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1 **A fish that uses a hydrodynamic tongue to feed on land**

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12 **Key words:** prey capture, mudskipper, newt, hyoid, tongue, kinematics

13 **Abstract**

14 To capture and swallow food on land, a sticky tongue supported by the hyoid and gill arch
15 skeleton has evolved in land vertebrates from aquatic ancestors that used mouth-cavity-
16 expanding actions of the hyoid to suck food into the mouth. However, the evolutionary pathway
17 bridging this drastic shift in feeding mechanism and associated hyoid motions remains unknown.
18 Modern fish that feed on land may help to unravel the physical constraints and biomechanical
19 solutions that lead to terrestrialization of fish feeding systems. Here, we showed that the
20 mudskipper emerges onto land with its mouth cavity filled with water, which it uses as a
21 protruding and retracting “hydrodynamic tongue” during the initial capture and subsequent intra-
22 oral transport of food. Our analyses link this hydrodynamic action of the intra-oral water to a
23 sequence of compressive and expansive cranial motions that diverge from the general pattern
24 known for suction feeding in fishes. However, the hyoid motion pattern showed a remarkable
25 resemblance to newts during tongue prehension. Consequently, although alternative scenarios
26 cannot be excluded, hydrodynamic tongue usage may be a transitional step onto which the
27 evolution of adhesive mucosa and intrinsic lingual muscles can be added to gain further
28 independence from water for terrestrial foraging.

29 **Background**

30 Identifying the functional modifications enabling transitions from water to land is key to our
31 understanding of how vertebrates managed to colonize land some 400 million years ago [1].
32 Although studies on skeletal adaptations during the fish-to-tetrapod transition have mainly
33 focused on adaptations of the locomotion system [2-4], modifications to the feeding system are
34 an equally important aspect of terrestrialization [5-8]. Fish rely on generating suction to draw
35 prey and surrounding water into the buccal cavity and to transport it within the mouth towards
36 the oesophagus [9, 10]. The hyoid is important for generating suction; it causes buccal volume
37 increase by depressing the floor of the buccal cavity and laterally abducting the suspensoria [11,
38 12]. On land, however, using flows of air to transport food is virtually impossible [13, 14].
39 Having passed this evolutionary barrier, modern basal terrestrial tetrapods (e.g., from the groups
40 *Lissamphibia*, *Lepidosauria*, and *Testudines*) use a tongue supported by the hyoid skeleton to
41 transport food towards the oesophagus [15-17]. The steps in the transformation of the hyoid (and
42 its associated muscles and ligaments) from a suction-generating structure to supporting and
43 moving the tongue, however, remain unknown.

44 Examination of extant amphibious fishes may help us better understand the mechanisms that led
45 to the recent evolution of a cranial musculoskeletal system specialized to operate in this novel
46 niche. These model systems provide insight in the basic physical constraints behind this key
47 macro-evolutionary change, and reveal biomechanical solutions for successfully making this
48 drastic shift in feeding environment [5, 18]. Probably the most successful group of fishes
49 capable of extended, terrestrial foraging excursions are mudskippers (Gobiidae, Oxudercinae).
50 Although the mechanics of the feeding system of mudskippers has been studied previously, these
51 studies focused either exclusively on the functioning of the oral jaws during the initial stages of

52 prey capture [8], or on pharyngeal jaw function during the final processing of prey near the
53 oesophagus entrance [19]. Consequently, it remains to be identified how terrestrial feeding is
54 completed in mudskippers, including the indispensable phase of transporting prey to the
55 posterior end of the buccal cavity. Interestingly, mudskippers come out on land with their
56 opercular and buccal cavities (anatomy shown in Fig. 1a) filled with water [20]. However,
57 whether this intra-oral water plays a role in feeding remains unknown [21]. The main goal of the
58 present study is to unravel how mudskippers capture prey and perform intra-oral transport of
59 prey on land. In addition, these findings will be discussed in the light of the evolution of
60 terrestrial feeding in early tetrapods by means of a comparison of hyoid kinematics between this
61 terrestrially feeding fish (i.e., mudskipper), a typical suction-feeding fish of generalized
62 morphology (*in casu* sunfish), and a model species for a tongue-using, basal terrestrial tetrapod
63 (*in casu* newt).

64 **Methods**

65 **Animals**

66 Five adult *Periophthalmus barbarus* (Linnaeus, 1766) (9.9 ± 1.8 cm standard length) originating
67 from Nigeria were obtained commercially. One additional adult individual was sacrificed using
68 an overdose of MS-222 (Sigma Chemical) and used for computed tomography (CT) scanning
69 (scanning protocol described previously in [8]). The four live animals were housed in individual
70 Plexiglas aquaria (35 x 18 x 30 cm) during testing and recording. The aquaria were equipped
71 with a Plexiglas ramp and a terrestrial excursion area with a transparent floor and sides. A
72 constant temperature of 27°C was maintained, with a 12:12 h light:dark cycle. The same set-up
73 was used to house two *Triturus carnifex* individuals (75 mm and 77 mm snout-to-vent length) to
74 be used for X-ray video recordings. These animals were collected in Lower Austria, Austria

75 with collection permission RU5-BE-18/022-2011 granted by the local government of Lower
76 Austria. *Lepomis gibbosus* (74 mm standard length) was wild-caught in Belgium and housed at a
77 room temperature of 20°C. All of the specimens used in this study were handled according to
78 University of Antwerp Animal Care protocols.

79 Kinematic analysis

80 Simultaneous high-speed videos were captured from lateral and ventral views of *P. barbarus*
81 feeding on pieces of Brown shrimp presented on the bottom of the terrestrial section of the
82 aquarium using two Redlake cameras (1280 × 1024 pixels; Redlake, San Diego, CA), a Redlake
83 MotionPro HS1000 and a MotionScope M3, at 500 frames per second. Several bright LEDs
84 provided the necessary illumination. The food items provided were approximately 7.5 mm in
85 length, which was somewhat less than 80% of the maximal gape size of the fish. At least five
86 prey-capture videos were recorded for each individual. Two video pairs per individual were
87 selected from these videos based on the quality of the image sharpness and contrast, to be used
88 for further analysis.

89 In addition to the external video recordings, high-speed X-ray videos were obtained for each of
90 the four individuals. These recordings were made using a Philips Optimus M 200 X-ray
91 generator (Royal Philips Electronics NV, Eindhoven, Netherlands) coupled to a 14 inch image
92 intensifier set to 6 inch zoom mode and a Redlake Motion Pro 2000 camera (1280 × 1024 pixels;
93 Redlake, San Diego, CA) recording at 500 frames per second. Prior to the recording sessions,
94 the animals were anesthetized using MS-222 to insert small, lead markers (<0.5 mm)
95 subcutaneously in close proximity to the dentary, premaxilla, hyoid, and skull roof using
96 hypodermic needles. The same procedure was followed for *L. gibbosus*. X-ray videos of *T.*
97 *carnifex* were recorded at 125 frames per second to improve image contrast. Two-dimensional

98 landmark coordinates were digitized using Didge (Alistair Collum, Creighton University, USA),
99 and were used to quantify the movement of the gape and hyoid during prey capture.

100 Volume and flow velocity modelling

101 The changes in the volume of the head and intra-oral cavities during feeding were calculated
102 using the approach described in a previous study on suction feeding in catfish [7]. This model is
103 based on the ellipse method for calculating the volume of biological objects using lateral and
104 ventral video recordings [22], and previously generated accurate predictions of suction flow
105 velocities in larval carp [22], snake-necked turtles [23], and air-breathing catfish [7]. The model
106 uses the upper and lower contour coordinates of the mudskipper's head excluding the eyes in the
107 lateral and ventral view. It also uses the coordinates of a longitudinal axis connecting the distal
108 tip of the operculum to the upper jaw tip. In the ventral view, this longitudinal axis was set from
109 the central point between the left and right opercula tips to the center of the snout tip. Next, the
110 contour coordinates were recalculated in the fish frame of reference for every frame of the
111 recording. Interpolation functions were used to extract the four corresponding contour
112 coordinates at 21 equally spaced intervals along the longitudinal axis. With these data, changes
113 in the width and height of the ellipses over time as well as changes in the volume of the 21
114 elliptical cylinders mimicking the head were calculated. For each elliptical cylinder, the profiles
115 of length and width versus time were filtered with a fourth-order zero-phase-shift low-pass
116 Butterworth filter to reduce landmark coordinate digitization noise (cut-off frequency of 15 Hz).
117 The internal dimensions of the oral and opercular cavities of the mudskipper at rest were
118 obtained through CT scan and scaled to match the head length of each individual animal. The
119 volume of the oral and opercular cavities was similarly divided into a series of 21 sections along
120 the same longitudinal axis as mentioned above. It was assumed that this situation (i.e., the

121 internal volume of the mouth cavity of the preserved specimen at rest) reflects the moment
122 before start of the prey-capture event. Subsequently, changes in the height and the width of the
123 head over time will cause changes in the width and height of the internal mouth volume ellipses
124 (assuming a constant volume for the head tissues the mudskipper). The law of continuity requires
125 each volume increase of the internal cavity to be filled with fluid immediately. This allowing
126 flow rates to be calculated as long as the mouth and opercular slits are not open at the same time,
127 which does not occur during terrestrial feeding in *P. barbarus*.

128 The height of the ellipses used in the model for *P. barbarus* were amended in function of the
129 movement of the hyoid. The high-speed X-ray videos showed the hyoid elevating between the
130 suspensoria without causing the outer contours to change from an external view. In order to
131 account for the change of internal volume of the oral cavity due to the externally invisible hyoid
132 elevation and depression, a spatiotemporal correction factor for hyoid movement was
133 implemented to the ellipse heights. This correction factor was based on the average profile of
134 hyoid movement (three captures \times two individuals). The amplitude and timing of the ellipse-
135 height correction factor was scaled to match the size of each individual and the timing of each
136 prey-capture event.

137 **Results**

138 Our biomechanical analysis based on dual-view high-speed videos and X-ray videos showed that
139 terrestrial capture and intra-oral food transport in *Periophthalmus barbarus*, the Atlantic
140 mudskipper, could best be described as a “hydrodynamic tongue”. As soon as the mouth starts
141 opening while pivoting the head about the pectoral fins to approach the prey, a convex meniscus
142 of buccal water was observed at the mouth aperture (Fig. 1b,c; first column). This water further

143 protruded out of the mouth (Fig. 1b,c; second column) and just before the jaws were placed
144 around the prey, the water contacted the prey and spread along the surface surrounding the prey
145 (Fig. 1b,c; third column). While the jaws were closing and the prey was engulfed, part of the
146 expelled water was sucked back into the buccal cavity (Fig. 1b,c; fourth and fifth columns) (see
147 Movie S1). Often, a single cycle of the gape and hyoid was sufficient to engulf and transport
148 prey to the pharyngeal jaw region of the buccal cavity (Fig. 1d) (see Movie S2). As this
149 “protrusion” and “retraction” of buccal water showed kinematical and functional resemblance to
150 tongue movement during feeding in lower tetrapods, we refer to it as a “hydrodynamic tongue”.
151 Note that this definition of a “hydrodynamic tongue” differs from previous uses of this term to
152 describe the more common intra-oral, posterior-flow-driven transport of prey by aquatic fishes
153 [24].

154 Mathematical modelling of the volume changes of the head and resulting intra-oral water
155 displacements (Fig. 1e) confirmed the forward and backward motion of the water observed
156 externally at the mouth region (Fig. 1b,c). Before the lunge at the prey, the small, valvular slits
157 at the dorso-posterior side of the opercula were closed. Consequently, the connected opercular
158 and buccal volumes could be regarded as a vessel with a small opening at the side of the mouth.
159 While the mudskipper accelerated forward and pivoted down towards the prey, the left and right
160 gill covers were adducted (on average between 0.1 and 0.025 s before the time of maximal
161 mouth opening) (zone p1 on Fig. 2a), and the hyoid was elevated (between 0.05 and 0.02 s
162 before the time of maximal mouth opening) (zone p2 on Fig. 2a). Because water is
163 incompressible, the decrease in volume resulting from these motions resulted in a flow of water
164 towards the mouth (first and second frame in Fig. 1e; time -0.10 to -0.02 in Fig. 2b). As this all
165 happened during forward acceleration of the head (peak accelerations approximately 6 m s^{-2}), the

166 inertia of the water mass cannot cause the anterior flow of water. This means that these
167 compressive motions were powered actively by the mudskipper's cranial muscles.

168 After the opercular and buccal compression caused protrusion of the hydrodynamic tongue, the
169 head volume increased and suction was generated. This expansion started just before the mouth
170 became maximally opened (time = 0 s) and occurred at the level of the hyoid and suspensorium
171 (zone p3 in Fig. 2a) and at the gill covers (zone p4 in Fig. 2a). Fluid flow velocities during
172 suction, which may partly include flows of air, were maximal very close to the time of maximal
173 gape and reach average peak values of 0.6 m s^{-1} at the mouth entrance (Fig. 2b). During the final
174 instants of opercular expansion (time = 0.07 s), the opercular slits opened. At the same time, the
175 mouth became fully closed. From this instant on, the opercular and buccal volumes could be
176 treated as a vessel with an opening at the opercular slits. Next, an anterior-to-posterior wave of
177 compression of the head (zone p5 in Fig. 2a) was formed to cause further posteriorly directed,
178 relatively low-speed fluid flow (Fig. 2b).

179 The opercular and buccal cavities were not always filled with water to the same level. Although
180 the volumetric changes described above occurred consistently, water was not always observed
181 protruding out of the mouth during feeding. To test the necessity of the hydrodynamic tongue for
182 terrestrial feeding, additional feeding events were recorded with high-speed X-ray video while a
183 high-performance absorbent was placed beneath the prey items to absorb the water expelled from
184 the buccal cavity. After this decrease of hydrodynamic tongue volume, the mudskipper was still
185 capable of grabbing the prey between the jaws. However, intra-oral transport of prey to the
186 pharyngeal jaws or oesophagus entrance without returning to the water was unsuccessful in 70%
187 of the feeding sequences (N = 18) (see Movie S3). Under normal circumstances, we observed
188 terrestrial feeding including unsuccessful intra-oral transport before moving out of the view of

189 the cameras in 36% of the cases (N = 24). This shows that the hydrodynamic tongue fails without
190 sufficient intra-oral water.

191 The mudskipper's hyoid motion pattern during terrestrial feeding was different from the general
192 pattern observed for aquatic feeding in fish. During suction feeding of a morphologically
193 generalized perciform fish, e.g., the pumpkinseed sunfish *Lepomis gibbosus*, depression of the
194 hyoid shortly followed the onset of mouth opening and reached its peak velocity near the instant
195 of maximum mouth opening, as exemplified with marker tracking on X-ray video (Fig. 3a),
196 which confirms previous kinematical results based on visible light video [25]. In terrestrially
197 feeding mudskippers, however, hyoid elevation persisted during the entire mouth opening phase,
198 and depression only started after the onset of mouth closing (Fig. 3b).

199 In contrast, a striking resemblance is observed between the kinematics of the hyoid underlying
200 the hydrodynamic tongue in the mudskipper and that of the hyobranchial elements supporting the
201 true tongue of salamandrids. Position tracking of a radio-opaque marker adhering to the tongue
202 skeleton of the Italian crested newt (*Triturus cristatus*) capturing prey on land during X-ray video
203 recordings showed elevation until past the time of maximum gape and a similarly long hyoid
204 depression delay as in mudskippers (Fig. 3b,c). This hyobranchial elevation helps to protrude
205 the tongue while the subsequent hyobranchial depression causes the tongue to be retracted [16].

206 **Discussion and conclusions**

207 The water retained in the buccal and opercular cavity of Atlantic mudskippers has a vital role
208 during terrestrial feeding. As the protrusion and retraction of this water mass was indispensable
209 for intra-oral transport of prey on land, this hydrodynamic tongue empowers mudskippers to
210 capture and swallow several prey sequentially without having to return to the water for

211 swallowing. In contrast, a different fish species previously described to capture prey on land, the
212 eel-catfish (*Channallabes apus*), does not hold water inside the mouth cavity, and always returns
213 immediately to the water for swallowing after having grabbed the prey between the jaws [14,
214 26]. Other species that only sporadically capture food on the shores, such as aquatic emydid
215 turtles [27] or pipid frogs [28], are also obligatory underwater swallows. Consequently, the
216 capacity to feed on multiple prey during terrestrial foraging, owing to their hydrodynamic
217 tongue, bring mudskippers up to a higher level of terrestrialization compared to these species.

218 Our results suggest that fish adapted to use a hydrodynamic tongue for feeding and swallowing
219 on land are likely to evolve a similar hyoid motion pattern as observed in primitive tetrapods
220 using an adhesive tongue to capture prey on land. Although the difference in hyoid kinematics
221 between the mudskipper and the aquatic suction-feeding sunfish is substantial (Fig. 3), a small
222 amount of buccal compression including hyoid elevation during a short time prior to expansion
223 has also been noted in preparation of aquatic suction feeding in several fish species [29-31]. Yet,
224 the amount of hyoid elevation and delay in depression relative to mouth opening in the
225 mudskipper is unprecedented in fish. Nevertheless, it is more likely that the cranial kinematics
226 of terrestrial feeding in mudskippers (Fig. 2, Fig. 3b) is derived from this preparatory phase of
227 aquatic suction feeding, rather than being the result of a newly gained motor pattern.

228 The evolution of prey prehension and swallowing by the tongue is considered to be a major step
229 in the terrestrialization of vertebrates [17]. However, due to the scarcity of fossil records of
230 hyobranchial elements of early tetrapods, reconstruction of the skeletal changes associated with
231 the evolution of an adhesive tongue is not possible [32]. Consequently, we are forced to rely
232 almost exclusively on mechanistic scenarios using information from modern systems subjected
233 to similar selection pressures to gain insight on how an adhesive tongue can evolve [1, 33].

234 Although tetrapodomorphs and modern sarcopterygians clearly differ in morphology from
235 mudskippers, the main functional elements of the mudskipper's hydrodynamic tongue are also
236 present in these groups: a hyoid capable of dorsal and ventral rotation, and adductable and
237 abductable gill covers (Fig. 2) [34, 35]. Similar usage of intra-oral water for terrestrial transport
238 of prey at some stage during early evolution of the tetrapod lineage can therefore not be excluded
239 *a priori* on morphological grounds.

240 The remarkable similarity in the hyoid's motion pattern between mudskippers and tongue-
241 protruding newts (Fig. 3b,c) calls for a reconsideration of the current general hypothesis about
242 the evolution of terrestrial feeding behavior in early tetrapods. This hypothesis states that
243 terrestrial prey *transport* by the tongue evolved first, while prey *capture* by a protruding tongue
244 is gained subsequently [36-38]. This hypothesis is based on kinematic similarity between the
245 externally observable hyoid depressions performed by suction feeding fish (see Fig. 3a) and the
246 depressing hyoid region of terrestrial salamanders during intra-oral transport of prey [36-38].
247 However, a fundamental hiatus in this hypothesis is that the tongue-based intra-oral transport by
248 modern terrestrial salamanders moves a prey that is already brought deep into the mouth cavity
249 by the foregoing protrusion and retraction of the tongue: it does not explain how the first land-
250 dwelling tetrapods managed to bring prey inside their mouth cavity. Consequently, this
251 hypothesis presents an incomplete scenario of the evolution of terrestrial feeding.

252 We propose two possible scenarios for the evolution of terrestrial feeding capability in early
253 tetrapods. A first one completes the classical hypothesis described above, while a second one
254 proposes mudskipper-like usage of buccal water to transport and swallow food on land to be an
255 intermediate evolutionary stage:

256 (1) Kinetic inertial transport of prey (i.e., generating a posterior shift of the prey by forward
257 accelerations of the head as observed in crocodilians [39] or monitor lizards [40] was
258 evolutionary gained to move prey from being held by the jaws to the level of the hyoid
259 inside the mouth cavity. A tongue evolved to perform salamander-like prey-transport
260 cycles to complete the final stages of intra-oral transport without using water, thereby
261 retaining the ancestral hyoid motion patterns of aquatic suction feeding [33].

262 (2) A tongue evolved to move prey grabbed in between the jaws. Doing so, an elevation
263 followed by a depression of the floor of the mouth by the hyoid skeleton is retained from a
264 behavior using buccal water for prey transport similar to mudskippers. Independence of
265 water for prey transport is gained by achieving closer contact between the elevated hyoid
266 and prey, coupled with the evolution of adhesive structures. A tongue able to protrude out
267 of the mouth is a logical extension of this behavior.

268 It remains an open question which of these two scenarios is the most plausible. The generally
269 large size of early tetrapods, and the presence of a mobile neck in tetrapodomorph fishes [6]
270 and in the earliest known terrestrial tetrapods [41] could be indicative of kinetic inertial
271 transport possibilities in analogy with the feeding style of crocodilians and monitor lizards.
272 However, modern tetrapods show no evidence for an intermediate evolutionary step in
273 combining tongue-retraction transport with foregoing inertial transport: feeding behaviors of
274 reptiles mapped on a phylogenetic tree suggests that their ancestor already used a protruding
275 tongue to capture prey, and so do virtually all extant amphibians that feed on land [42]. The
276 latter may be indicative of a tongue evolving directly to mediate in intra-oral food uptake close
277 to or outside the jaws, which is in line with the second scenario. In that case, kinematic patterns
278 of water-mediated, terrestrial feeding similar to the one discovered here for mudskippers, may

279 have been important precursor behaviors in the colonization of land. An already established
280 kinematic pattern of the future tongue-bone could then allow a gradual anatomical
281 specialization towards water-independent terrestrial feeding through the increase of the
282 adhesive capacity of the tissues that eventually will form the tongue.

283 **Ethics**

284 All experiments conducted on the animals for this study were approved by the University of
285 Antwerp ethical animal welfare committee.

286 All of the specimens used in this study were handled according to University of Antwerp Animal
287 Care protocols.

288 **Data accessibility**

289 The datasets supporting this article have been uploaded as part of the Supplementary Material.

290 **Competing interest**

291 We have no competing interests

292 **Author contributions**

293 All authors contributed in collecting data; K.B.M. analysed the data. K.B.M and S.V.W. wrote
294 the manuscript; all authors discussed the results and commented on the manuscript.

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301 **References:**

- 302 1. Hsieh, S.-T.T. 2010 A locomotor innovation enables water-land transition in a marine fish.
303 *PloS one* **5**, e11197.
- 304 2. Shubin, N.H., Daeschler, E.B. & Jenkins, F.A., Jr. 2006 The pectoral fin of Tiktaalik roseae
305 and the origin of the tetrapod limb. *Nature* **440**, 764-771. (doi:10.1038/nature04637).
- 306 3. Ijspeert, A.J., Crespi, A., Ryzko, D. & Cabelguen, J.M. 2007 From swimming to walking
307 with a salamander robot driven by a spinal cord model. *science* **315**, 1416-1420.
308 (doi:10.1126/science.1138353).
- 309 4. Pierce, S.E., Clack, J.A. & Hutchinson, J.R. 2012 Three-dimensional limb joint mobility in the
310 early tetrapod Ichthyostega. *Nature* **486**, 523-526. (doi:10.1038/nature11124).
- 311 5. Ashley-Ross, M.A., Hsieh, S.T., Gibb, A.C. & Blob, R.W. 2013 Vertebrate land invasions-
312 past, present, and future: an introduction to the symposium. *Integr Comp Biol* **53**, 192-196.
313 (doi:10.1093/icb/ict048).
- 314 6. Daeschler, E.B., Shubin, N.H. & Jenkins, F.A., Jr. 2006 A Devonian tetrapod-like fish and the
315 evolution of the tetrapod body plan. *Nature* **440**, 757-763. (doi:10.1038/nature04639).
- 316 7. Van Wassenbergh, S., Aerts, P. & Herrel, A. 2006 Scaling of Suction Feeding Performance in
317 the Catfish *Clarias gariepinus**. *Physiological and Biochemical Zoology* **79**, 43-56.
- 318 8. Michel, K.B., Adriaens, D., Aerts, P., Dierick, M. & Wassenbergh, S.V. 2014 Functional
319 anatomy and kinematics of the oral jaw system during terrestrial feeding in *Periophthalmus*
320 *barbarus*. *Journal of morphology* **275**, 1145-1160. (doi:10.1002/jmor.20291).

- 321 9. Alexander, R. 1970 Mechanics of the feeding action of various teleost fishes. *Journal of*
322 *Zoology* **162**, 145-156.
- 323 10. Muller, M. & Osse, J. 1984 Hydrodynamics of suction feeding in fish. *The Transactions of*
324 *the Zoological Society of London* **37**, 51-135.
- 325 11. Muller, M. 1989 A Quantitative Theory of Expected Volume Changes of the Mouth during
326 Feeding in Teleost Fishes. *Journal of Zoology* **217**, 639-661.
- 327 12. Aerts, P. 1991 Hyoid Morphology and Movements Relative to Abducting Forces during
328 Feeding in *Astatotilapia-Elegans* (Teleostei, Cichlidae). *Journal of morphology* **208**, 323-345.
329 (doi:DOI 10.1002/jmor.1052080308).
- 330 13 Herrel, A., Van Wassenbergh, S. & Aerts, P. 2012 Biomechanical Studies of Food and Diet
331 Selection. *eLS*. (doi:10.1002/9780470015902.a0003213.pub2).
- 332 14. Van Wassenbergh, S. 2013 Kinematics of terrestrial capture of prey by the eel-catfish
333 *Channallabes apus*. *Integr Comp Biol* **53**, 258-268. (doi:10.1093/icb/ict036).
- 334 15. Bramble, D.M. & Wake, D. 1985 Feeding mechanisms of lower tetrapods. In *Functional*
335 *vertebrate morphology* (ed. D.M.B. M. Hildebrand, K. F. Liem, D. B. Wake), pp. 230-261.
336 Cambridge, Harvard University Press.
- 337 16. Miller, B.T. & Larsen, J.H. 1990 Comparative Kinematics of Terrestrial Prey Capture in
338 Salamanders and Newts (Amphibia, Urodela, Salamandridae). *Journal of Experimental Zoology*
339 **256**, 135-153. (doi:DOI 10.1002/jez.1402560204).

- 340 17. Reilly, S.M. & Lauder, G.V. 1989 Kinetics of Tongue Projection in *Ambystoma-Tigrinum* -
341 Quantitative Kinematics, Muscle Function, and Evolutionary Hypotheses. *Journal of*
342 *morphology* **199**, 223-243. (doi:DOI 10.1002/jmor.1051990208).
- 343 18. Markey, M.J. & Marshall, C.R. 2007 Terrestrial-style feeding in a very early aquatic tetrapod
344 is supported by evidence from experimental analysis of suture morphology. *Proceedings of the*
345 *National Academy of Sciences of the United States of America* **104**, 7134-7138. (doi:DOI
346 10.1073/pnas.0701706104).
- 347 19. Sponder, D.L. & Lauder, G.V. 1981 Terrestrial feeding in the mudskipper *Periophthalmus*
348 (*Pisces, teleostei*) - a cineradiographic analysis. *Journal of Zoology* **193**, 517-530.
- 349 20. Stebbins, R.C. & Kalk, M. 1961 Observations on the natural history of the mud-skipper,
350 *Periophthalmus sobrinus*. *Copeia* **1961**, 18-27.
- 351 21. Clayton David, A. 1993 Mudskippers. In *Oceanogr. Mar. Biol. Annu. Rev* (pp. 507-577.
352 Aberdeen, Aberdeen University Press.
- 353 22. Drost, M.R. & Vandenboogaart, J.G.M. 1986 A Simple Method for Measuring the Changing
354 Volume of Small Biological Objects, Illustrated by Studies of Suction Feeding by Fish Larvae
355 and of Shrinkage Due to Histological Fixation. *Journal of Zoology* **209**, 239-249.
- 356 23. Aerts, P., Van Damme, J. & Herrel, A. 2001 Intrinsic mechanics and control of fast cranio-
357 cervical movements in aquatic feeding turtles. *American Zoologist* **41**, 1299-1310.
- 358 24. Liem, K.F. 1990 Aquatic Versus Terrestrial Feeding Modes - Possible Impacts on the
359 Trophic Ecology of Vertebrates. *American Zoologist* **30**, 209-221.

- 360 25. Lauder, G.V. 1980 Evolution of the feeding mechanism in primitive actionopterygian fishes:
361 a functional anatomical analysis of Polypterus, Lepisosteus, and Amia. *Journal of morphology*
362 **163**, 283-317.
- 363 26. Van Wassenbergh, S., Herrel, A., Adriaens, D., Huysentruyt, F., Devaere, S. & Aerts, P.
364 2006 Evolution: a catfish that can strike its prey on land. *Nature* **440**, 881.
365 (doi:10.1038/440881a).
- 366 27. Stayton, C.T. 2011 Terrestrial feeding in aquatic turtles: environment-dependent feeding
367 behavior modulation and the evolution of terrestrial feeding in Emydidae. *The Journal of*
368 *experimental biology* **214**, 4083-4091. (doi:10.1242/jeb.060574).
- 369 28. Measey, G.J. 1998 Terrestrial prey capture in *Xenopus laevis*. *Copeia*, 787-791.
- 370 29. Lauder, G. 1985 Aquatic feeding in lower vertebrates. In *Functional vertebrate morphology*
371 (ed. D.M.B. M. Hildebrand, K. F. Liem, D. Wake), pp. 210-229. Cambridge, Massachusetts,
372 Harvard Univ. Press.
- 373 30. Hernandez, L.P., Barresi, M.J. & Devoto, S.H. 2002 Functional morphology and
374 developmental biology of zebrafish: reciprocal illumination from an unlikely couple. *Integr*
375 *Comp Biol* **42**, 222-231. (doi:10.1093/icb/42.2.222).
- 376 31. Sanford, C.P.J. & Wainwright, P.C. 2002 Use of sonomicrometry demonstrates the link
377 between prey capture kinematics and suction pressure in largemouth bass. *Journal of*
378 *Experimental Biology* **205**, 3445-3457.

- 379 32. Schoch, R.R. 2001 Can metamorphosis be recognised in Palaeozoic amphibians? *Neues*
380 *Jahrb Geol P-A* **220**, 335-367.
- 381 33. Reilly, S. 1996 The metamorphosis of feeding kinematics in *Salamandra salamandra* and the
382 evolution of terrestrial feeding behavior. *The Journal of experimental biology* **199**, 1219-1227.
- 383 34. Downs, J.P., Daeschler, E.B., Jenkins, F.A., Jr. & Shubin, N.H. 2008 The cranial
384 endoskeleton of *Tiktaalik roseae*. *Nature* **455**, 925-929. (doi:10.1038/nature07189).
- 385 35. Bemis, W.E. & Lauder, G.V. 1986 Morphology and function of the feeding apparatus of the
386 lungfish, *Lepidosiren paradoxa* (Dipnoi). *Journal of morphology* **187**, 81-108.
387 (doi:10.1002/jmor.1051870108).
- 388 36. Reilly, S.M. & Lauder, G.V. 1990 The Evolution of Tetrapod Feeding-Behavior - Kinematic
389 Homologies in Prey Transport. *Evolution* **44**, 1542-1557. (doi:10.2307/2409336).
- 390 37. Gillis, G. & Lauder, G. 1995 Kinematics of feeding in bluegill sunfish: is there a general
391 distinction between aquatic capture and transport behaviors? *Journal of Experimental Biology*
392 **198**, 709-720.
- 393 38. Reilly, S. 1995 The ontogeny of aquatic feeding behavior in *Salamandra salamandra*:
394 stereotypy and isometry in feeding kinematics. *The Journal of experimental biology* **198**, 701-
395 708.
- 396 39. Cleuren, J. & Devree, F. 1992 Kinematics of the Jaw and Hyolingual Apparatus during
397 Feeding in *Caiman-Crocodilus*. *Journal of morphology* **212**, 141-154. (doi:DOI
398 10.1002/jmor.1052120205).

399 40. Elias, J.A., McBrayer, L.D. & Reilly, S.M. 2000 Prey transport kinematics in Tupinambis
400 teguixin and *Varanus exanthematicus*: conservation of feeding behavior in ‘chemosensory-
401 tongued’ lizards. *Journal of Experimental Biology* **203**, 791-801.

402 41. Ahlberg, P.E., Clack, J.A. & Blom, H. 2005 The axial skeleton of the Devonian tetrapod
403 *Ichthyostega*. *Nature* **437**, 137-140. (doi:10.1038/nature03893).

404 42. Nishikawa, K. & Schwenk, K. 2001 Ingestion in Reptiles and Amphibians. *eLS*.
405 (doi:10.1038/npg.els.0001835).

406

407 **Figure captions**

408 **Fig.1.** Morphology and kinematics of terrestrial feeding in *Periophthalmus barbarus*. (A) Cut-
409 out section of a scanning 3D-reconstruction illustrates the anatomical elements and their colour
410 codes. Ventral view (B) and lateral view (C) high-speed video frames showing successive stages
411 of feeding, and illustrating the water protruding out of the mouth (light blue contours). X-ray
412 video frames at identical stages are shown in (D) and the outlines of the jaws, hyoid and prey
413 (orange contours) are mapped. (E) Representation of the volumetric ellipse model with the
414 internal volume illustrated by white bars and the flow velocity at 20%, 50% and 80% of the head
415 length are shown by the direction, length and color of the arrows (see Fig. 2b for color legend).

416 **Fig. 2.** Intra-oral rate of cross-sectional area change and flow velocity during prey capture in
417 *Periophthalmus barbarus*. (A) Spatiotemporal-interpolated and averaged (2 captures \times 4
418 individuals) rate of change in the cross-sectional area as a function of the position along the
419 head, showing successive compression and expansion events (time 0 = maximal mouth opening).
420 (B) The corresponding intra-oral flow velocities along the anterior-to-posterior axis showing
421 initially forward (blue colouring) and then backward motion (yellow to red colouring) of fluid
422 with respect to the head (dashed line = zero flow velocity).

423 **Fig. 3.** Comparison of gape and hyoid kinematics during prey capture. Data are derived from
424 landmark tracking on high-speed X-ray videos with lead markers inserted subcutaneously (top
425 row; including the reference frames). A strong difference is observed between the hyoid
426 kinematics of a suction-feeding sunfish (A; 8 captures \times 1 individual) and the terrestrial capture
427 of prey by the mudskipper (B; 3 captures \times 2 individuals) (e.g., in hyoid depression delay or

428 hdd). The latter shows a striking resemblance with terrestrial feeding in newts (C; 4 captures \times 2
429 individuals). Error ribbons, 1 s.e.m.

430 **Supplementary material:**

431 *Supplementary movie S1*: Simultaneous lateral and dorsal view of *Periophthalmus barbarus*
432 feeding on land. Video playback is slowed down by 20 times from the original high-speed videos
433 recorded at 500 Hz.

434 *Supplementary movie S2*

435 Title: X-ray video of *Periophthalmus barbarus* capturing and swallowing prey on land. Markers
436 on the fish and prey allowed position tracking during feeding. Video playback is slowed down 50
437 times.

438 *Supplementary movie S3*

439 Title: X-ray video of terrestrial feeding by *Periophthalmus barbarus* on a substrate covered with
440 a high-performance absorbent material. The mudskipper successfully captures the prey with its
441 jaws, but then fails to perform intra-oral transport of prey on land. Video playback is slowed
442 down 50 times.





