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Extreme premaxillary protrusion in the king-of-the-salmon, *Trachipterus altivelis*

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Abstract

The king-of-the-salmon, *Trachipterus altivelis* (Lampriformes), has an unusual set of oral jaws which allow it the ability to protrude the entire upper jaw, containing the premaxilla and the maxilla bones, to extreme distances. Here, we provide a short description of the cranial anatomy and mechanism of jaw protrusion in *T. altivelis* using hand-drawn illustrations (by KF), supplemented by CT-scans. We then place the protrusion abilities of *T. altivelis* into context by comparing anatomical jaw protrusion with protrusion from other members of the Lampriformes, other unrelated species with highly protrusile jaws, and unrelated species with more stereotypical amounts of jaw protrusion. Through these comparisons we demonstrate that *T. altivelis* is indeed, capable of some of the most extreme premaxillary protrusion as of yet discovered, even when taking into account the extreme morphological modifications that facilitate said protrusion. That is to say, *T. altivelis* can protrude the premaxilla farther than one would predict from the length of the ascending process alone.

KEYWORDS
fish, jaw protrusion, lampriforms, prey capture

1 | INTRODUCTION

The king-of-the-salmon, *Trachipterus altivelis* (Lampriformes), is unique among fishes for its incredible length and quite monsterous appearance. Indeed, these midwater denizens appear, for all purposes, like creatures conjured from medieval lore. Adding to this creature-esque collection of traits is a remarkable set of jaws. The jaws of *T. altivelis*, like most teleost (bony) fishes, consists of a mobile upper and lower jaw. The upper jaw is composed of two elements, the maxilla and premaxilla. The lower jaw is a single mobile element, the mandible, which is, in turn, comprised of the dentary and the anguloarticular. In *T. altivelis*, however, the premaxilla is particularly protrusile (i.e., able to project to extreme lengths), anteriorly, away from the head.

Protrusile jaws, in general, are thought to play an important role in the translation of suction for capturing prey. Upper jaw protrusion is heralded as a key evolutionary innovation in the fishes for its exceptional contribution to aquatic prey capture (Liem, 1980). When the upper jaws are protruded towards the prey item, a small, rounded mouth-opening is created which enhances the flow of water into the head (Motta, 1984). For the most part, protrusile jaws are associated with suction feeding. To wit, a recent study examining both extinct (fossil) and extant fishes examined jaw protrusion as a metric for suction production ability and found this simple measure to be remarkably robust (Bellwood, Goatley, Bellwood, Delbarre, & Friedman, 2015). Protrusile jaws are thought to be particularly important for capturing elusive prey; those prey items with a high probability of being able to escape an oncoming predator (Motta, 1984; Norton & Brainerd, 1993; Wainwright et al., 2001; Wainwright, McGee, Longo, & Hernandez, 2015). Examples of extreme protrusion, such as that seen in *T. altivelis*, tend to be found in isolated taxa from highly speciose clades of fishes, and/or in species where it is presumed that competition for resources is high, and selection is driving change towards more and more extreme morphologies as resources are partitioned (Bellwood et al., 2015).

Little is known of the ecology of *T. altivelis*. The name “king-of-the-salmon” is derived from the original Makah tribes of the Pacific Northwest (Jordan & Starks, 1895). *T. altivelis* are more widely known

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[†]Deceased

for being deep midwater residents, whose diet appears to include planktonic organisms such as amphipods, copepods, euphausids, fish larvae, juvenile fish, squid, and octopods (Hart, 1973; Shenker, 1983). Much of what is known about this species is obtained from stranded specimens, which occurs with some regularity along the western coast of the United States.

In this study, we provide an overview of the cranial anatomy of *Trachipterus altivelis* using hand-drawn illustrations and CT-images. We provide a short description of the mechanism of jaw protrusion in *T. altivelis*. We then place the protrusion abilities of *T. altivelis* into context by comparing anatomical jaw protrusion with protrusion from other members of the Lampriformes, other unrelated species with highly protrusile jaws, and unrelated species with more stereotypical amounts of jaw protrusion.

2 | METHODS

2.1 | Anatomy

The cranial anatomy of *Trachipterus altivelis* Kner, 1859 is illustrated here from drawings completed by hand from an approximately 200 cm specimen caught in a salmon set net off South Beach, San Juan Island by salmon fishermen. It was brought, freshly dead, to the Friday Harbor Laboratories where it was photographed. The underlying mechanism of jaw protrusion was determined via direct examination/manipulation of the skeletal material and tissue/ligamentous connections. The fish was subsequently fixed in formalin for 2 days, and then dissected and carefully drawn by KL in pencil on large format paper, which was later inked. The dissection process was destructive and the specimen was not saved. However, the drawing process was observed by AS, and the drawings immediately scanned digitally for preservation.

The drawings are supplemented by CT-images of a 14.3 cm juvenile specimen of *T. altivelis* (UW 158445), obtained using a Bruker Skyscan 1,173 at 65 kV, 123 mA, and a voxel resolution of 28.4 μm. The resulting projections were reconstructed in NRECON (Bruker, NL) and the stack was visualized in the free, open source 3D-Slicer (https://www.slicer.org/) and Amira (Thermo Fisher). The slice data are available at the open access MorphoSource.org (image ID 46926). While this specimen is much smaller than the specimen that was hand-drawn, it is difficult to scan larger specimens due to technical limitations and due to the poor condition of most specimens upon acquisition. This smaller specimen was fully intact, without damage from fishing gear, allowing the greatest chance of imaging the bones in their proper positions.

All aspects of the research complied with requirements of the University of Washington institutional animal care and use committee.

2.2 | Comparative analysis

In order to place the extreme anatomy and putative protrusion ability into context, we collected data from three species groups: (a) other members of the Lampriformes; (b) unrelated species with highly protrusile jaws; and, (c) unrelated species with more stereotypical amounts of jaw protrusion. For all species, the length of the ascending process of the premaxilla was measured, as a potential indicator of maximum premaxillary protrusion. This simple approach was validated by Bellwood et al. (2015) in a careful analysis of over 200 species of fishes. This approach can be particularly useful as it allows for the utilization of species that are rarely collected alive. However, we also measured protrusion distance based either upon manual protrusion of the premaxilla away from the head to the fullest extent possible without damage (e.g., "anatomical" protrusion, sensu Arena, Ferry, & Gibb, 2012), or via video recordings of active protrusion during high-effort prey capture events by those species (e.g., "functional" protrusion, sensu Arena et al., 2012). Anatomical protrusion was measured from fresh specimens as well as from images obtained for the purpose of illustrating maximum premaxillary protrusion. Measurements were obtained from images (still and video) using NIH Image J. The method of data collection employed for each species varied based upon multiple factors, including the ease of obtaining specimens, and is elaborated upon below (see also Appendix 1). In all cases, protrusion was measured directly as the maximum distance away from the resting or fully retracted position.

From the Lampriformes we attempted to sample broadly. These are midwater fishes with silvery bodies and red fins, a character shared by all members of the clade. Species obtained included: (a) king of the salmon (*Trichipterus altivelis*, Trichipteridae); (b) the oarfish (*Regalecus* sp., Regalecidae); (c) the sailfin velifer (*Velifer hypselopterus*, Veliferidae); which, along with *Lampris guttatus* (next), is not highly elongate, (d) the opah (*Lampris guttatus*, Lampridae); (e) the tube-eye (*Stylephorus chordatus*, Stylephoridae); and (f) the crestfish (*Eumecichthyes fiski*, Lophotidae). The only missing representatives are the tapertails (Radiicephalidae). Specimens of *T. altivelis* and *Regalecus* sp. were obtained from additional strandings, and *L. guttatus* from commercial fishermen, all off the southern California coast, USA (see also Appendix 1 for specimen information). Maximum premaxillary protrusion data for *T. altivelis*, *Regalecus* sp., and *L. guttatus* were obtained via directly manipulating fresh specimens by one of us. Length of the ascending process of the premaxilla and maximum premaxillary protrusion for *S. chordatus* was obtained from anatomical drawings specifically for the purpose of illustrating maximum protrusion from Pietsch (1978). Similarly, data for *V. hypselopterus* were obtained from images from Coetzer (2017) and Priede (2017). Data for *E. fiski* were obtained from images by Bray (2017).

For comparison, we selected species who potentially exhibit extreme amounts of premaxillary protrusion. These are: (a) the bay snook (*Petenia splendida*, Cichlidae), a freshwater neotropical cichlid that inhabits slow moving streams and shallow lakes; (b) the slingjaw wrasse (*Epibulus insidiator*, Labridae), a tropical reef species; (c) the hogfish (*Lachnolaimus maximus*, Labridae), another tropical wrasse species which is also durophagous in addition to being piscivorous; (d) the john dory (*Zeus faber*, Zeidae), another coastal marine fish that lives near the sea floor; (e) the stone scorpionfish (*Scorpaena mystes*, Scorpaenidae), a shallow-dwelling marine reef fish that rests on the bottom and lies in wait for prey; (f) the boarfish (*Capros aper*, Caproidae), the only fairly deep-dwelling species studied, but which lives on the bottom associated with substrate; and, (g) the copperband butterflyfish (*Chelmon rostratus*, Chaetodontidae), which is a tropical reef-dweller. Each of these species consumes elusive prey; the latter two are zooplanktivores, and the remainder are partially or fully piscivorous. They have elongate jaws and/or obviously enlarged oral cavities. The cichlids and wrasses included here have, arguably, the largest amount of protrusion ever recorded (Lauder & Liem, 1981; Waltzek & Wainwright, 2003; Westneat & Wainwright, 1989). The cichlid and labrid groups, in particular, are extremely speciose, with over 1,500 known cichlids and around 600 known labrids (Nelson, 2006). Both of these clades are known for their relatively rapid, and recent, speciation events, which have been attributed, in part, to prey capture and processing abilities (Waltzek & Wainwright, 2003). For reference, the scorpaenids and cheatodontids each have over 200 species, the caproids only 12 species, and the zeids six species (Nelson, 2006). Length of the ascending process of the premaxilla and maximum premaxillary protrusion data for *E. insidiator*, *S. mystes*, and *C. rostratus* were obtained from existing video images of these species capturing elusive prey obtained by one of us (see also Appendix 1 for specimen information). Care was taken to obtain maximum premaxillary protrusion for each species for the purposes of the comparisons here, and length of the ascending process of the premaxilla was measured from images where the entire skeletal element was clearly visible. Maximum premaxillary protrusion for *Z. faber* was obtained from images at the Monaco Nature Encyclopedia (Mazza, n.d.). Images of *L. maximus* are from McIntrye (2018), and *C. aper* images are from Hoem (2018). In each case, extreme care was taken to utilize only photographs in lateral view, clearly illustrating maximum protrusion, and in which the entire premaxilla is clearly visible (which is why there are not more species included here from on-line sources). Data for *P. splendida* are published in Waltzek and Wainwright (2003).

Species with more typical amounts of premaxillary protrusion were used to essentially validate our method of data collection against the data from Bellwood et al. (2015), so we could then use their model as a baseline for average jaw protrusion. These were species with no obvious modifications to the oral jaws in the manner of the previously described species. We modified the approach of Bellwood et al. (2015), who standardized premaxillary lengths to body lengths in order to account for variation in body size. Because the Lampriformes are highly elongate, we instead used head length, defined as the distance from the anterior tip of the snout, which is the anterior tip of the premaxilla when it is fully retracted into the head, to the posterior margin of the opercular opening. Using those fish species without elongate bodies and with "typical" amounts of jaw protrusion, we verified that this correction did not cause our species' premaxillary protrusion estimates to be biased relative to the predictive curve created by Bellwood et al. (2015). The use of this model allowed us to place our species of study into a much larger context and provided a baseline for determining if protrusion that was truly "extreme," meaning it fell outside of the confidence intervals of the predictive relationship quantified by Bellwood et al. (2015). We included: (a) the pearlscale butterflyfish (*Chaetodon xanthurus*, Chaetodontidae); (b) the cheek-lined wrasse (*Oxycheilinus digrammos*, Labridae); (c) the lingcod (*Ophiodon elongatus*, Hexagrammidae); (d) the oscar (*Astronotus ocellatus*, Cichlidae); (e) the killifish (*Kryptolebias marmoratus*, Kryptolebidae); (f) the mosquitofish (*Gambusia affinis*, Poecilidae); and, (g) the molly (*Poecilia sphenops*, Poecilidae). Each of these species has been included in previous publications by one or more of the authors, and data were collected from existing video images that contributed to those publications (see also Appendix 1). While data were available from multiple individuals and multiple capture events for each species, care was taken, as above, to use the maximum premaxillary protrusion recorded for each species for the purposes of the comparisons here. Length of the ascending process of the premaxilla in these same individuals was measured either from images where the skeletal element was clearly visible or from the same individuals that had been subsequently preserved. Data for *A. ocellatus* are also published in Waltzek and Wainwright (2003).

3 | RESULTS

3.1 | Anatomy

While it is not the aim of this paper to completely review the cranial anatomy of *T. altivelis*, it must be acknowledged that the most enigmatic feature of the anatomy of *T. altivelis* is the unusually long premaxillary process. The ascending process of the premaxilla is so long it creates a small bump on the top of the head when fully retracted.

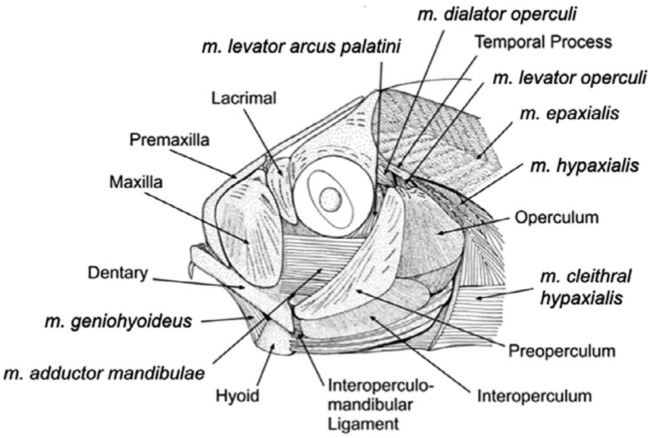

FIGURE 1 Lateral view of the cranial anatomy of *T. altivelis* drawn by hand by KL. Muscles and bones are labeled. Muscles are preceded by the "m"

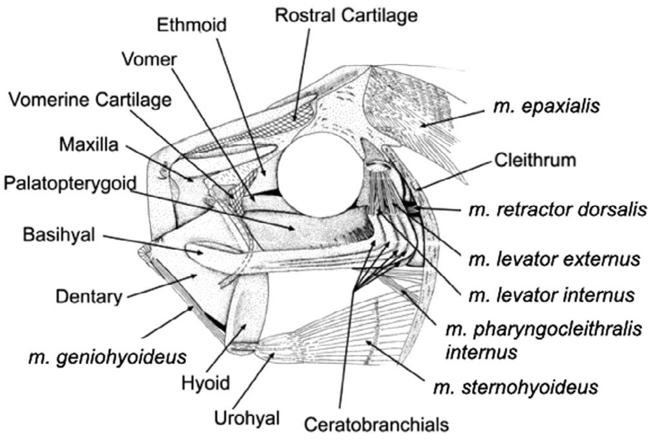

FIGURE 2 Medial view of the cranial anatomy of *T. altivelis* drawn by hand by KL. Muscles and bones are labeled. Muscles are preceded by the "m"

The maxilla is "paddle-shaped" at its anterior end, and also has an elongate ascending process akin to the premaxilla (Figure 1). These are certainly associated with premaxillary protrusion, as the mechanism of premaxillary protrusion in *T. altivelis* appears to resemble the typical mechanism for percomorphs (see also Alexander, 1967). However, notably, the maxilla also protrudes along with the premaxilla. Briefly, when the lower jaw is depressed, the upper jaw is subsequently pulled anteriorly and ventrally via ligamentous connections (Figure 2). The ascending process of the premaxilla glides along the rostral surface of the skull, causing the entire premaxilla + maxilla complex to be projected largely ventrally, toward the rotating lower jaw. However, the premaxilla + maxilla also rotate dorsally, which reduces the degree to which the open mouth is ultimately projected downwards. This rotation is facilitated by an additional strap-like ligamentous connection from the posterior corner of the dentary to the head of the maxilla (denoted by an asterisk, Figure 3). Thus, as the dentary rotates ventrally, tension on this ligament will rotate the maxilla dorsally while it is also moving anteriorly. The resultant mouth opening is projected anteriorly. Movement of the descending process of the premaxilla, also serves to laterally occlude the sides of the open mouth (thought to prevent prey from escaping through the sides of the mouth; Motta, 1984). The unusually shaped maxillae also contribute strongly to this occlusion.

A ventral view of the hyoid region confirms that lower jaw depression is also via the usual linkages in percomorph fishes (Figure 4). The *m. sternohyoideus* extends from the pectoral girdle to the hyoid region. Contraction of the *m. sternohyoideus* pulls the hyoid linkage posteriorly, which, combined with contraction of the *m. geniohyoideus*, serves to depress the dentary.

The bones in the hand-drawn specimen were thin, and not obviously mineralized. Although we did not explicitly test for the degree of mineralization, our CT-scans obtained from *T. altivelis* further demonstrate this; the bones are rather lace-like in the images (Figure 5). Indeed, upon handling, many of the bones broke easily and had a porous structure, lacking any obvious (to visual inspection) form of reinforcement.

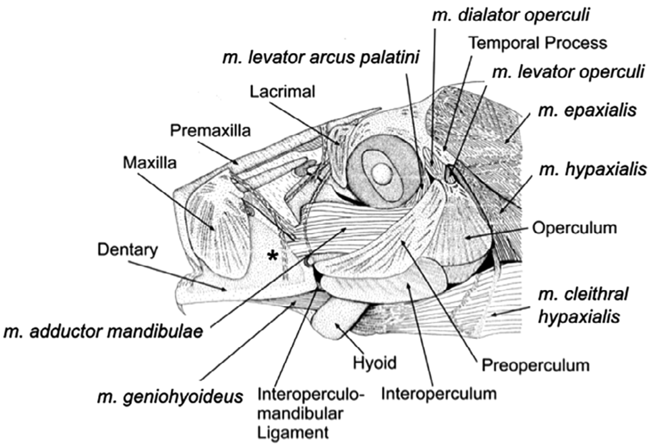

FIGURE 3 Lateral view of the cranial anatomy of *T. altivelis* with the jaws protruded, drawn by hand by KL. Muscles and bones are labeled. Muscles are preceded by the "m."

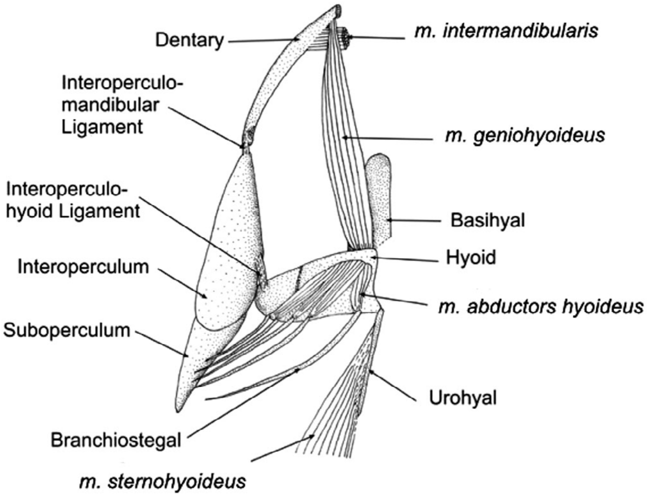

FIGURE 4 Ventral view of one side (fish right side) of the cranial anatomy of *T. altivelis* drawn by hand by KL. Muscles and bones are labeled. Muscles are preceded by the "m"

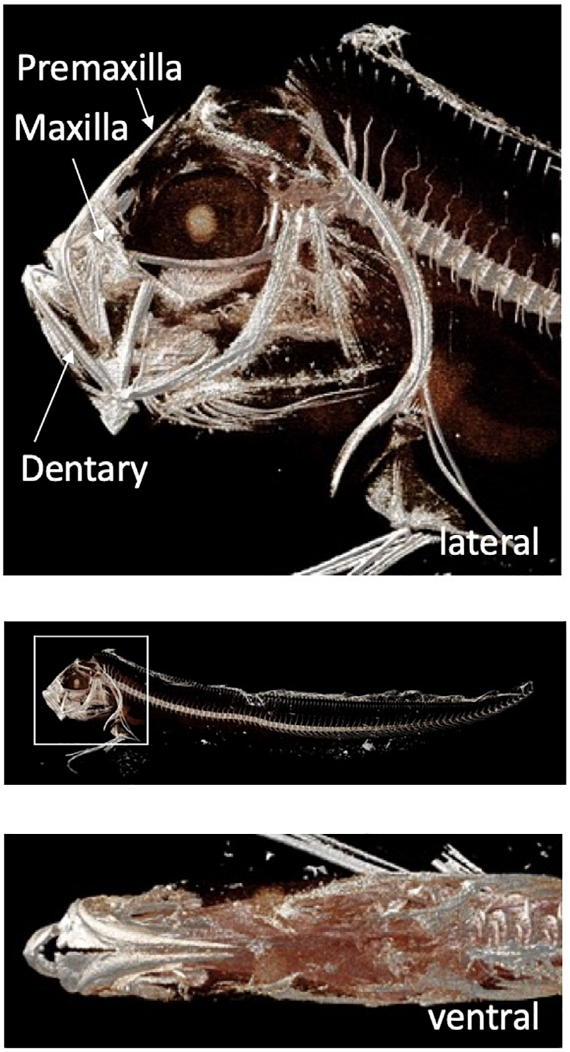

FIGURE 5 Anatomy of *T. altivelis* revealed via CT imaging. The center panel shows the entire specimen. The white box denotes the cranial region, which is enlarged in the top and bottom panels. Above is the lateral view, and below is the ventral view. Both are labeled accordingly

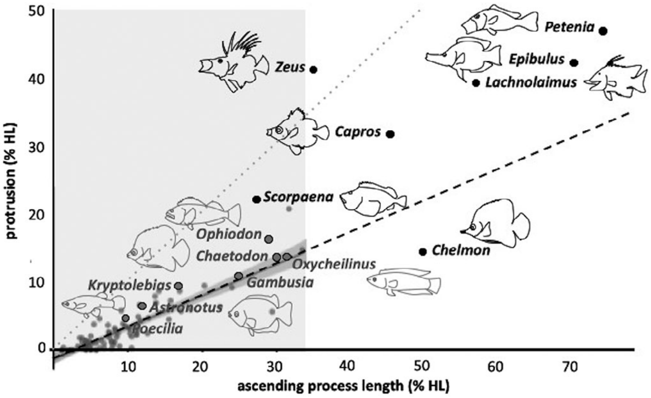

FIGURE 6 Premaxillary protrusion expressed as a percentage of head length versus the length of the ascending process of the premaxilla also expressed as a percentage of head length for non-lampriform protruders. Shown in grey are the data from Bellwood et al. (2015), and the confidence intervals around their regression. The grey box indicates the limit of inference space from this regression. The dashed line is an extension of the slope from Bellwood et al. (2015). The dotted line indicates a 1:1 relationship between protrusion and premaxillary length (when expressed as %HL). The seven species with typical amounts of jaw protrusion are indicated with grey points outlined with black. The seven species capable of extreme protrusion are indicated with solid black points. Outlines of each of the species are provided to give some indication of body shape; length is not to scale

3.2 | Comparative analyses

The seven species characterized as "typical" in their premaxillary protrusion abilities all fell within the range of data points presented by Bellwood et al. (2015). This suggested to us that our approach of using head length (HL) to account for differences in body size was a reasonable approach in this context, or at least as reasonable as body length (Figure 6).

When the species characterized as having extreme premaxillary protrusion are compared with typical protruders, it is necessary to extrapolate beyond the original dataset of Bellwood et al. (2015). If the same trend is extended, however, it would appear that most extreme protruders are performing well above what might be predicted from the length of the ascending process alone (Figure 6). This is probably not surprising given these species' characterization as extreme protruders. *Petenia splendida* clearly produces the most premaxillary protrusion, when scaled to head length; however, *Epibulus insidiator* is quite close, followed by *Lachnolaimus maximum*. *Zeus faber* also is rightly considered an extreme protruder; even though protrusion distance is not as impressive as *P. splendida* or *E. insidiator*, the ratio of protrusion distance to ascending process length is *above* the 1:1 line, indicating that *Z. faber* can protrude the premaxilla to distances exceeding the actual length of the premaxilla. *Capros aper* and *S. guttata* are moderate protruders, with *C. rostratus* actually underperforming given the length of the ascending process of the premaxilla.

When we examine the performance of the Lampriformes, *T. altivelis* exhibits more protrusion than *P. splendida* (i.e., farther to the right; Figure 7). *Trachipterus altivelis* outperforms the remainder of the Lampriformes studied, and each of the remaining species falls quite neatly, and surprisingly, directly onto the relationship observed by Bellwood et al. (2015).

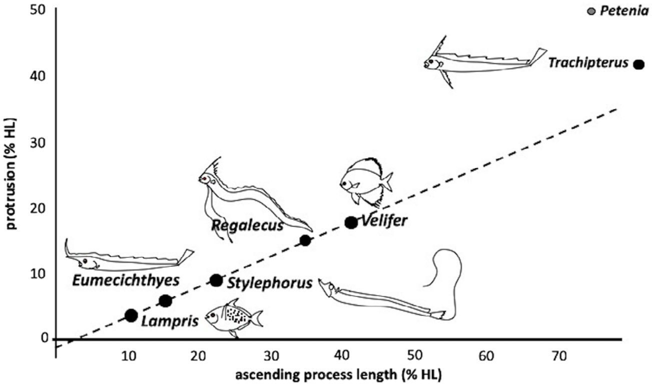

FIGURE 7 Premaxillary protrusion expressed as a percentage of head length versus the length of the ascending process of the premaxilla also expressed as a percentage of head length for the Lampriformes. The dashed line is the extension of the slope from Bellwood et al. (2015), as in Figure 6. The datapoint for *Petenia splendida* is shown for comparison. Outlines of each of the species are provided to give some indication of body shape; length is not to scale

4 | DISCUSSION

While this manuscript is a somewhat brief overview of the premaxillary protrusion abilities and underlying mechanism in *Trachipterus altivelis*, we note several important findings. First, and most obviously, *T. altivelis* does appear to have earned the title of "most extreme" in terms of premaxillary protrusion. The distance to which the upper jaw is protruded anteriorly away from the head exceeds that of any other known species.

However, a secondary, and quite surprising finding, is the pattern of protrusion ability for the remainder of the Lampriformes examined here. That the lampriforms should fall along the line for the remainder of teleosts in Figure 6 is quite telling. First, it suggests that the premaxilla length, which is the primary variable used for predicting protrusion ability here and in other studies, scales with body length, and in the same manner as for other, perhaps all, fishes. In other words, the protrusion ability of this group of fishes is to be expected for their head and premaxillary lengths, and is, in that sense, not really remarkable at all. The premaxilla itself may be considered remarkable, however, what it can do with that extra length is not.

Finally, the truly remarkable species are likely those that fall well above the line in Figure 7. These are species who protrude the premaxilla farther than the average fish with the same premaxillary length, or farther than one would predict from premaxillary length alone. These include species such as *P. splendida* and *E. insidiator*, but also *Z. faber*. *Z. faber* is not found as far to the right as *P. splendida* and *E. insidiator* in Figure 6, but it does demonstrate the greatest positive deviation from the line, which indicates that *Z. faber* can effectively "do more" with its premaxilla than other species included here. This finding suggests that measures of "extreme" protrusion likely need to take into account more than simple linear displacement of the element. To wit, *T. altivelis* demonstrates *both* an extreme anatomy and the ability to protrude the already extreme premaxilla farther than predicted from premaxillary length alone.

As an aside, the gut was examined in an attempt to gain further insight into this species' ecology. The gut was empty, but the anatomy was unusual and potentially suggestive of extreme foraging habits. There were hundreds of very small diverticuli lining the gut, which suggest to us a mechanism for increasing digestive surface area and/or efficacy. This species has been described as a deep-midwater forager on crustacean zooplankton (Hart, 1973; Shenker, 1983), which is consistent with such mechanisms. While much work remains regarding the ecology of *T. altivelis* and its relatives, it is certain that this fish holds many surprises yet in store. As technology increases, and our ability to observe and work with organisms such as *T. altivelis* improves, the utility of drawings such as these (by KL) will surely retain their place as valuable contributions to the understanding of an organisms' ecomorphology.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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