture may rely upon novel morphological modifications not found in more widespread ram- or suction-based feeding mechanisms. To assess this evolutionary hypothesis, we describe the trophic anatomy of 16 cyprinodontiform species, selected to broadly represent the order as well as capture intrageneric variation. The group appears to have undergone gradual morphological changes to become increasingly specialized for picking and scraping behaviors. We also identify a suite of functional characters related to the acquisition of a novel and previously undescribed mechanism of premaxillary protrusion and retraction, including: modification of the “premaxillomandibular” ligament (which connects each side of the premaxilla to the ipsilateral mandible, or lower jaw), a novel architecture of the ligaments and bony elements that unite the premaxillae, maxillae and palatine bones, and novel insertions of the adductor muscles onto the jaws. These morphological changes to both the upper and lower jaws suggest an evolutionary trend within this group toward increased reliance on picking individual prey from the water column/substrate or for scraping encrusting material from the substrate. We propose that the suite of morphological characters described here enable a functional innovation, “picking,” which leads to novel trophic habits. *J. Morphol.* 270:645–661, 2009. © 2008 Wiley-Liss, Inc.

**KEY WORDS:** adductor mandibulae; premaxillary protrusion; Cyprinodontiformes; feeding

## INTRODUCTION

The speciose and diverse Cyprinodontiformes (Teleostei) are generally considered to be a group of generalized “midwater omnivores” feeding on small, non-elusive, benthic and planktonic organisms (Weisberg, 1986; Motta et al., 1995; Mansfield and Macardle, 1998). However, this description does not do justice to the unusual feeding behaviors

and mechanisms found within the group. Though some cyprinodontiform fishes are indeed mid-water omnivores (e.g., Hunt, 1953), many species appear to capture prey by means of an unusual “picking” mode of prey capture (Ferry-Graham et al., 2008).

Picking is a form of biting prey capture employed to procure prey items in the water column, at the air–water interface, or loosely attached to the substrate (Horn and Ferry-Graham, 2006). Biting and suction behaviors typical of teleosts are often considered feeding modes where trade-offs occur because jaws typically can be optimized for producing force *or* operating at high velocities, but not for both (as reviewed in Westneat, 2004). Increased feeding velocity is often associated with enhanced suction production, whereas in biting behaviors suction performance is compromised to enable the jaws to remove attached prey by force. Although forceful movements of the jaw characterize strong biting, less forceful but more controlled movements of the jaw characterize picking (Ferry-Graham et al., 2008). Picking prey from the water column requires fine control of the jaws, but does not require large forces to be produced. Thus picking likely requires a suite of morphological features different from those typically observed in teleostean lineages that are considered either strong biters or suction feeders.

In addition, more derived members of Cyprinodontiformes, particularly species within the Poeci-

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liidae, often obtain prey via a scraping behavior, where the jaws are placed in direct contact with the substrate and epiphytic material is removed using a combing action of the teeth (Gibb et al., in press). Scraping by cichlid fishes has been well described, for example, where anatomical changes to the oral jaws increase gape and facilitate increased contact between the teeth and the substrate (Liem, 1980; Bouton et al., 1998). We hypothesize that poeciliids and some cyprinodontids have independently evolved a different set of anatomical “tools” used for this feeding mode.

Studies examining feeding morphology among cyprinodontiform species have revealed significant trophic polymorphisms (Turner and Grosse, 1980; Holtmeier, 2001). Such findings suggest that the trophic anatomy of this order may lend itself to a variety of feeding modes (Hernandez et al., 2008). To appropriately evaluate potential trophic polymorphisms, however, we must first understand phylogenetic changes in cyprinodontiform oral jaws. This study, which is well supported by several morphological analyses of cyprinodontiform relationships (Rosen and Bailey, 1963; Parenti, 1981; Costa, 1998; Ghedotti, 2000), specifically examines how the trophic apparatus is modified across Cyprinodontiformes in light of these different functional roles.

We describe the evolution of morphological features associated with picking and scraping behaviors by examining several cyprinodontiform species with special emphasis on Poeciliidae and Cyprinodontidae (see Fig. 1). As Poeciliidae demonstrates exceptional trophic diversity we sampled extensively within this clade to understand variation at this level. Specifically, we describe the osteology of the anterior jaws, the morphology of the adductor mandibulae muscle complex (the primary jaw closing muscle in teleosts), and the associated ligamentous attachments required to produce feeding movements. The specific aims of this study are to: 1) describe the musculoskeletal structure of the anterior jaws in the Cyprinodontiformes; 2) assess the morphological changes that have occurred within these trophic structures; and 3) propose both proximate performance consequences as well as ecological and evolutionary consequences associated with these morphological changes.

## MATERIALS AND METHODS

The following live specimens were obtained from commercial suppliers, sacrificed according to Northern Arizona University IACUC approved protocols (NAU IACUC #04-007) and used as representative taxa: *Kryptolebias marmoratus*, *Fundulus rubrifrons*, *Gambusia affinis*, *Heterandria formosa*, *Jordanella floridae*, *Xiphophorus helleri*, and *Poecilia sphenops*. Additional specimens were obtained from museums and from the collections of colleagues and were used to assess intra-clade and intra-generic variation in feeding morphology: *Atherinops californiensis*, *Fundulus grandis*, *F. similis*, *F. chrysotus*, *G. holbrooki*, *Cyprinodon variegatus*, *Floridichthys carpio*, *Jordanella floridae*, and *Poecilia latipinna*. In all cases except *Atherinops*

*californiensis*, which were frozen, specimens were preserved in 10% formalin and subsequently stored in 70% ethanol prior to our receipt of the specimens.

For the morphological description, fresh and preserved specimens were dissected and briefly immersed in iodine to facilitate identification of muscle fiber orientation. Approximately 10 specimens from each representative species were dissected to determine musculoskeletal architecture and to assess inter-individual variation in feeding morphology. Additional specimens were cleared and stained using a protocol presented in Dingerkus and Uhler (1977) with modifications by Potthoff (1984). Cleared and stained specimens were used to assess the shape of the bones and cartilages of the anterior jaws.

Line-drawn illustrations of specimens were made from photographs taken using an Olympus DP12 digital camera attached to an Olympus SZX12 dissecting microscope, or with an Olympus SZX-DA camera lucida attached to the same dissecting microscope. Digital illustrations of skeletal and muscle morphology were constructed using Canvas (ver. X for OS X), Adobe Illustrator (ver. 10.0.3 for OS X), and a Wacom drawing pad.

The morphological analysis included characterization of the following feeding structures: premaxilla, maxilla, anguloarticular, dentary, and palatine bones and the adductor mandibulae muscle complex. As previous research has shown that the adductor mandibulae complex is the primary muscle complex involved in jaw closing movements, a brief review of its morphology is warranted here. Most teleosts are characterized by four major divisions of the adductor mandibulae complex: A1, A2, A3, and A $\infty$ . Although there is some variation in the origin and insertion of the divisions of the adductor mandibulae across species, teleosts tend to follow a consistent pattern. A1 generally originates from the preopercle, quadrate, symplectic, hyomandibular, or pterygoid bones and inserts on the maxilla, purportedly to assist in premaxillary protrusion (Alexander 1967b; Ballintijn et al., 1972; Motta, 1984). A2 also commonly originates from the preopercle, quadrate, symplectic, hyomandibular, or pterygoid bones, usually deep (i.e., medial to) to the origin of A1, and inserts on the lower jaw—on either the anguloarticular or dentary, or on both, as is seen in strong biters (e.g., Hernandez and Motta, 1997). A3 is typically the most medial division and appears to vary the least, characteristically arising from the ventral aspect of the suspensorium and inserting on the medial side of the dentary, or on the anguloarticular (Winterbottom, 1974). A $\infty$  originates from the medial surface of the ventral-most region of the quadrate and inserts on the dentary, filling most of the Meckelian fossa.

We also characterized changes to the ligaments of the anterior jaws across Cyprinodontiformes. To describe the ligaments associated with jaw movements, we assessed morphological changes to the ethmomaxillary, palatomaxillary, “premaxillomandibular”, premaxillomaxillary, maxillolacrimal, as well as the ligaments that tie the medial hooks of the maxillae to the ascending processes of the premaxilla. The ethmomaxillary connects the anterior end of the ethmoid to the dorsal head of the maxilla. The palatomaxillary connects the dorsal end of the palatine to the dorsal end of the maxilla. The “premaxillomandibular” ligament connects the lateral face of the descending arm of the premaxilla to the medial side of the lower jaw. It should be noted that premaxillomandibular ligaments described in other species (Nandida; Liem, 1970) show a completely different architecture, thus rendering the homology uncertain. Although its homology is uncertain, we use the term premaxillomandibular to refer to this ligament when describing its condition in the species examined here because it obviously connects the premaxilla to the mandible. The premaxillo-maxillary ligament connects the ventral ends of the maxilla to the premaxilla. The maxillolacrimal connects the lacrimal to the maxilla.

## RESULTS

We first describe the osteology of the anterior jaws, the ligamentous anatomy, and the jaw mus-

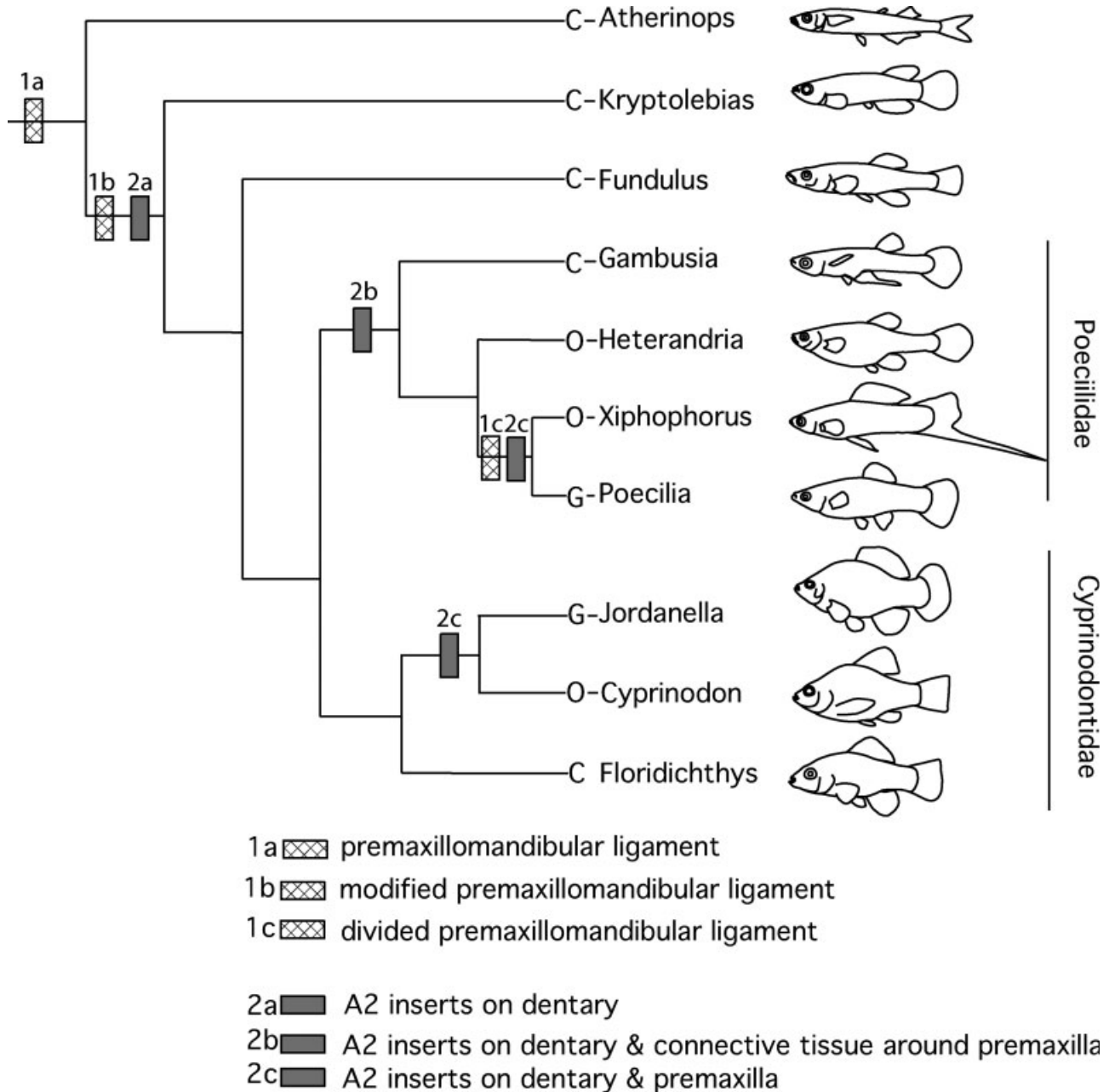


Fig. 1. Cladogram of species examined in this study. Character states are as noted on the figure. Larger atheriniform and cyprinodontiform relationships are after Costa (1998), Ghedotti (2000), and Parenti (2005). Relationships within the Cyprinodontidae are after Parker and Kornfeld (1995). Diet data are from published literature (Hunt, 1953; Zaret and Rand, 1971; Naiman, 1975; Davis, 1981; Arthington, 1989; D'Avanzo and Valiela, 1990; Hurlbert and Mulla, 1981; Taylor, 1992; Belk and Lydeard, 1994; Schaefer et al., 1994; Motta et al., 1995). C, benthic and midwater micro-carnivore; G, grazing herbivore; O, omnivore.

culature of *Kryptolebias marmoratus*, the most basal cyprinodontiform examined here. We describe each of the more derived clades only to the extent that they differ from this basal anatomy or the anatomy of previously described species. Additionally, for each genus in which more than one species was examined, we provide a brief synopsis of intra-generic variation within these trophic structures. This synopsis is especially relevant for Cyp-

rinodontidae, where we find the greatest variation and for which several genera were examined.

#### Musculoskeletal Aspects of the Anterior Jaws in Cyprinodontiforms

***Kryptolebias marmoratus* (see Fig. 2), *Manogrove rivulus*.** In the most basal species examined, the aplocheloid *Kryptolebias marmoratus*,

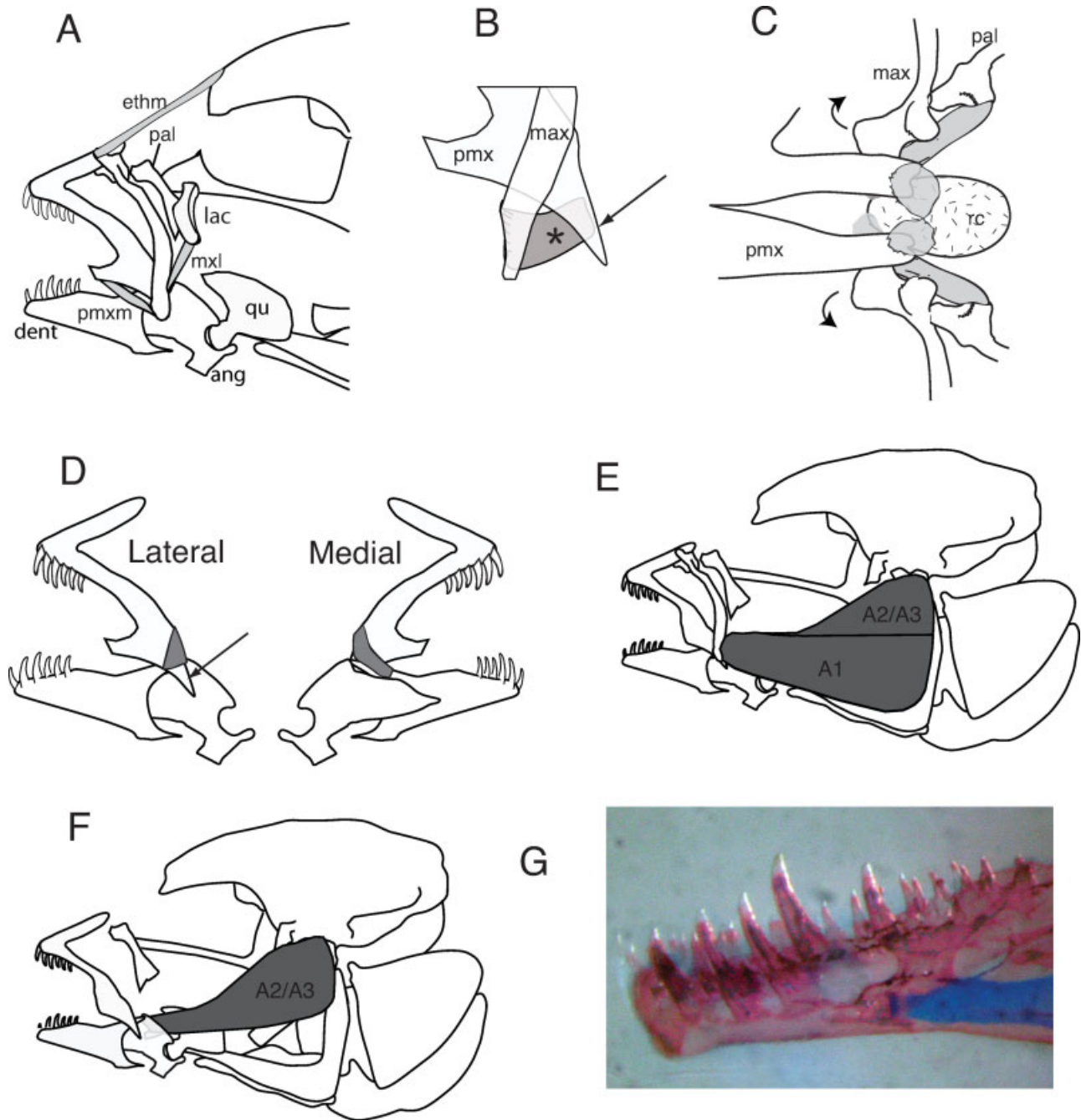


Fig. 2. Oral jaw morphology of *Kryptolebias marmoratus*. (A) Lateral view of cranial bones showing the ligaments that secure the maxilla to adjacent bones, ethmomaxillary (ethm), maxillolacrimal (mxl), and premaxillo-maxillary (pmxm). (B) Close-up view of premaxillo-maxillary ligament that may assist in premaxillary protrusion (to clarify connections, the ligament is illustrated in a relaxed state, and longer than that seen in fixed specimens). (C) Dorsal aspect of oral jaws showing rostral cartilage and all ligaments tying the ascending processes of the premaxillae to the medial hooks of the maxillae. (D) Lateral and medial views of the premaxillomandibular ligament. (E) Lateral view of the cranial anatomy showing AM A2/A3 after removal of A1. (F) Lateral view of the cranial anatomy showing AM A2/A3 after removal of A1. (G) Caniniform dentition on dentary. pmx, premaxilla; max, maxilla; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; rc, rostral cartilage; lac, lacrimal.

the overall architecture of the bony elements comprising the anterior jaws shows a typical teleostean morphology (Fig. 2A). As in all species examined here, the maxilla is adjacent to and slightly

lateral to the descending arm of the premaxilla. Relative to many other Cyprinodontiformes, the ascending arm of the premaxilla is long, and bears a distinct gap at the distal tip (a character used to

differentiate primitive versus derived state of the oral jaws within Cyprinodontiformes; Parenti, 1981; Fig. 2C). Ventral to the point at which the premaxilla attaches to the lower jaw, the descending arm of the premaxilla has a ventrally projecting spine (Fig. 2B,D arrow). This ventral portion of the descending arm of the premaxilla fits into a shallow groove within the ventromedial edge of the maxilla.

At its ventral extreme, the rostral edge of the maxilla has a thick, taut ligament that turns medially to attach to the medial face of the premaxilla (Fig. 2B). This taut connection is such that lateral rotation of the maxilla pulls the premaxilla forward. The arm of the maxilla is relatively thin, but has a pronounced "bowed" shape, which has previously been shown to characterize aplocheloids (Parenti, 1981).

The dorsal aspect of the maxilla is more complex: a distinct lateral process and a bent "hook" form the dorsal portion of the maxilla (Fig. 2C). The lateral process serves as a site of attachment for the ethmomaxillary ligament (Fig. 2A). When the lower jaw is fully adducted there is considerable overlap between the medial hook of the maxilla and the ascending processes of the premaxillae (Fig. 2C). In the lower jaw, a patent coronoid process of the dentary, as well as ventral process of the anguloarticular result in a firm articulation of the anguloarticular and dentary (Fig. 2A). The teeth on both the premaxilla and dentary are comprised of one peripheral row of larger caniniform teeth, with several rows of smaller caniniform teeth behind it (Fig. 2G).

The rostral, slightly anteriorly directed, articular facet of the palatine abuts the dorsal aspect of the maxilla, just below a lateral process upon which a thick ethmomaxillary ligament attaches (Fig. 2A). The palatine and maxilla articulate via a small, cartilaginous, articular surface on the palatine. A thick, fibrous ligament attaches the dorsal process of the palatine with the medial hook of the maxilla (Fig. 2C).

Ligamentous tissue connects the anterior-dorsal region of a large rostral cartilage to the tips of the ascending process of the premaxilla (Fig. 2C). This connective tissue indirectly connects the ascending process of the premaxilla to the medial hook of the maxilla, such that anterior movement of the medial hook of the maxilla pulls on this rostral cartilage and associated ventral ligaments, thereby pulling the premaxilla forward (Fig. 2C). The connective tissue that connects the dorsal and ventral aspects of the rostral cartilage to the ascending processes of the premaxillae and the medial arms of the maxillae, respectively, is not comprised of typical parallel-fibered collagen tissue. The anterior end of the rostral cartilage is, instead, surrounded by relatively diffuse connective tissue, which rather loosely binds these elements together.

Several ligaments attach to the maxilla, allowing little motion of this element to occur, other than rotation along its long axis (Fig. 2A). *Kryptolebias marmoratus*, which was only recently separated from the genus *Rivulus* (Hrbek and Larson, 1999; Costa, 2004; Vermeulen and Hrbek, 2005; Hrbek et al., 2007), is unlike other rivulids in that it has a triangular lacrimal (Fig. 2A); this triangular shape is like most other aplocheloids (Costa, 1998). Other rivulids that have been studied are characterized by a unique and strongly twisted lacrimal (Parenti, 1981; Costa, 1998). A thick maxillolacrimal ligament connects the ventral region of the maxilla to the ventral edge of the lacrimal in *K. marmoratus*. Thick ethmomaxillary ligaments attach the rostral margins of the ethmoid to the lateral head of the maxilla. The relatively thin, slightly twisted, maxilla is held at its ventral extreme by the maxillolacrimal (mxl of Fig. 2A) and premaxillo-maxillary ligament (pmxm), and at the dorsal extreme by the ethmomaxillary ligament (ethm). The architecture of the ligaments that join the maxilla to the other bony elements of the head (Fig. 2A) is such that when the maxilla is rotated, as would be expected to occur when the jaw is lowered and/or A1 contracts, the medial hook of the maxilla rotates anteriorly, pulling the ascending processes of the premaxillae forward.

*Kryptolebias marmoratus* has a premaxillomandibular ligament that connects the caudolateral edge of the premaxilla with the caudal edge of the anguloarticular and dentary (Fig. 2D). This small ligament originates from the ventral-most edge of the lateral dentigerous arm of the premaxillae, then wraps around the posterior edge of the premaxilla before turning anteriorly to attach to the medial aspect of the dentary and/or anguloarticular bone, adjacent to the insertion of the adductor mandibulae A2 (Fig. 2D). Importantly, this ligament does *not* insert on the posterior margin of the premaxilla, but rather moves freely along the caudal edge of this bone when the jaws are manipulated. In *K. marmoratus*, this ligament is relatively small and appears to be comprised of typical collagenous ligament.

*Kryptolebias marmoratus* has a very large, single branch of adductor mandibulae A1, which inserts on the ventral third of the maxilla via a broad, muscular insertion (Fig. 2E). However, a smaller "incipient" subdivision of A1 is also present (potentially the beginning of division A1 $\beta$ ; not shown). The belly of A2 is difficult to distinguish from the belly of A3 (although the belly of A3 is larger and more medial); however, A2 inserts partially on the caudal edge of the coronoid process of the dentary as well as on the anguloarticular, whereas A3 has a well-developed tendon that inserts on the medial face of the anguloarticular (Fig. 2F). As in most teleosts, A $\omega$  originates from the medial surface of the ventral-most portion of

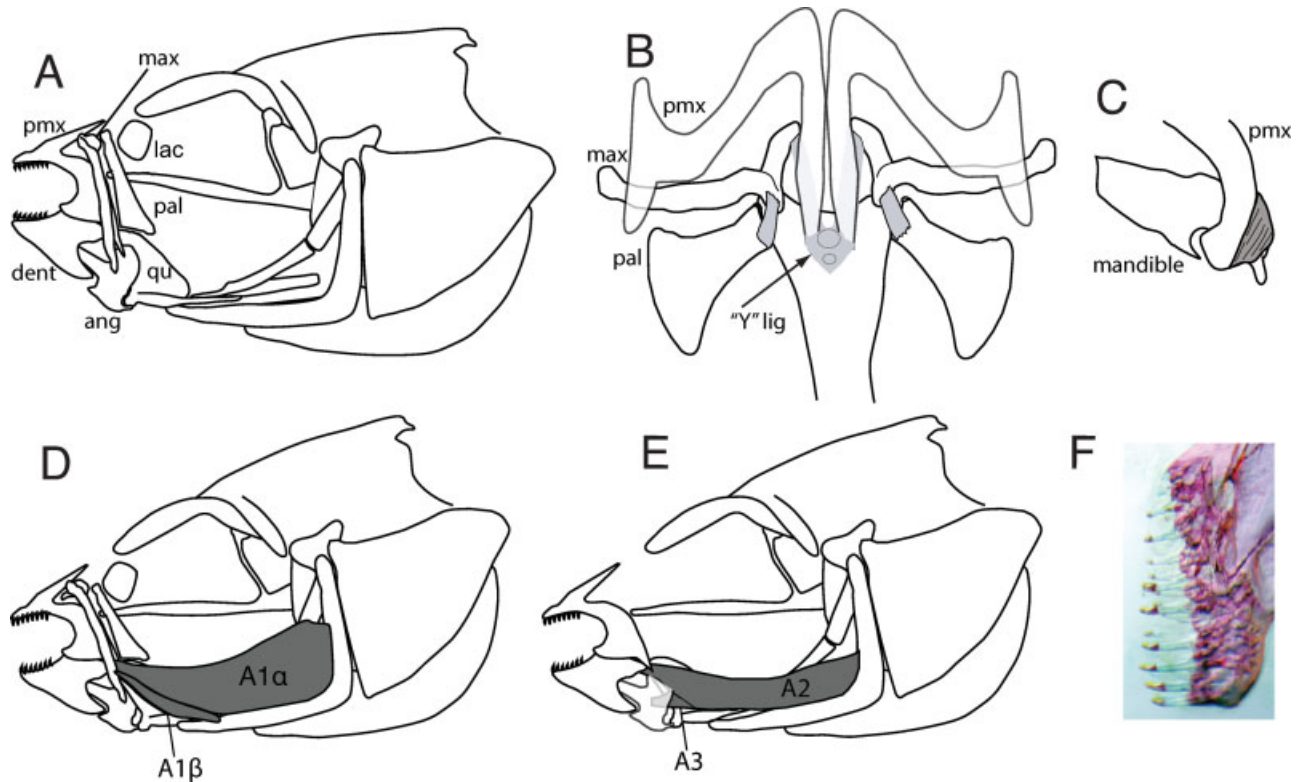


Fig. 3. Oral jaw morphology of *Fundulus rubrifrons*. (A) Lateral view of cranial bones. (B) Dorsal aspect of oral jaws showing rostral cartilages and ligaments tying the ascending processes of the premaxillae to the medial hooks of the maxillae. (C) Lateral view of the premaxillomandibular ligament. (D) Lateral view of the cranial anatomy showing the adductor mandibulae complex. (E) Lateral view of the cranial anatomy showing AM A2/A3 after removal of A1. (F) Caniniform dentition on premaxilla. pmx, premaxilla; max, maxilla; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; eth, ethmoid; lac, lacrimal.

the quadrate and inserts on the dentary, filling most of the Meckelian fossa. Because the morphology of  $A_0$  is not different among taxa used in this study, we will not describe the morphology of this branch for other cyprinodontiform species.

***Fundulus rubrifrons* (see Fig. 3), red-faced topminnow.** Within *Fundulus rubrifrons*, a basal member of the Cyprinodontidae (Fundulidae being the outgroup to Cyprinodontidae + Poeciliidae; Parenti, 2005), the bony elements comprising the anterior jaw are generally similar to those of *Kryptolebias marmoratus* (Fig. 3A).

The ventral end of the maxilla is relatively thin, but with a straight, blade-like morphology that does not connect with the ventral end of the premaxilla, as in *Kryptolebias marmoratus*. Although there is still a taut premaxillo-maxillary ligament attaching the ventral extremes of the maxilla and premaxilla, these connections are not as robust as those seen in *K. marmoratus*. The dorsal end of the maxilla of *Fundulus rubrifrons* is markedly different from that of *K. marmoratus*. A distinct dorsolateral process for attachment of the ethmo-maxillary ligament is not present. Moreover, while elongate, the medial hook does not have the bent shape seen in *K. marmoratus*, rather it subtly

curves anteriorly, remaining adjacent to (but not ventral to) the ascending process of the premaxilla (compare Figs. 2C and 3B). The curved dorsal aspect of the maxilla articulates with the anterior edge of the ethmoid. A relatively thick meniscus is seen at the contact point between the ethmoid and the maxilla, where the maxilla likely articulates (not shown). Such an articulation and corresponding meniscus were not seen in *K. marmoratus*.

Unlike in *Kryptolebias marmoratus*, where the rostral cartilage was quite large (Fig. 2C), *Fundulus rubrifrons* has two smaller rostral cartilages (one may be an accessory cartilage). The medial hook of the maxilla is attached ventrally to the ascending process of the premaxilla via a thick, Y-shaped ligament within which these two distinct rostral cartilages are embedded (Fig. 3B). Alexander (1967b) previously described the combined ligament and embedded rostral cartilages in *F. rubrifrons* as the "rostral cartilage." Alternatively, we propose that this thick ligament contains discrete rostral cartilages embedded within it. The ethmo-maxillary ligament has been lost, which is a synapomorphy of cyprinodontoids (Parenti, 1981; Costa, 1998). Although still present, the maxillolacrimal ligament has changed architecture signifi-

cantly in *F. rubrifrons* and the lacrimal bone itself is more rectangular in shape. Importantly, this ligament attaches to the maxilla approximately 2/3 of the way up its shaft.

Several rows of similarly sized caniniform teeth line the dentary and premaxilla (Fig. 3F).

The palatine in *Fundulus rubrifrons* is shaped differently from that seen in *Kryptolebias marmoratus*. Within *F. rubrifrons*, the palatine is characterized by a blunt facet, which serves as both a site of articulation and as a site of ligamentous connection with the maxilla. The point of articulation is at the maxilla's most dorsal aspect where the medial hook begins curving anteriorly. A thick ligament also attaches the palatine to the medial process of the maxilla (Fig. 3B). Within *F. rubrifrons*, the premaxillomandibular ligament is wider and covers a slightly larger portion of the ventrolateral face of the premaxilla than that in *K. marmoratus* (Fig. 3C).

In contrast to the adductor musculature of the aplocheloids, *Fundulus rubrifrons* is characterized by two distinct divisions of adductor mandibulae A1 (A1 $\alpha$  and A1 $\beta$ ; Ballantijn et al., 1972), both inserting on the ventral third of the maxilla. A1 $\beta$  inserts muscularly on the ventrolateral edge of the maxilla, whereas A1 $\alpha$  inserts more medially, via a short, discrete tendon.

To assess the degree of intrageneric muscular variation, we also examined the adductor mandibulae complex within specimens of *Fundulus similis*, *F. chrysotus*, and *F. grandis*. *Fundulus spp.* showed little variation except in the size of different divisions of the AM complex and slight differences in insertions of the different divisions.

***Gambusia affinis* (see Fig. 4), mosquitofish.** In *Gambusia affinis*, a relatively basal member of the Poeciliidae, the premaxilla is relatively shorter than that seen in either *Kryptolebias marmoratus* or *Fundulus rubrifrons* (Fig. 4A). Moreover, from a dorsal aspect, the ascending process of the premaxilla in *G. affinis* is more blunt and triangular in shape, with a broadened connection with the descending arm of the premaxilla (Fig. 4B).

The maxilla of *Gambusia affinis* is more robust than that of *Fundulus rubrifrons*, with a wider ventral end (a condition previously described for poeciliids; Parenti, 1981; Costa, 1998). In *G. affinis* the maxilla has both an expanded dorsolateral process, and a slightly curved, but flattened medial projection. Importantly, unlike both *Kryptolebias marmoratus* and *F. rubrifrons*, there is little overlap in dorsal aspect between the medial hook of the maxilla and the ascending process of the premaxilla (Fig. 4B).

Neither the coronoid nor the posteroventral process of the dentary is as long as those seen in *Fundulus rubrifrons*, thus the anguloarticular and dentary are not tightly linked (Fig. 4A). An elongate ventral process characterizes the anguloartic-

ular (Costa, 1998). Several rows of caniniform teeth line both the dentary and premaxilla (Fig. 4E). The darker tips of the teeth suggest that the enamel may incorporate iron (Fig. 4E).

The head of the palatine is shaped like a hammer (Fig. 4A), with a broad anterior head articulating with a process on the dorsal edge of the shaft of the maxilla (Fig. 4B). The broad, cartilaginous facet at the anterior end of the palatine (a synapomorphy of poeciliids; Costa, 1998) suggests that there is significant movement or contact with the maxilla against this process.

Rostral cartilages have been lost. Unlike in *Kryptolebias marmoratus* and *Fundulus rubrifrons*, taut ligaments do not tie the ascending process of the premaxilla to the medial arm of the maxilla. Although there are still loose ligaments connecting these two elements, ligaments are thinner and not taut. Importantly, without taut connections between the ascending process of the premaxilla and the medial hook of the maxilla, it appears unlikely that twisting of the maxilla can transfer force to the premaxilla and thereby effect protrusion.

The slightly wider maxilla (relative to that of *Fundulus rubrifrons*) allows for more distinct insertions of A1 $\alpha$  and A1 $\beta$ . A2 and A3 are still somewhat interconnected, however the bulk of A2 originates from the suspensorium (deep to A1) and inserts muscularly on the dorsocaudal edge of the dentary. A small dorsal section of A2 appears to insert on ligamentous tissue that invests the premaxilla. The bulk of A3 is found deep to A2 and inserts on the medial face of the anguloarticular via a discrete tendon (Fig. 4D). Examination of *Gambusia holbrooki* revealed only subtle size differences in the different divisions of the AM complex and the premaxillomandibular ligament.

***Heterandria formosa* (see Fig. 5), least killifish.** One obvious difference between *Heterandria formosa* and other cyprinodontiforms is that the posteroventral process of the dentary has been lost, thus this bone is significantly shorter (Fig. 5A). The ascending arm of the premaxilla is also quite short, relative to other taxa, with a wide base where the ascending arm abuts the descending arm (Fig. 5B). The ventral edge of the descending arm of the premaxilla has a strongly recurved shape, with a distinct ventral spine (see arrowhead, Fig. 5A).

When compared with the other species described thus far, *Heterandria formosa* has the simplest dorsal process and shortest medial hook of the maxilla. Importantly, the medial hook of the maxilla is separated widely from the ascending process of the premaxilla (Fig. 5B), a trait with clear functional implications. Because of this separation, within fresh specimens of *H. formosa*, the anterior movement of the premaxilla does not result in rotation of the maxilla. The maxilla appears to form a stable base from which the premaxilla

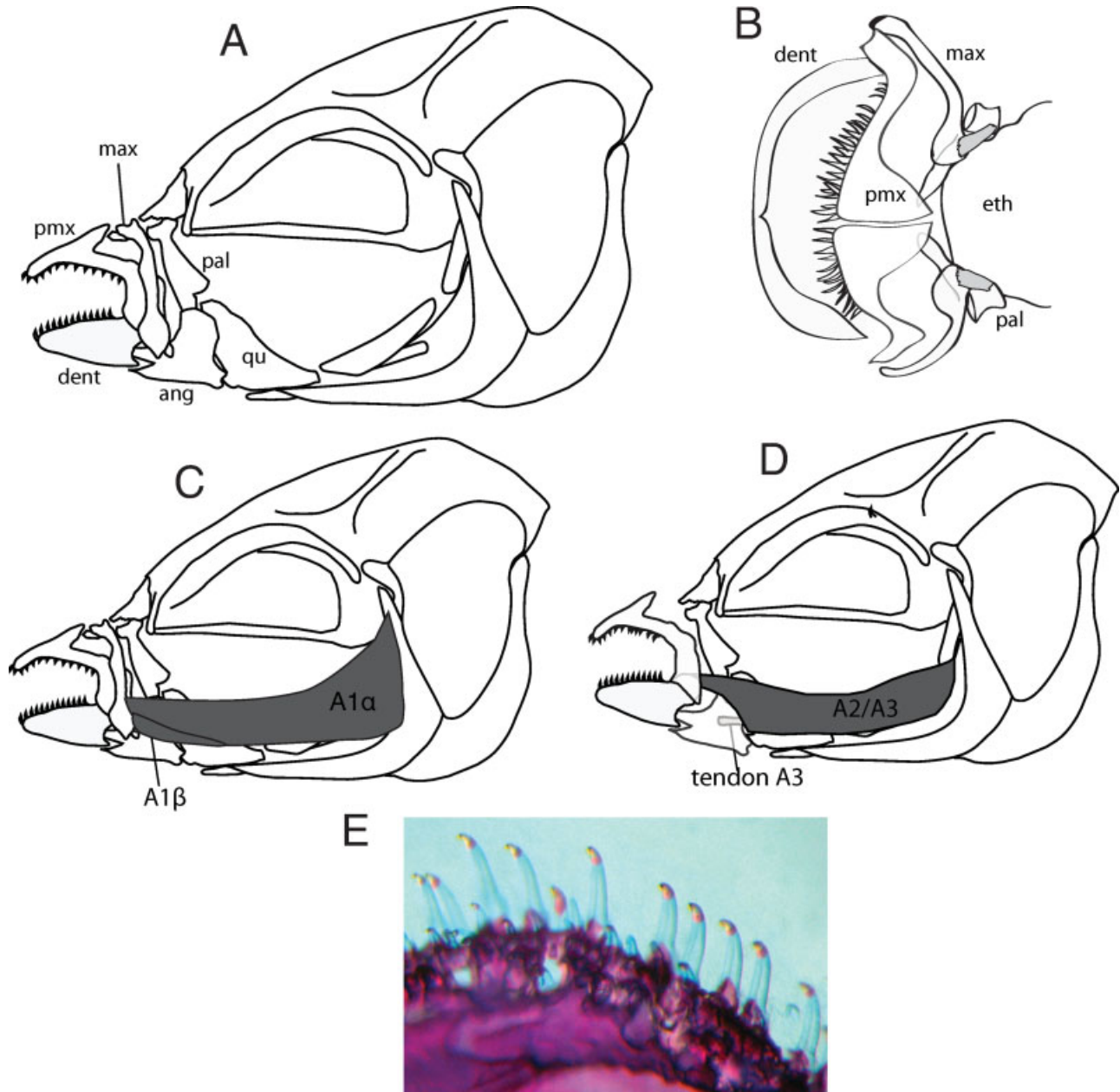


Fig. 4. Oral jaw morphology of *Gambusia affinis*. (A) Lateral view of cranial bones. (B) Dorsal aspect of oral jaws showing the palatamaxillary ligament. (C) Lateral view of the cranial anatomy showing the adductor mandibulae complex. (D) Lateral view of the cranial anatomy showing AM A2/A3 after removal of A1. (E) Caniniform dentition on dentary. pmx, premaxilla; max, maxilla; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; eth, ethmoid.

protrudes. Moreover, we note that manual ventral rotation of the lower jaw in fresh specimens generates synchronized movement of the dentary and premaxilla, with little, if any, concomitant movements of the maxilla.

The anguloarticular and dentary of the lower jaw do not interdigitate strongly (Fig. 5A). Several rows of pointed, slightly spatulate teeth line both the dentary and premaxilla.

The palatine has a reduced articular facet when compared with *Gambusia affinis*. However, given that *Heterandria formosa* is a secondarily miniaturized species (Rosen and Bailey, 1963), we suggest that major functional implications should not be attached to this finding. Though the palatine is small, a patent articular facet suggests that there is significant movement or pressure from the maxilla against this process (Fig. 5B).



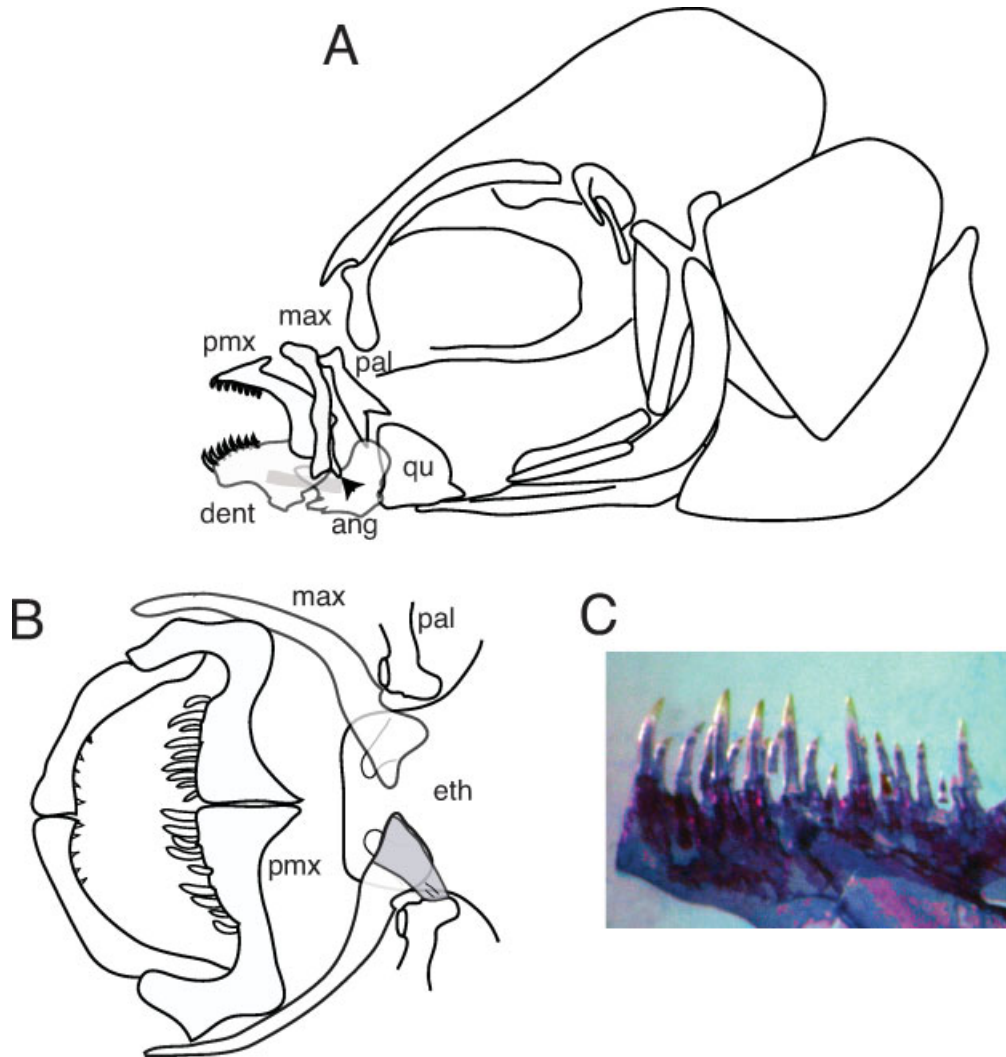


Fig. 5. Oral jaw morphology of *Heterandria formosa*. (A) Lateral view of cranial bones, note pronounced spine on descending arm of the premaxilla (arrowhead). (B) Dorsal aspect of oral jaws showing the palatamaxillary ligament on the left side. The right side is rendered transparent to show the size and shape of the medial aspect of the maxilla. (C) Pointed, slightly spatulate dentition on dentary. pmx, premaxilla; max, maxilla; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; eth, ethmoid.

The connections between the palatine and maxilla are generally similar to those seen in *Gambusia affinis*. The point of articulation between the palatine and maxilla is ventral to the dorsal process of the maxilla. In *Kryptolebias marmoratus* and *Fundulus rubrifrons*, the point of articulation was near the dorsal end of the maxilla, whereas in *Heterandria formosa*, the point of articulation is clearly upon the arm of the maxilla (Fig. 5B). A palatamaxillary ligament connects the dorsal head of the palatine to the small dorsolateral process of the maxilla.

***Poecilia sphenops* (see Fig. 6), molly.** Within *Poecilia sphenops* we see significant morphological changes in the architecture of the jaw elements relative to more basal members. The strongly recurved descending arm of the premax-

illa is more robust (from the lateral aspect) than in most other cyprinodontiforms. The ascending process of the premaxilla is shorter than in *Gambusia affinis*, but not as short as in *Heterandria formosa*, with wide bases merging with a markedly wider descending arm of the premaxilla (Fig. 6A,B).

Although the ventral arm of the maxilla is similar in shape to that of *Gambusia affinis*, the dorsal portion, which articulates with the neurocranium, is more complex. The broad lateral process has a pronounced ridge running dorsoventrally along its face, and the medial hook is longer and even more complex in shape than in *G. affinis* (Fig. 6B). Importantly, there is no overlap between the ascending process of the premaxilla and the medial hook of the maxilla.

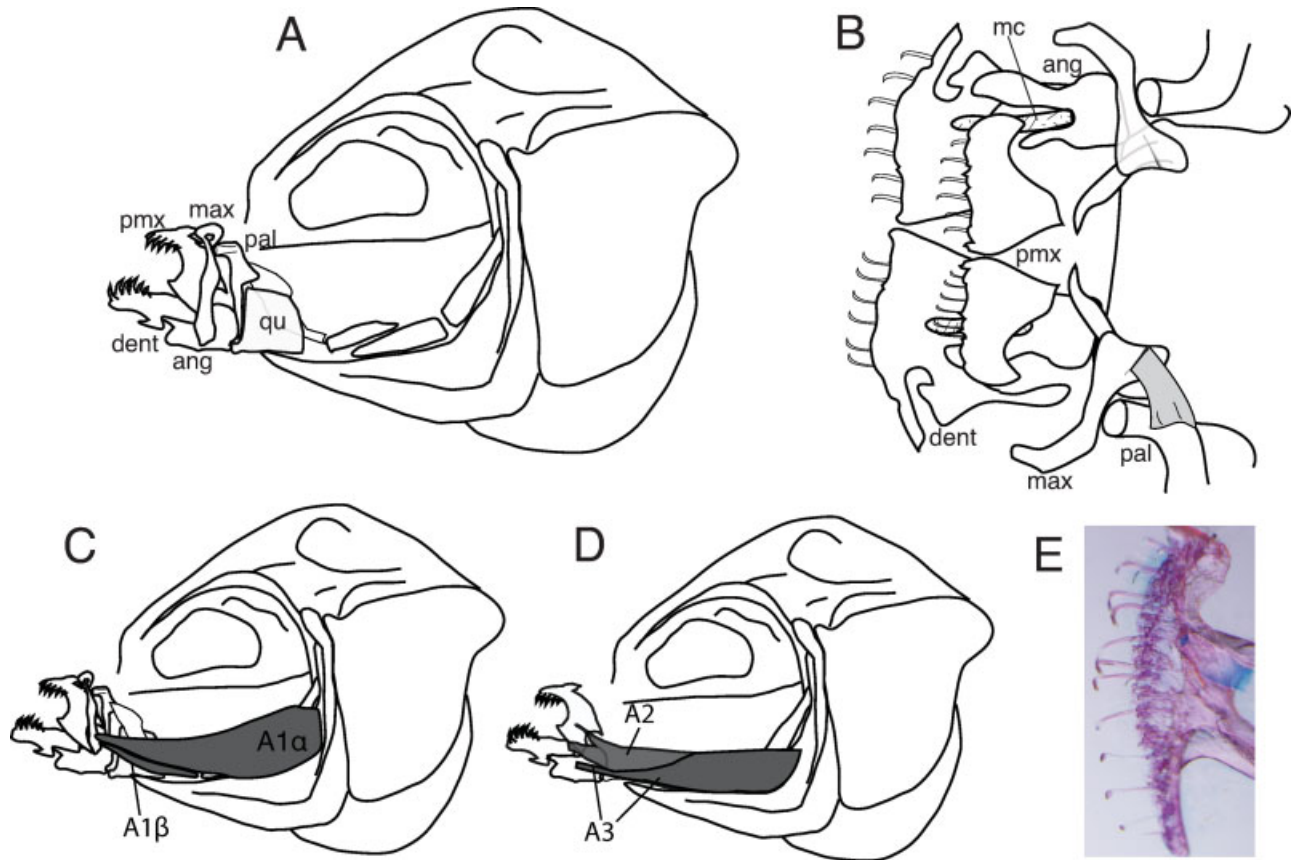


Fig. 6. Oral jaw morphology of *Poecilia sphenops*. (A) Lateral view of cranial bones. (B) Dorsal aspect of oral jaws showing the palatamaxillary ligament on the left side. The right side is rendered transparent to show the size and shape of the medial side of the maxilla. (C) Lateral view of the A1. (D) Medial view of the cranial anatomy showing AM A2/A3. (E) Hooked, elongated teeth with shorter teeth at their base. pmx, premaxilla; max, maxilla; mc, Meckels cartilage; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; eth, ethmoid.

The posteroventral process of the dentary is short, resulting in a loose connection between the anguloarticular and dentary. The coronoid process of the dentary is widely separate from the coronoid process of the anguloarticular. A patent Meckels cartilage unites the disarticulated bony elements of the lower jaw (Fig. 6B). One row of thin, elongated, hooked teeth are peripheral to several rows of smaller, less recurved teeth (Fig. 6E).

The palatine has a prominent facet where it articulates with the maxilla (Fig. 6A,B). As in most other poeciliids examined, the palatine articulates with the shaft of the maxilla, ventral to the dorsal process of the maxilla. This is markedly different than the architecture of *Fundulus rubrifrons* and *Kryptolebias marmoratus*, where articulation was at the dorsal-most portion of the maxilla. Such differences in sites of articulation likely affect jaw mechanics. The palatine curves anteriorly and has only one articular facet. A thick palatamaxillary ligament attaches the dorsal aspect of the palatine to a thin, elevated process on the dorsolateral process of the maxilla (Fig. 6B).

The premaxillomandibular ligament connecting the premaxilla and lower jaw is complex, splitting into two elements.

In most teleosts, A3 originates deep to A2, as has been described here for more basal cyprinodontiforms. In *Poecilia sphenops* and *Xiphophorus helleri* (see Fig. 7), both A2 and A3 comprise one superficial mass that forms the bulk of the adductor mandibulae. In *P. sphenops* A2 bifurcates such that a large proportion of this division goes to the premaxilla (Fig. 6D). The insertion of A2 in *P. sphenops* is via a discrete tendon to the caudal edge of the dentary, whereas the insertion of A2 on the upper jaw is via a less discrete tendinous connection to the anterior premaxilla.

Examination of *Poecilia latipinna* revealed no intrageneric variation in morphology. Although A2/A3 appeared smaller than in *P. sphenops*, there were no notable differences in muscular architecture between these species.

***Xiphophorus helleri* (see Fig. 7), Swordtail.** Within *Xiphophorus helleri*, also a poeciliid, the overall architecture of the bony elements compris-

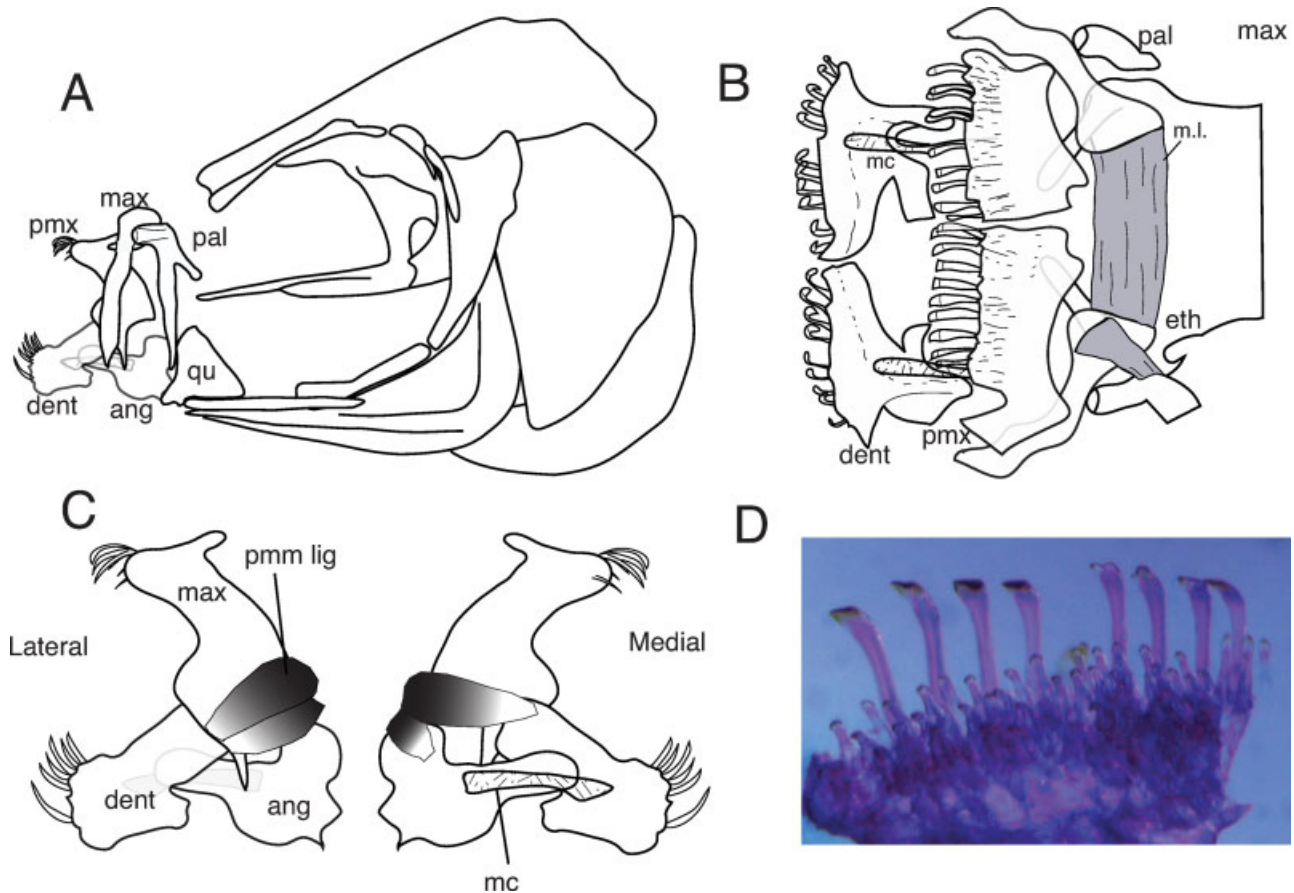


Fig. 7. Oral jaw morphology of *Xiphophorus helleri*. (A) Lateral view of cranial bones, showing unique architecture of premaxillae. (B) Dorsal aspect of oral jaws showing the palatomaxillary ligament, as well as a ligament (m.l.) connecting the dorsal heads of the maxillae. (C) Lateral and medial view of the premaxillomandibular ligament, showing the increased complexity of this ligament. Dark portions of this ligament represent hyaline cartilage whereas lighter areas connote more typical collagenous tissue. (D) Spatulate, straight edged dentition on outer row with rows of smaller teeth behind. pmx, premaxilla; max, maxilla; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; eth, ethmoid; m.l., maxillary ligament; pmm, premaxillomandibular ligament; mc, Meckel's cartilage.

ing the anterior jaws has undergone significant changes relative to the other species studied here. Although the basic shape of elements is unchanged, the manner in which they articulate with one another has changed. In a resting state, the premaxilla is largely laterally occluded by the maxilla. This does not reflect an increase in the size of the maxilla, but rather reflects a posterior shift in the resting position of the premaxilla (compare Figs. 7A and 6A). The greatly reduced ascending process of the premaxilla is shifted laterally (Fig. 7B).

The dorsal process of the maxilla has a very complex shape, with a prominent dorsolateral shelf of bone, and a large twisted medial hook (Fig. 7B). There is an overlap between the medial hook of the maxilla and the modified ascending process of the premaxilla (Fig. 7B). However, the long medial hook of the maxilla may serve as a strut against which the premaxilla can be protruded, because, as seen in *Heterandria formosa*, manually rotating

the lower jaw causes little movement of the maxilla.

The extremely foreshortened lower jaw contains a visible gap between the dentary and anguloarticular that is partially filled by a patent Meckel's cartilage (Fig. 7C). Although a discrete coronoid process of the dentary is visible, the posteroventral process is significantly shortened (Fig. 7C). One row of elongated, straight-edged, recurved, spatulate teeth lines both the dentary and premaxilla. These larger teeth are followed by several rows of shorter, slightly spatulate teeth (Fig. 7D).

Unlike in other poeciliids examined, a thick maxillary ligament (m.l.) connects the two dorsal processes of the maxillae (Fig. 7B).

As in *Poecilia sphenops* the greatly modified premaxillomandibular ligament connecting the premaxilla and lower jaw is split into two elements (Fig. 7C). Although one portion of this ligament curves around the back of the premaxilla to attach to the dentary, as described for other species, an

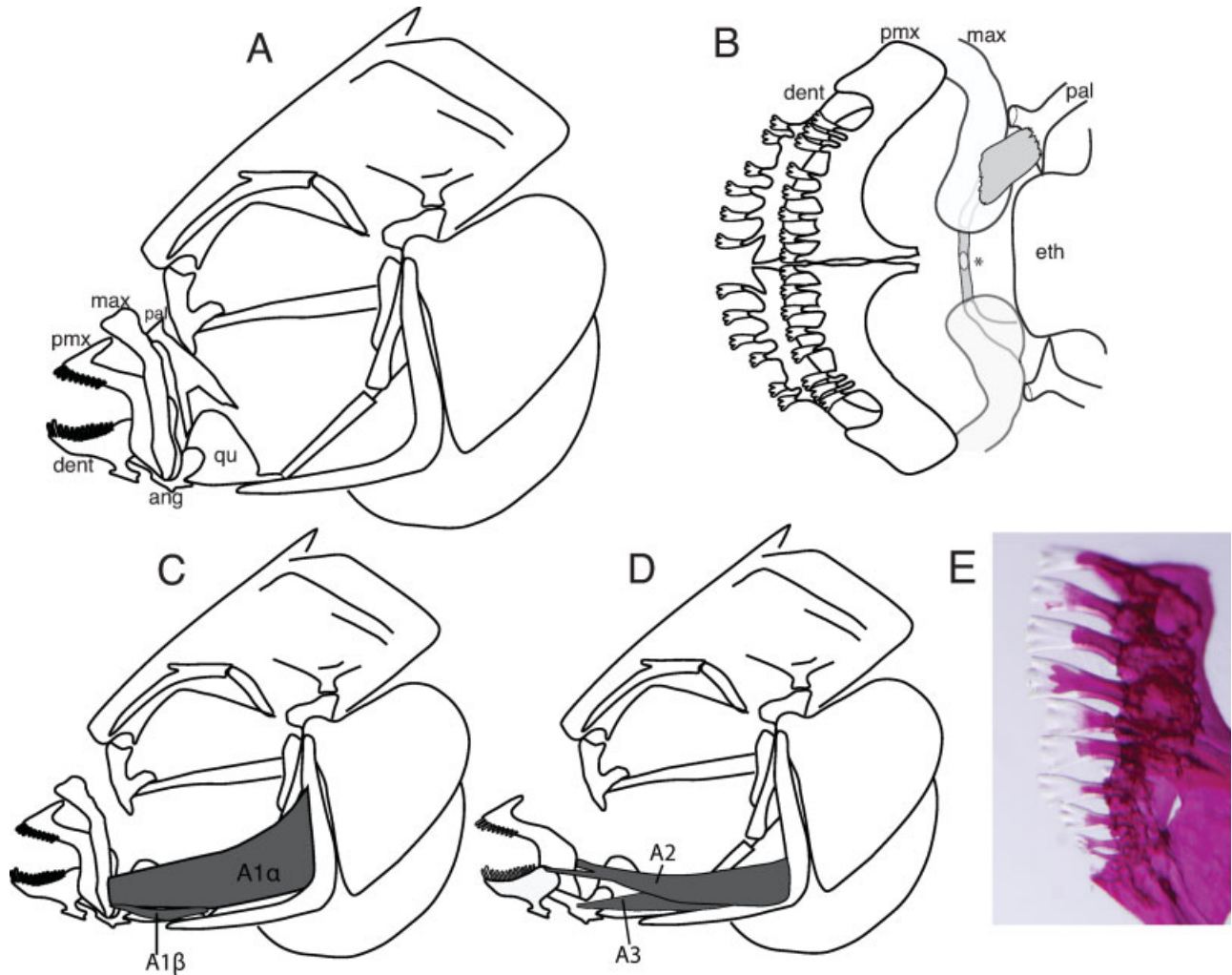


Fig. 8. Oral jaw morphology of *Jordanella floridae*. (A) Lateral view of cranial bones. (B) Dorsal aspect of oral jaws showing a thick palatamaxillary ligament, and a patent ligament between the medial hooks of the maxilla that holds a small (perhaps vestigial) rostral cartilage. (C) Lateral view of adductor mandibulae A1. (D) Medial view showing AM A2/A3 after removal of A1. (E) Tricuspid dentition on dentary. pmx, premaxilla; max, maxilla; pal, palatine; dent, dentary; ang, anguloarticular; qu, quadrate; eth, ethmoid.

additional component of this ligamentous structure also inserts on the anguloarticular. Thus, the single, relatively simple ligament observed in *Kryptolebias marmoratus*, *Fundulus rubrifrons*, and *Gambusia affinis* is now divided distally to attach to both the coronoid process of the dentary (adjacent to the insertion of A2) and the anguloarticular. Moreover, the material comprising this complex ligament has changed, with a large portion of what appears to be hyaline-cell cartilage (Benjamin, 1989) located between the collagenous attachment points of the ligament (LPH pers. obs.).

A3 originates on the preopercular and the bulk of its muscle fibers are largely located within the caudal half of the suspensorium. A2 originates not solely from the suspensorium, but also from the rostral, ligamentous face of A3. Thus, A2 and A3 form a tightly coupled mass where the more

rostral portion constitutes A2, and the more caudal portion constitutes A3. A2 has a small, but discrete, tendon that inserts on the premaxilla, while the remainder of A2 inserts on the coronoid process of the dentary via a robust tendon.

***Jordanella floridae* (see Fig. 8) American flagfish.** Within *Jordanella floridae*, a member of Cyprinodontidae (sister family to Poeciliidae; Parenti, 2005), the general cyprinodontiform osteology of the anterior jaws is retained; however, we also see significant morphological changes with possible functional implications (Fig. 8A). Although many basal features characterized the osteology, the musculature is characterized by several derived traits seen in poeciliid species.

As in *Poecilia sphenops*, the ascending process of the premaxilla is short, however, as in *Fundulus rubrifrons*, it is relatively narrow where it merges

with the descending arm of the premaxilla (Fig. 8B).

As is characteristic for cyprinodontids (Parenti, 1981), *Jordanella floridae* shows an expanded dorsolateral process of the maxilla. However, the medial hook of the maxilla is smaller, and more pointed, than in the other species examined.

In contrast to *Poecilia sphenops*, the posteroven-tral process of the dentary of *Jordanella floridae* is not foreshortened. Patent coronoid and posteroven-tral processes of the dentary create a more tightly articulated lower jaw than is seen in the more derived poeciliids. A single row of tricuspid teeth is found on both the premaxilla and dentary (Fig. 8E).

The palatine is shaped like a hammer with an anterior articulating facet (as described for other species) but also with a pointed posterior process (Fig. 8B; Character 29 in Costa, 1998). A thick lig-ament arises from this posteriorly oriented process and curves to attach to the dorsolateral process of the maxilla.

As in *Poecilia sphenops*, loose tissue connects the ascending process of the premaxilla to the medial hook of the maxilla. Interestingly, although the rostral cartilage is lost within most poeciliids, in this cyprinodontid a small, non-staining rostral cartilage can be seen within the ligament tying together the medial hooks of the maxillae (Fig. 8B\*).

The premaxillomandibular ligament connecting the premaxilla and lower jaw is similar to that described for *Fundulus rubrifrons*.

The adductor mandibulae shows a combination of character states when compared with the species studied thus far. Although A2/A3 fibers are intermingled, in *Jordanella floridae* A3 is deep to A2 and therefore unlike the muscular complex described for *Poecilia sphenops* and *Xiphophorus helleri* (Figs. 6D vs. 8D). However, A2 bifurcates at its distal end, into relatively equal halves, to insert on both the premaxilla and dentary. Although there is a muscular insertion to the caudolateral edge of the premaxilla (and associated connective tissues), a long tendinous insertion goes to the dentary. A3 inserts on the medial side of the angulo-articular.

The adductor mandibulae complex of other cyp-rinodontids suggests that there may be significant variation in trophic musculature within this fam-ily. *Floridichthys carpio* does not show the clear insertion of A2 on the premaxilla that charac-terizes *Jordanella floridae*; whereas A2 still inserts on the coronoid process of the dentary, there is no evidence of muscle fibers going to the premaxilla. *Cyprinodon variegatus* has jaw musculature more like *J. floridae*, whereby A3 is deep to A2. How-ever, as seen in *Poecilia sphenops*, the bulk of A3 is caudal to the bulk of A2. Additionally, *C. varie-gatus* has a premaxilla more like that seen in *Fun-dulus rubrifrons* or *Kryptolebias marmoratus*, with

a pronounced ascending process. In *C. variegatus*, A2 attaches by a distinct tendon to the coronoid process of the dentary, but also extends a few fibers to the premaxilla. As seen in *Heterandria formosa* and *Gambusia affinis*, muscle fibers from A2 actually attach to the ligaments surrounding the premaxilla, instead of attaching directly to the bone. It is possible that this architecture is repre-sentative of a transitional state between no inser-tion (as is seen in more basal cyprinodontiforms) and a discrete muscle attaching to the premaxilla (as is seen in *J. floridae*).

## DISCUSSION

We posit that in the course of cyprinodontiform evolution, several mechanisms have arisen that protrude and retract the jaws. Specifically, changes to three key anatomical features of the feeding mechanism appear to be involved (see Fig. 1): 1) changes in the architecture of the major jaw closing muscle, the adductor mandibulae complex; 2) specialization of a ligament that connects the upper and lower jaws (premaxillomandibular ligament); and, 3) pronounced changes in other ligamentous attachments that connect anterior elements of the feeding apparatus. This research differs from previous work in emphasizing the importance of ligamentous attachments in the evolu-tion of trophic systems.

### Architecture and Novel Insertions of Adductor Mandibulae A2

In most teleosts, A2 inserts on the anguloarticu-lar (Winterbottom, 1974). Even when A2 is second-arily duplicated, both divisions typically insert on the anguloarticular (Friel and Wainwright, 1997). Within even the most basal cyprinodontiform examined here, however, at least a portion of A2 inserts on the dentary. This may suggest that, even during their earliest evolutionary history, cyprinodontiforms had an unusual architecture of the adductor mandibulae complex.

Although we see insertion of A2 on the dentary as early as *Kryptolebias marmoratus*, a patent coronoid process of the dentary creates a relatively caudal insertion within the lower jaw in more basal cyprinodontiforms. The evolutionary trend toward foreshortened jaws, brought about by the decreased size of the coronoid process, moves the insertion of A2 rostrally in more derived poeciliids. Such a rostral migration may allow force to be more directly transmitted to the anterior lower jaw, which likely facilitates direct application of muscle force to the teeth. It should be noted that the loss of a prominent coronoid process might simultaneously lead to decreased mechanical advantage during feeding because of a shortened lever arm. Moreover, given the intramandibular

bending seen in derived poeciliids (Gibb et al., 2008), this rostral shift may decouple the anterior and posterior lower jaw. Such decoupling may allow fish to procure prey using quasi-independent movements of the anterior jaw tips.

Controlled movements of the upper jaws are also possible given the acquisition of a novel branch of A2 inserting on the premaxilla within more derived poeciliids and cyprinodontids. We see muscle fibers impinging on ligaments surrounding the premaxilla within *Gambusia affinis*, and the evolutionary trend toward direct muscular control of the upper jaw continues in more derived members of Poeciliidae. Such a novel architecture of the adductor mandibulae complex likely allows for controlled adduction of the jaws; both upper and lower jaw elements would serve as third-order levers that are simultaneously moved toward one another—mechanically, the jaws would function similarly to a pair of forceps.

The rostral shift in insertion of A2 on the dentary and the insertion of A2 on the premaxilla appear to constitute a gradual transformation of the feeding apparatus. Although A2 inserts on the dentary in all species examined, the foreshortening of the dentary has generated a gradual anteriorly-directed shift in the insertion of this key jaw adductor. Moreover, within the poeciliids examined here, muscle fibers initially impinge upon the connective tissues surrounding the premaxilla and ultimately come to insert directly on the premaxilla. Early in teleostean evolutionary history, muscle fibers impinged on the primordial ligament, eventually generating a new division of the adductor mandibulae, A1 (Schaeffer and Rosen, 1961). We see a similar gradual transformation within derived poeciliids, where migration of muscle fibers eventually generates a new insertion for A2. Thus, evolution of the adductor musculature within this clade likely constitutes an example of gradual evolution of a derived trait.

The transformation of the adductor mandibulae complex within Cyprinodontiformes is strikingly similar to the changes that have been observed within the Loricarioidea. Schaefer and Lauder (1986, 1996) described the functional transformation of the anterior jaws within Loricarioidea (the armored catfishes), where relatively little protrusion is demonstrated by basal taxa but pronounced protrusion coupled with independent movements of the upper jaw characterize derived members of this clade. Within the species examined here, we observe a similar gradual transformation of the adductor mandibulae complex—from species that show a “typical” teleostean morphology of the adductor mandibulae to species that possess the derived character of a branch of A2 that inserts on the premaxilla. Schaefer and Lauder (1986, 1996) proposed that such a historical transformation was associated with a functional specialization for algal

scraping. The similarity between these feeding mechanisms may represent functional convergence between Loricarioidea and Cyprinodontiformes.

Interestingly, the likely independent origin of a premaxillary insertion of A2 in both derived poeciliids and cyprinodontids (see Fig. 1) is correlated with the acquisition of dentition generally associated with scraping. Both the rake-like teeth of *Poecilia sphenops* and *Xiphophorus helleri*, as well as the tricuspid teeth of *Jordanella floridae* have been correlated with a scraping feeding mode (Yamaoka, 1983; Yagishita and Nakabo, 2003).

### Acquisition of a Novel Ligament Connecting the Upper and Lower Jaws

One of the most significant changes seen during the course of cyprinodontiform trophic evolution is the reorganization of the ligaments that connect the various osteological elements of the anterior jaws. Within all the species examined here, a premaxillomandibular ligament connects the descending arm of the premaxilla to the dentary (Hernandez et al., 2008). Although a premaxillomandibular ligament providing a taut connection between these two elements has been previously described for other taxa (Schaeffer and Rosen, 1961), the architecture of the cyprinodontiform ligament is unique. When the dentary is depressed, this ligament pulls the premaxilla forward. Moreover, this ligament significantly varies in morphology among cyprinodontiform species.

We suggest that the unique architecture of this ligament will enhance premaxillary protrusion. It has previously been suggested that a ligamentous attachment between the premaxilla and lower jaw could improve protrusion ability (Schaeffer and Rosen, 1961; Motta, 1982, 1984). It is important to note that because this ligament is not constrained where it wraps around the posterior edge of the premaxillae, the premaxilla will follow the movement of the lower jaw directly during mandibular (lower jaw) depression. Therefore, the range of premaxillary protrusion produced during mouth opening is likely determined directly by the degree of lower jaw depression. Given that *Poecilia sphenops* has been shown to produce extreme gape angles ( $>120^\circ$ ; Ferry-Graham et al., 2008; Gibb et al., 2008), the type of ligamentous attachment we describe here likely facilitates maximal upper jaw protrusion.

Although the attachment of this ligament to the lateral face of the descending arm of the premaxilla is relatively conserved among all species, the attachment to the lower jaw varies among the different species examined. This ligament attaches to either the dentary or anguloarticular bone (or to both), and the location of this attachment usually corresponds with the location of the insertion of A2 onto the lower jaw. Moreover, there is a pronounced change in the type of connective tissue

that comprises the ligament. In *Kryptolebias marmoratus*, *Fundulus rubrifrons*, *Gambusia affinis*, and *Jordanella floridae* it is largely comprised of fibrous, collagenous tissue whereas in more derived poeciliids it appears increasingly cellular (LPH; pers. obs.). Within more derived poeciliids (*Poecilia sphenops*) it appears to be composed largely of hyaline cell cartilage (Benjamin, 1989).

Within some poeciliids (e.g., *Xiphophorus helleri* and *Poecilia sphenops*), the premaxillomandibular ligament has become bifurcated distally to attach to both the anguloarticular and dentary (see Fig. 1). Moreover, examination of fresh specimens suggests that the tissue composition of this ligament has changed, with the basal condition showing more collagenous fibers whereas the derived condition shows increasingly cellular tissue, such as the hyaline cell cartilage seen in *Poecilia sphenops* (Benjamin, 1989). *Poecilia sphenops*, more than the other species examined here, relies on repeated scraping motions of the jaws to graze on epiphytic algae (Zaret and Rand, 1971, Gibb et al., in press). This modified premaxillomandibular ligament may confer a looser connection between the jaw elements. Scraping parrotfish demonstrate looser connections among the different bones of the oral jaw apparatus (Bellwood and Choat, 1990) as do girellids that use scraping (Yagishita and Nakabo, 2003). A loose connection is thought to allow for the production of larger gapes for increasing contact with the substrate for scraping.

### Architectural Changes Associated With Premaxillary Protrusion

Although considerable research has attempted to elucidate mechanisms of premaxillary protrusion across teleost taxa (e.g., Alexander, 1967b; Motta, 1984), we suggest that the ligamentous attachments that produce and coordinate these movements have been neglected. Here we show how changes in the premaxillomandibular as well as other key ligaments likely affect the protrusion mechanism used in this clade. The varied shapes of osteological elements (maxillae, palatines, dentaries, premaxillae, and neurocranium), coupled with varying configurations of the ligaments that connect these elements to one another, likely determine both the underlying mechanism and functional implications of this type of premaxillary protrusion.

The aplocheloid *Kryptolebias marmoratus* served as our representative outgroup taxa. Within *K. marmoratus* the taut ethmomaxillary ligament and the architecture of the palatomaxillary ligament combine to restrict the movement of the maxilla to lateral rotation. Thus, lowering the jaw and/or contracting A1 will result in outward rotation of the medial hooks of the maxillae (Fig. 2C), which will in turn pull the ligaments that connect

the maxillae to the ascending processes of the premaxillae (via the rostral ligament) anteriorly and help project the upper jaw. Although the size of the rostral cartilage(s) is reduced, a similar situation occurs in *Fundulus* (Alexander, 1967a). Thus, in these two basal groups (aploceloids and fundulids) premaxillary protrusion is accomplished (or at least assisted) by “twisting” of the maxilla (Eaton, 1935; Alexander, 1967a).

The first major modification to this system is a loss or significant reduction in the rostral cartilages and associated ligaments that attach the medial hooks of the maxillae to the ascending processes of the premaxillae. Alexander (1967a) noted the loss of these structures in *Xiphophorus helleri*, concluding that twisting of the internal hooks of the maxillae did not contribute to premaxillary protrusion. Clearly, without a taut ligament uniting these elements, premaxillary protrusion cannot be effected by lateral rotation or twisting of the maxilla. Coupled with this change is a foreshortening of the ascending process of the premaxilla. Notably, within most poeciliids and cyprinodontids, there is little if any overlap between the ascending processes of the premaxillae and the medial hooks of the maxillae—a necessary configuration for premaxillary protrusion to occur via maxillary rotation.

Pronounced premaxillary protrusion is typically associated with a greatly lengthened ascending process (Eaton, 1935; Lauder and Liem, 1981; Westneat and Wainwright, 1989). Within cyprinodontiforms, significant protrusion can still be accomplished with an evolutionary decrease in the length of the ascending process. It is worth noting however that increased premaxillary protrusion in other species is correlated with increased stealth during a suction feeding event (Motta, 1984). In contrast, the role of increased premaxillary protrusion in improving biting, picking, and scraping performance (the role it likely serves within cyprinodontiforms) is still largely unexamined (but see Ferry-Graham et al., 2008). A novel means of protrusion whereby increased protrusion is decoupled from increased length of the ascending process may facilitate the evolution of feeding modes beyond the ubiquitous ram- or suction-based mechanisms. For example, poeciliids trying to scrape algae by applying their mouths fully to the substrate might be constrained in the maneuverability of the jaws by very long ascending processes.

In these higher cyprinodontiform taxa, there is also a significant change in both the shape of bones and the architecture of ligaments connecting the maxilla to the rest of the feeding apparatus. The basal condition is rotation between the maxilla and the palatine at the dorsal extreme of the maxilla (Figs. 2 and 3A), whereas the more derived condition is to have the point of articulation more ventrally located, on the arm of the

maxilla. This derived condition should serve to brace the maxilla, rather than to effect its rotation. Indeed, Schaeffer and Rosen (1961) as well as Motta (1984) have suggested that the maxilla acts as a brace against which the premaxilla is protruded. Indeed, depression of the lower jaw effects little maxillary movement but generates significant protrusion of the premaxillae in more derived members of Poeciliidae.

Although there are substantial changes to the bony elements of the feeding apparatus within cyprinodontiforms, changes in ligamentous and muscular attachments may be just as important in enhancing novel feeding modes. We have described changes in the ligamentous architecture of the oral jaws that likely result in a functional transformation from premaxillary protrusion via twisting of the maxilla to a new, novel means of premaxillary protrusion that employs a novel ligamentous coupling of the upper and lower jaws by a greatly modified premaxillomandibular ligament. During the course of this transition, there is a concomitant loss of the rostral cartilages, loss of the ligaments that attach the rostral cartilages to the jaws, reduction of the ascending processes of the premaxillae, and a significant increase in the size and complexity of the premaxillomandibular ligament. We suggest that within this group such changes facilitate a general transition towards precision-based picking and scraping feeding modes.

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