1   Symposium Article

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15   **Abstract**
16   Studies of vertebrate feeding have predominantly focused on the bones and muscles of the head,
17   not the body. Yet, postcranial musculoskeletal structures like the spine and pectoral girdle are
18   anatomically linked to the head, and may also have mechanical connections through which they
19   can contribute to feeding. The feeding roles of postcranial structures have been best studied in
20   ray-finned fishes, where the body muscles, vertebral column, and pectoral girdle attach directly
21   to the head and help expand the mouth during suction feeding. Therefore, I use the anatomy and
22   motion of the head-body interface in these fishes to develop a mechanical framework for
23   studying postcranial functions during feeding. In fish the head and body are linked by the
24   vertebral column, the pectoral girdle, and the body muscles that actuate these skeletal systems.
25   The morphology of the joints and muscles of the cranio-vertebral and hyo-pectoral interfaces
26   may determine the mobility of the head relative to the body, and ultimately the role of these
27   interfaces during feeding. The postcranial interfaces can function as anchors during feeding: the
28   body muscles and joints minimize motion between the head and body to stabilize the head or
29   transmit forces from the body. Alternatively, the postcranial interfaces can be motors: body
30   muscles actuate motion between the head and body to generate power for feeding motions. The
31   motor function is likely important for many suction-feeding fishes, while the anchor function
32   may be key for bite- or ram-feeding fishes. This framework can be used to examine the role of
33   the postcranial interface in other vertebrate groups, and how that role changes (or not) with
34   morphology and feeding behaviors. Such studies can expand our understanding of muscle
35   function, as well as the evolution of vertebrate feeding behaviors across major transitions such as
36   the invasion of land and the emergence of jaws.

37 **Title:** What fish can teach us about the feeding functions of postcranial muscles and joints

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39 **Running Title**: Postcranial structures in feeding

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Abstract

Studies of vertebrate feeding have predominantly focused on the bones and muscles of the head, not the body. Yet, postcranial musculoskeletal structures like the spine and pectoral girdle are anatomically linked to the head, and may also have mechanical connections through which they can contribute to feeding. The feeding roles of postcranial structures have been best studied in ray-finned fishes, where the body muscles, vertebral column, and pectoral girdle attach directly to the head and help expand the mouth during suction feeding. Therefore, I use the anatomy and motion of the head-body interface in these fishes to develop a mechanical framework for studying postcranial functions during feeding. In fish the head and body are linked by the vertebral column, the pectoral girdle, and the body muscles that actuate these skeletal systems. The morphology of the joints and muscles of the cranio-vertebral and hyo-pectoral interfaces may determine the mobility of the head relative to the body, and ultimately the role of these interfaces during feeding. The postcranial interfaces can function as anchors during feeding: the body muscles and joints minimize motion between the head and body to stabilize the head or transmit forces from the body. Alternatively, the postcranial interfaces can be motors: body muscles actuate motion between the head and body to generate power for feeding motions. The motor function is likely important for many suction-feeding fishes, while the anchor function may be key for bite- or ram-feeding fishes. This framework can be used to examine the role of the postcranial interface in other vertebrate groups, and how that role changes (or not) with morphology and feeding behaviors. Such studies can expand our understanding of muscle function, as well as the evolution of vertebrate feeding behaviors across major transitions such as the invasion of land and the emergence of jaws.

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Introduction

Vertebrate feeding studies have focused on the bones and muscles of the head, with much less known about the interaction between the head and body or the roles of postcranial bones and muscles. This is not surprising, as it is the cranial structures—tongues, jaws, beaks, teeth—that directly contact food, and the muscles of the head that attach directly to these elements. Cranial motions are often externally visible and can be directly related to acquiring and ingesting food, while postcranial structures such as the vertebral column, pectoral girdle, and associated body muscles are usually neither visible nor directly interacting with the food. However, these postcranial structures may also be acting as part of the feeding apparatus.

The head and body are anatomically linked, and there is reason to expect they are also mechanically linked. In tetrapods, the head is connected to the trunk and limbs by the neck, while in non-tetrapod fishes the body muscles of the trunk attach directly to the cranial skeleton (Evans, 1939; Shubin et al., 2015). By linking the head and body, this postcranial interface has the potential to transmit forces or even power from the body to the head. What role the postcranial musculoskeletal system plays in feeding will depend on the morphology of these muscles and joints, as well as their behavior during feeding. Understanding the role of postcranial structures during feeding can bring new insights into the mechanics and evolution of vertebrate feeding behaviors, as well as how the demands of feeding may have shaped the head-body interface.

The feeding role of the postcranial interface has been most widely recognized in suction-feeding fishes. In non-tetrapod bony fishes ("bony fishes" hereafter) that primarily capture food by suction the body muscles and pectoral girdle have long been studied as part of the feeding

107   apparatus (Alexander, 1967; Gregory, 1933; Tchernavin, 1953), as they are capable of

108   contributing to mouth expansion during suction feeding. First, the dorsal body muscles (epaxials)

109   are the only muscles that cross the craniovertebral joint and can rotate the head dorsally to

110   increase the dorsoventral height of the mouth cavity (Fig. 1A). Second, the ventral body muscles

111   (hypaxials) can retract the pectoral girdle to expand the mouth cavity ventrally and caudally, via

112   linkages with the hyoid apparatus and lower jaw (Fig. 1A). As a result, the body muscles,

113   vertebral column, and pectoral girdle have been studied during feeding in a wide range of

114   suction-feeding fishes (reviewed in Anker, 1974; Ferry-Graham and Lauder, 2001; Lauder, 1985;

115   Schaeffer and Rosen, 1961; Westneat, 2006). Therefore, bony fishes are an excellent system for

116   exploring the role of postcranial musculoskeletal systems during feeding, and may offer insights

117   that can be applied to other vertebrate systems as well.

118

119   Outside of bony fishes, relatively little is known about the feeding functions of postcranial

120   structures, nor is there a mechanical framework for understanding postcranial motion and

121   morphology in the context of feeding. This is due in part to the difficulty of visualizing the *in*

122   *vivo* motion of deep structures like the pectoral girdle, vertebral column, and the muscles

123   actuating them. Additionally, measuring motion between the head and body requires a new

124   frame of reference. Many feeding studies measure motion relative to the cranium, making it

125   impossible to determine how the cranium itself is moving relative to the body. X-ray

126   Reconstruction of Moving Morphology (XROMM) has made it possible to visualize bones like

127   the vertebral column and pectoral girdle in live animals, by combining biplanar X-ray video with

128   3D digital bone models (Brainerd et al., 2010). The skeletal animation produced by XROMM

129   also allows bone motions to be measured in multiple, anatomically relevant frames of reference,

130   (e.g., Camp and Brainerd, 2014; Menegaz et al., 2015). Additionally, sonomicrometry and

131   fluoromicrometry use sound or biplanar X-ray video, respectively, to measure *in vivo* muscle

132   length.

133

134   With the ability to directly image and measure postcranial structures now available, the

135   mechanical interface between head and body is an exciting area for exploration. The goal of this

136   paper is to propose a framework for how the postcranial body structures can contribute to

137   feeding, based on our knowledge from bony fishes. I first describe the anatomical connections

138   between the head and body in bony fishes, and then propose mechanical functions for the

139   postcranial interfaces during feeding. Lastly, I examine how this mechanical framework may be

140   applied across the major vertebrate groups, highlighting areas that are ripe for further research.

141

142   **Anatomy of the postcranial interface**

143   *Cranio-vertebral interface*

144   In bony fishes, the head and body are connected by two musculoskeletal systems: dorsally by the

145   cranio-vertebral interface and ventrally by the hyoid-pectoral interface. The cranio-vertebral

146   interface consists of the bones, joints, and muscles that connect the cranium and the vertebral

147   column. The neurocranium and the vertebral column directly articulate in most fish at the

148   craniovertebral joint (but see Schnell et al., 2008) between the basioccipital and the rostralmost

149   vertebral body (Fig. 1A). This joint is crossed dorsally and laterally by the epaxials: segmented

150   body muscles whose W-shaped myomeres extend along the vertebral column from the

151   neurocranium to the caudal fin (Fig. 1). Thus, the epaxial muscles, and only these muscles, have

152   a line of action to produce flexion between the head and body. This flexion is usually described

153   as dorsal rotation or elevation of the neurocranium relative to the body, and has been measured

154   in many bony fishes (reviewed in Lauder, 1985; Schaeffer and Rosen, 1961).

155

It remains unclear which vertebral joints contribute to cranial elevation in suction-feeding fishes, or how this role relates to vertebral morphology. Traditionally, the vertebral column of fish has been split into abdominal and caudal regions (Rockwell et al., 1938), but there is developmental (Johanson et al., 2005; Morin-Kensicki et al., 2002) and morphological (Nowroozi et al., 2012) evidence for a cervical region immediately caudal to the head (Fig. 1C) in at least some species. The presence and extent of a cervical region has not yet been broadly examined across bony fishes, nor whether it contributes to cranial elevation. Nevertheless, morphologically distinct anterior vertebrae are found in many fishes, such as the Weberian apparatus of ostariophysians (e.g., Bird and Hernandez, 2007), and some have been hypothesized to directly relate to cranial elevation (Huet et al., 1999; Jimenez et al., 2018; Lauder and Liem, 1981; Lesiuk and Lindsey, 1978). For most fishes cranial elevation is likely not achieved by flexion at the craniovertebral joint alone, and the center of cranial rotation is further posterior at approximately the level of the pectoral girdle's posttemporal-supracleithrum joint (Fig. 1A) based on morphology, specimen manipulation (Gregory, 1933), 2D (Carroll et al., 2004), and 3D (Jimenez et al., 2018) kinematics analysis. This implies that some number intervertebral joints on either side of that center are also dorsally flexed to generate cranial elevation. For example, in largemouth bass (*Micropterus salmoides*), the center of cranial rotation was between the second and fourth vertebrae (Jimenez et al., 2018), within the cervical region (Fig. 1B). Alternatively, the pivot-feeding sygnathiform fishes have centers of cranial rotation at, or rostral to, the cranio-vertebral joint (Roos et al., 2010), and may achieve cranial elevation by flexion primarily about this joint (de Lussanet and Muller, 2007). Given the morphological and behavioral diversity of fishes, the number and location of intervertebral joints contributing to the dorsal postcranial interface likely varies among species or even feeding behaviors.

179

180 Large regions of the epaxial muscles may contribute to cranial elevation, and therefore be

181 considered part of the cranio-vertebral interface. The epaxial muscles have long been known to

182 activate during suction feeding in many fishes (Wainwright et al., 1989), and in the largemouth

183 bass that activity extends over halfway down the body (Thys, 1997). These muscles are not only

184 active, but also shorten from the head to about halfway down the body in at least two species:

185 largemouth bass (Camp and Brainerd, 2014) and bluegill sunfish (Camp et al., 2018). This

186 demonstrates that large regions of the epaxial muscles, likely extending beyond the region of

187 dorsally flexing intervertebral joints, can contribute to the cranio-vertebral interface during

188 feeding. Like the vertebrae, no morphological distinction has been found to indicate which

189 regions of the epaxial muscles contribute to cranial elevation.

190

191 *Hyo-pectoral interface*

192 Ventrally, the head and body are linked by the hyo-pectoral interface: the bones of the pectoral

193 girdle, and the muscles that connect it to the hyoid apparatus and the body. In most bony fishes

194 the pectoral girdle is made up of a series of articulated bones, the most dorsal of which typically

195 articulates with the epiotic bones in the caudal region of the neurocranium (Gosline, 1977) (Fig.

196 1A). Ventrally, the cleithrum is linked to the hyoid apparatus by the sternohyoideus muscle and

197 to the body and vertebral column by the hypaxial muscles (Fig. 1A). These muscles control the

198 cranio-caudal position of the cleithrum and can generate rostrodorsal (protraction) or

199 caudoventral (retraction) sagittal-plane rotations at the cleithrum-supracleithrum joint. During

200 feeding, the hypaxial muscles can shorten to retract the pectoral girdle, which in turn retracts and

201 depresses the hyoid apparatus and contributes to mouth expansion (Camp and Brainerd, 2014;

202 Muller, 1987; Van Wassenbergh et al., 2007b). The sternohyoideus muscle may also shorten

203 during pectoral girdle retraction as in bluegill sunfish (Camp et al., 2018), or it may act as a

204 ligament to transmit motion to the hyoid, as in largemouth bass (Camp and Brainerd, 2014) and

205 clariid catfishes (Van Wassenbergh et al., 2007b). It has also been proposed that the

206 sternohyoideus could shorten against an immobile cleithrum—held in place by the hypaxials—to

207 retract the hyoid apparatus (Lauder and Lanyon, 1980), but this has yet to be demonstrated

208 experimentally.

209

210 As with the epaxial muscles, it is not anatomically obvious what proportion of the hypaxial

211 muscles are involved. Activity has only been recorded in the rostralmost regions of the hypaxials

212 (Lauder and Lanyon, 1980; Lauder and Norton, 1980; Lauder, 1981), but large regions (from the

213 pectoral girdle to halfway down the body) of the hypaxials muscles shorten during pectoral

214 girdle retraction in largemouth bass (Camp and Brainerd, 2014) and bluegill sunfish (Camp et

215 al., 2018). While cleithrum retraction has been measured in multiple species, it is unknown

216 whether this is due solely to rotation about the cleithrum-supracleithrum joint or whether more

217 dorsal pectoral girdle joints also contribute (Gosline, 1977; Muller, 1987).

218

219 **Mechanical Framework**

220 As described above, the postcranial interface has multiple anatomical connections to the head

221 and can contribute kinematically to mouth expansion through cranial elevation and/or hyoid

222 retraction. These mechanical connections lead to two proposed feeding functions of the

223 postcranial interface.

224

225 First, the postcranial interface may act as a motor: generating power that is then transmitted to

226 the head during mouth expansion (Fig. 2). In order to generate power (the product of force and

227 velocity), muscles must actively shorten to generate force and positive velocity. To allow this

228 muscle shortening and power transmission to the head, there must also be flexion of the skeleton

229 at the postcranial interface. Thus, for the cranio-vertebral interface to act as a motor, there should

230 be motion (dorsal flexion) at the craniovertebral and/or intervertebral joints, and epaxial muscle

231 shortening. Similarly, for the hyo-pectoral system power production must be accompanied by

232 rotation (retraction) of the pectoral girdle and hypaxial shortening. In summary, if the postcranial

233 interface is functioning as a motor to power feeding motions, then the interfacing body muscles

234 should be active and shortening, and the neurocranium or pectoral girdle should rotate relative to

235 the body (Fig. 2).

236

237 Second, the postcranial interface may act as an anchor to stabilize the head and transmit forces

238 from the body (Fig. 2). The interfacing muscles may actively generate force, but not shorten or

239 generate power, which would move rather than stabilize the head. Therefore, there is no joint

240 motion at the interface: no dorsal flexion of the neurocranium or retraction of the pectoral girdle.

241 In this way the postcranial interfaces can provide stable attachment sites for the cranial muscles

242 that insert on the neurocranium or pectoral girdle. Such stability may also be important for

243 transferring forces from the locomotion system (body and fins) to the head. Anchoring is also

244 required during suction feeding: if either the neurocranium or pectoral girdle were free to move,

245 they would be sucked towards the center of the mouth by the sub-ambient pressure in the mouth

246 cavity (e.g.,Carroll et al., 2004). The postcranial interfaces must at least generate force to

247 overcome this pressure. In summary, if the postcranial interface is functioning as an anchor, then

248 the muscles should be active but not shortening and the neurocranium and pectoral girdle should

249 not move relative to the body (Fig. 2).

250

251 The mechanical functions of 'motor' and 'anchor' are somewhat simplistic and likely represent

252 two extremes along a spectrum of roles for the postcranial interface during feeding. These

253 musculoskeletal systems can do more than just generate force or power, and may switch roles

254 within or between feeding behaviors. However, the motor and anchor roles still provide a useful

255 framework for examining postcranial function in suction-feeding bony fishes and other

256 vertebrates. The motor function is clearly important for suction feeding fishes, as substantial

257 power is required to expand the mouth fast and forcefully enough to accelerate a bolus of water

258 and prey into the mouth. While it has long been recognized that the muscles of the head are too

259 small to be the sole source of suction power (Aerts et al., 1987; Alexander, 1970; Elshoud-

260 Oldenhave, 1979), recent studies have shown that that epaxial and hypaxial muscles generate

261 over 90% of the required power for suction strikes (Camp et al., 2015; Camp et al., 2018). In

262 some suction feeding fishes, however, cranial elevation is minimal or absent (Van Wassenbergh

263 et al., 2009), implying the cranio-vertebral interface may have an anchoring role in these species.

264 Anchoring the postcranial interface may function to transmit force or stabilize cranial muscle

265 attachment sites, but it prevents the body muscles from contributing power. Given the predicted

266 importance of body muscle power for mouth expansion, it seems unlikely that both postcranial

267 interfaces would act as anchors during suction feeding. However, if only one interface is acting

268 as a motor to power suction expansion, then the other must be an anchor to resist the mouth

269 cavity collapsing. For example, if the hyo-pectoral interface alone powers suction expansion,

270 then the cranio-vertebral interface must anchor the neurocranium so it is not accelerated ventrally

271 by the sub-ambient pressure of the mouth cavity. In order to expand the mouth cavity

272 dorsoventrally, i.e., by increasing the angle between the neurocranium and the pectoral girdle,

273 both interfaces must function together as motors or a motor-anchor pair. Suction feeding fish

274   may even be able to modify the role (anchor vs. motor) of an interface depending on prey type

275   and position (Van Wassenbergh et al., 2006).

276

277   **Postcranial feeding roles across vertebrates**

278   While this framework has been developed based on suction feeding fishes, I expect it can be

279   usefully applied to studying how the postcranial interface contributes to other feeding behaviors

280   and vertebrates. All vertebrates have anatomical connections between the head and body—

281   although the specific structures and muscles vary—and therefore have the potential for

282   postcranial structures to contribute mechanically to feeding. While there are fewer studies

283   outside of suction-feeding bony fishes, I use the motor-anchor framework to develop informed

284   hypotheses about postcranial function during feeding.

285

286   *Cartilaginous Fishes*

287   Chondrichthyians, the sharks, chimaeroids, and rays, are the other major group of aquatic

288   vertebrates, and while some are specialized suction feeders this is not the predominant mode of

289   prey capture as in bony fishes (Wilga et al., 2007). The cranio-vertebral interface of

290   chondrichthyians is broadly similar to that of bony fishes in that the chondrocranium directly

291   articulates with the vertebral column at the craniovertebral joint (Fig. 3A), which is spanned by

292   the epaxial muscles. While a cervical region has not been identified in this group, the anterior

293   vertebrae may have distinct morphologies, such as the synarcual of chimaeroids and rays formed

294   by fusion of two or more of the most cranial vertebrae (Claeson, 2011; Johanson et al., 2015),

295   and expanded basiventrals in some sharks and rays (Claeson and Hilger, 2011). It remains

296   unclear how or if these vertebral morphologies contribute to motion between the chondrocranium

297   and vertebral column (Claeson and Hilger, 2011), although cranial elevation is usually minimal

298   in most sharks and rays including suction-feeding specialists (Ajemian and Sanford, 2007; Wilga

299   and Sanford, 2008; Wu, 1994) (but see Fouts and Nelson, 1999). This suggests that in most

300   chondrichthyians the cranio-vertebral interface, including specialized anterior vertebrae like the

301   synarcual, may function as an anchor to stabilize the head during feeding. The ram- and bite-and-

302   tear feeding behaviors of sharks rely on accelerating the body to ram into prey (Motta and Wilga,

303   2001), so transmitting force from the body to the head may be an important function of the

304   postcranial interface.

305

306   The pectoral girdle of sharks does not articulate with the cranium at all and is caudally displaced

307   compared to bony fishes (Fig. 3). Despite this, in at least one suction-feeding shark (the white-

308   spotted bamboo shark) pectoral girdle retraction and hypaxial muscle shortening was recorded

309   during feeding (Camp et al., 2017), consistent with a motor function for the hyo-pectoral

310   interface. This pectoral girdle retraction occurred relatively late (Camp et al., 2017), and mouth

311   expansion was likely powered by the hypobranchial muscles rather than the axial muscles as in

312   bony fish (Ramsay, 2012). The role of the pectoral girdle and axial muscles in suction-feeding

313   rays (e.g., Dean and Motta, 2004) has yet to be examined, although morphology suggests limited

314   pectoral girdle mobility (Da Silva and De Carvalho, 2015). Much remains to be discovered about

315   the function of the postcranial interfaces in cartilaginous fishes, and studying this group may also

316   help us understand the role of the postcranial interface for feeding in stem gnathostomes.

317

318   *Bony fishes*

319   The role of the postcranial interfaces during suction feeding in bony fishes is discussed above,

320   but less is known about their role in other behaviors such as ram-feeding, biting, scraping,

321   filtering, winnowing. Mechanically, these behaviors rely less on powerful mouth expansion, and

322 instead require force and work to be exerted on the food. The epaxial muscles are often still

323 active at least during biting (e.g., Alfaro et al., 2001), and anchoring of the postcranial interface

324 may aid the function of cranial muscles during these feeding behaviors. For example, the

325 interfaces may stabilize the head during ram and ram-filter feeding (as it is propelled forward by

326 whole-body acceleration), or transmit body forces to the head during bite-and-tear feeding where

327 food is gripped with jaws, and pulled or twisted off by body motions. Alternatively, motor

328 functions of the cranio-vertebral and hyo-pectoral interfaces may still be important for these

329 feeding modes; more data on body muscle shortening and neurocranium and pectoral girdle

330 kinematics are needed to test this. Most actinopterygian biters, scrapers, and filterers can also

331 suction feed, with little evidence of performance trade-offs between these two behaviors (Liem,

332 1980; Van Wassenbergh et al., 2007a). This suggests the body muscles may be quite versatile

333 and multi-functional within a single individual, as well as across species.

334

335 *Tetrapods*

336 Unlike bony and cartilaginous fishes, tetrapods have an anatomically distinct postcranial

337 interface: the neck, which spans from the head to the pectoral girdle. The cervical vertebrae of

338 the neck allow three-dimensional motion and positioning of the head during feeding (e.g.,

339 Gussekloo and Bout, 2005; Snively et al., 2014). In addition to driving head motions, the

340 postcranial interface may contribute mechanically to feeding. Suction-feeding salamanders and

341 turtles can use the cranio-vertebral and hyo-pectoral interfaces as motors, with cranial elevation

342 and pectoral girdle retraction as in suction-feeding fishes (Aerts et al., 2001; Lauder and Shaffer,

343 1985; Lauder and Prendergast, 1992; Van Damme and Aerts, 1997; Van Damme et al., 2001).

344 Presumably this allows the body muscles to contribute power to suction feeding, as in bony

345 fishes, despite the separation of the head and body by the neck. For at least the cranio-vertebral

346 interface, this motor function is not limited to suction feeding as cranial elevation has also been

347 observed during feeding lizards (Herrel and Vree, 1999; Herrel et al., 1995) and caiman (Cleuren

348 and de Vree, 1992), although in these ram- and bite-feeders it is most likely used to widen the

349 mouth opening before biting down on food.

350

351 The craniovertebral interface is also likely to be used by many tetrapods as an anchor to stabilize

352 the head and transmit forces from the body. There are qualitative and anecdotal reports of

353 tetrapods holding food in the jaws while motions of the neck and/or body are used to dislodge or

354 tear the food (e.g., Van Valkenburgh, 1996). In some feeding behaviors—like diving at high

355 speeds or the precise occlusion of mammalian chewing—head stabilization may be crucial, and

356 the anchoring of the craniovertebral interface may be important. However, more studies are

357 needed to better understand how tetrapods use the craniovertebral interface, and how these

358 functions correspond to vertebral morphology. For example, does all cranial elevation in

359 salamanders result from rotation about their single cervical vertebrae (Fig. 3C), or are more

360 caudal intervertebral joints also contributing? Conversely, are all the cervical vertebrae in lizards

361 (Fig. 3D) contributing to cranial elevation?

362

363 The hyo-pectoral interface has received even less study in tetrapods, but is most often associated

364 with anchor functions in these vertebrates. The morphology of the pectoral girdle skeleton varies

365 widely across tetrapods and some elements (Jenkins, 1974) or even the entire girdle may be

366 absent (e.g., Tsuihiji et al., 2012). Not only is the pectoral girdle of tetrapods separated from the

367 head, but its roles supporting the rib cage or forelimbs may prevent substantial motion of the

368 girdle (Heiss et al., 2018). And unlike bony and cartilaginous fishes, tetrapods have a muscular

369 tongue, derived from hypobranchial muscles which still attach to elements of the pectoral girdle

370   and/or hyoid apparatus (Diogo et al., 2008). One possibility is that stability of the pectoral girdle

371   may be important for the tongue's functions during feeding. More research is needed to examine

372   the role of the hyo-pectoral interface during feeding in tetrapods, and understand how pectoral

373   girdle morphology relates to feeding behaviors.

374

375   A broader understanding of the feeding roles of the postcranial interface across vertebrates, not

376   just bony fishes, can lead to exciting and important evolutionary questions. First, there are good

377   reasons to hypothesize that the axial muscles of the postcranial interface were involved in the

378   feeding of early stem gnathostomes. Stem gnathostomes already possessed the musculoskeletal

379   elements of the postcranial interfaces. The evolution of the epaxial and hypaxial muscles and the

380   pectoral girdle predate the cranial muscles and vertebrate jaw (Brazeau and Friedman, 2015;

381   Forey and Janvier, 1993; Kusakabe et al., 2011). Epaxial-powered cranial elevation is an

382   important mechanism of mouth-opening—for suction, ram, and bite feeding—used across extant

383   bony fishes, and inferred to be ancestral for this group (Schaeffer and Rosen, 1961). Early jawed

384   vertebrates such as the arthrodire placoderms, may also have used epaxial-powered cranial

385   elevation to feed (Anderson and Westneat, 2007; Anderson, 2010; Trinajstic et al., 2007).

386   Although we don't yet know if the same is true of hypaxial-powered pectoral girdle retraction,

387   this motion has been observed in bony and cartilaginous fishes (Camp and Brainerd, 2014; Camp

388   et al., 2017) and W-shaped hypaxial muscles were present in placoderms (Trinajstic et al., 2007).

389   As we better understand the form-function relationships of the postcranial interface in living

390   fishes, we may be able to infer its role during feeding in early vertebrates.

391

392   Second, as vertebrates colonized terrestrial habitats, how did the function of the postcranial

393   interface change, and how did this influence the evolution of postcranial morphology and feeding

394 behaviors? The morphology and mechanics of the postcranial interface changed substantially in

395 tetrapods. The pectoral girdle was initially separated from the head by the neck in

396 tetrapodamorph fishes (Shubin et al., 2015; Shubin et al., 2006), and then co-opted to support the

397 forelimbs and rib cage in terrestrially locomoting tetrapods. Suction feeding was no longer

398 feasible in the low-density, low-viscosity air of the terrestrial environment, so food had to be

399 captured by mouth-closing rather than powerful mouth expansion (Heiss et al., 2018; Neenan et

400 al., 2014). As a result of these anatomical and mechanical changes, what happened to the role of

401 the postcranial interface during feeding in tetrapods? Most studies of the pectoral girdle and

402 vertebral column in early tetrapods and tetrapodamorph fishes have focused on their role in

403 locomotion (e.g., Pierce et al., 2013; Shubin et al., 2006), while feeding studies have focused on

404 the jaws and skull (e.g., Neenan et al., 2014). But could these interfaces have still acted as

405 motors during feeding, as they do in many bony fishes? As we discover more about the feeding

406 functions of the postcranial interfaces of modern tetrapods and bony fishes, we can start to

407 answer these questions.

408

409 **Conclusions**

410 Understanding the feeding functions of the postcranial interface is an exciting research area, with

411 much still to be discovered. This paper provides a preliminary framework for understanding the

412 function of the postcranial interface during feeding—as an anchor or a motor—which may be

413 revised or replaced as more data are collected. Currently, comparative data on musculoskeletal

414 function of the cranio-vertebral and hyo-pectoral interfaces are scarce, and more studies are

415 desperately needed. With recent advances in visualizing and recording musculoskeletal function,

416 I hope more feeding studies will include these postcranial elements, leading to a more complete

417 understanding of their form-function relationships, evolutionary morphology, and muscle

418 function.

419

429

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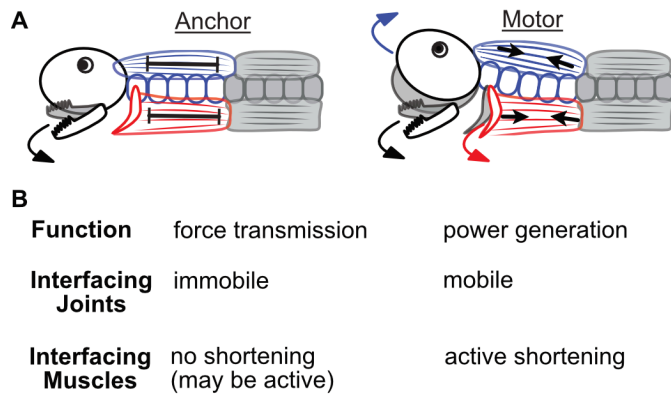621   for jaw protrusion in elasmobranchs. J Morphol 222, 175-190.
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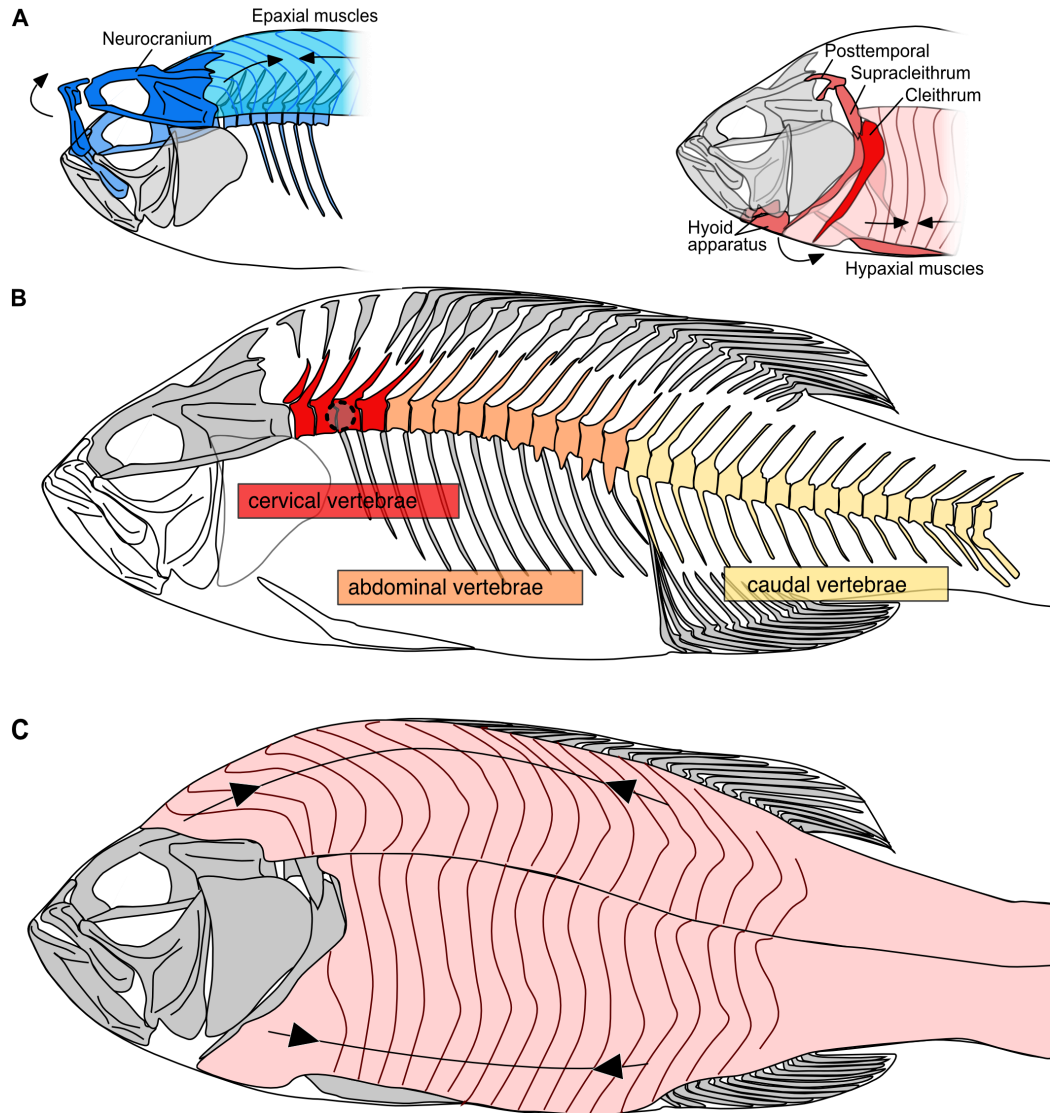
Figure 1. Anatomy and function of the postcranial interface during feeding in fish, based on

largemouth bass (*Micropterus salmoides*). (**A**) The dorsal, cranio-vertebral interface (in blue) can

contribute to mouth expansion as epaxial muscle shortening produces dorsal flexion at the

craniovertebral joint to rotate (elevate) the cranium. The ventral, hyo-pectoral interface (in red)

can contribute to expansion by hypaxial muscle shortening to caudally rotate (retract) the

pectoral girdle, which in turn retracts and depresses the hyoid. (**B**) The vertebral column can be

divided into three regions: caudal (yellow), abdominal (orange), and cervical (red) as defined by

(Nowroozi et al., 2012). The average center of neurocranial rotation measured from largemouth

633   bass (Jimenez et al., 2018) is indicated by a black, dashed circle. (**C**) The epaxial and hypaxial

634   musculature, with the regions that shorten during feeding indicated with black arrows (Camp and

635   Brainerd, 2014) extend far beyond the cervical vertebrae and center of neurocranial rotation

636   shown in **B**.

637

638

A   Anchor   Motor

B

Function	force transmission	power generation
Interfacing Joints	immobile	mobile
Interfacing Muscles	no shortening (may be active)	active shortening

639

640   **Figure 2.** Mechanical roles of the cranio-vertebral and hyo-pectoral systems during feeding. (**A**)

641   Schematic of the postcranial interfaces (unfilled, colored-outlines) as either motors or anchor,
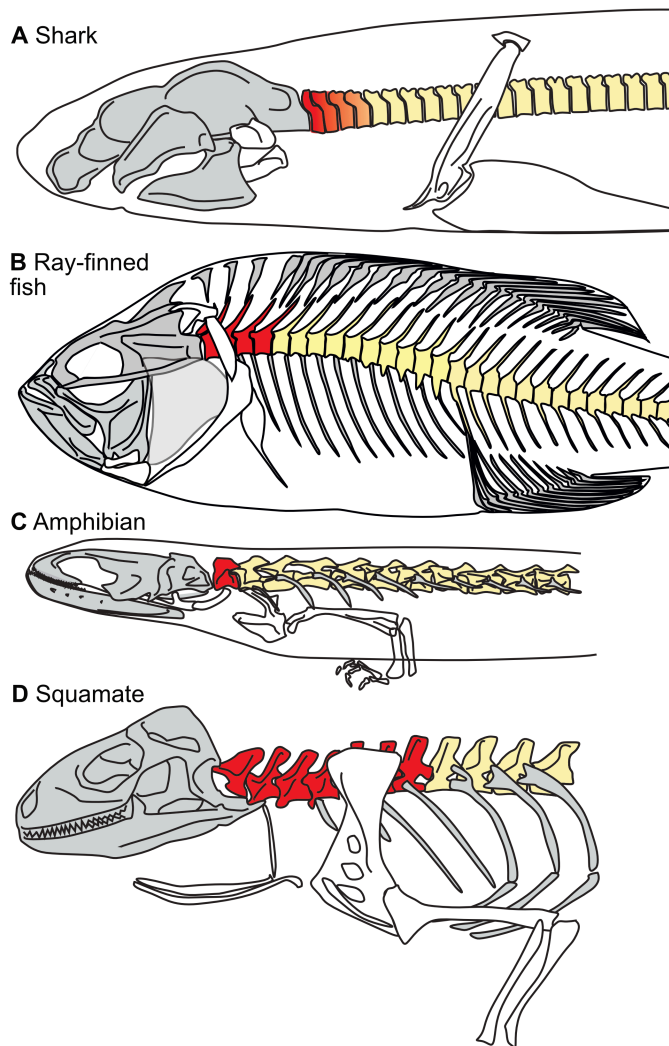
642   relative to the rest of the body (filled, grey outlines). (**B**) Each role is hypothesized to have

643   distinct mechanical functions, interfacing joints motions (relative to the body), and interfacing

644   muscle behaviors. (Online figure in color).

645

646

Figure 3. Comparative skeletal anatomy of the postcranial interfaces from different vertebrate groups. The pectoral girdle and hyoid apparatus are shown in white (unfilled) and the vertebral column in yellow, with the cervical vertebrae highlighted in red. The red-to-yellow gradient in the shark (**A**) indicates vertebrae that may be morphologically distinct, although not referred to as a cervical region (see Claeson and Hilger, 2011). Schematic diagram of (**A**) shark (*Chiloscyllium plagiosum*), (**B**) ray-finned fish (*Micropterus salmoides*), (**C**) salamander (*Pleurodeles waltl*), (**D**) lizard (*Iguana iguana*). Online version in color.