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1 Cambrian cinctan echinoderms shed light on feeding in
2 the ancestral deuterostome

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17

18 **Abstract**

19

20 Reconstructing the feeding mode of the latest common ancestor of deuterostomes is key to
21 elucidating the early evolution of feeding in chordates and allied phyla; however, it is debated
22 whether the ancestral deuterostome was a tentaculate feeder or a pharyngeal filter feeder. To
23 address this, we evaluated the hydrodynamics of feeding in a group of fossil stem-group
24 echinoderms (cinctans) using computational fluid dynamics. We simulated water flow past
25 three-dimensional digital models of a Cambrian fossil cinctan in a range of possible life
26 positions, adopting both passive tentacular feeding and active pharyngeal filter feeding. The
27 results demonstrate that an orientation with the mouth facing downstream of the current was
28 optimal for drag and lift reduction. Moreover, they show that there was almost no flow to the
29 mouth and associated marginal groove under simulations of passive feeding, whereas
30 considerable flow towards the animal was observed for active feeding, which would have
31 enhanced the transport of suspended particles to the mouth. This strongly suggests that
32 cinctans were active pharyngeal filter feeders, like modern enteropneust hemichordates and
33 urochordates, indicating that the ancestral deuterostome employed a similar feeding strategy.

34

35 **Keywords:**

36 echinoderms, deuterostomes, evolution, feeding, functional morphology, computational fluid
37 dynamics

38

39

40 **1. Introduction**

41

42 Deuterostomes are one of the three major clades of bilaterian animals. Molecular
43 phylogenetics has helped resolve the relationships of the main deuterostome phyla (chordates,
44 echinoderms and hemichordates) [1–3], but despite extensive study of their anatomy,
45 development and phylogeny for over a century, important aspects of the early evolutionary
46 history of deuterostomes remain unclear [4]. Feeding is one such outstanding issue; it was
47 long speculated that the ancestral deuterostome had tentacles for collecting food from the
48 water column, like modern crinoids and pterobranch hemichordates [5–7], but more recently
49 it has been proposed that it had a pharynx with gill slits for actively generating feeding
50 currents, similar to enteropneust hemichordates, urochordates, cephalochordates and larval
51 lampreys [8–10]. Distinguishing between these competing hypotheses is problematic because
52 it is disputed whether the latest common ancestor of deuterostomes had a pterobranch-like
53 body plan (with tentacular feeding), or an enteropneust-like body plan (with pharyngeal filter
54 feeding) [4].

55

56 The fossil record provides an alternative means of differentiating these two hypotheses
57 through the inference of feeding modes in the earliest fossil forms, and could thus inform on
58 the ancestral feeding strategy of deuterostomes. Although the early record of most
59 deuterostome phyla is patchy and incomplete [4], echinoderms possess a rich record dating
60 back to the Cambrian [11,12] because a mineralized skeleton was among their first derived
61 traits [13]. Several groups of pre-radiate fossil stem-group echinoderms (*Ctenoimbricata*,
62 ctenocystoids and cinctans) are especially important, as they document the earliest steps in
63 the assembly of the echinoderm body plan and retain plesiomorphic characters of the
64 ancestral deuterostome [14–16]. Cinctans are the best understood of these groups in terms of
65 their anatomy and functional morphology, and so have the greatest potential for elucidating
66 deuterostome evolution; however, their mode of feeding is controversial. It is widely

67 accepted that cinctans were sessile epibenthic suspension feeders with an anterolateral mouth
68 and one or a pair of marginal grooves [7,14,17–20], but it is debated whether they were
69 passive suspension feeders with a system of tentacles, analogous to crinoids [19,20], or active
70 pharyngeal filter feeders, similar to urochordates [14,21].

71

72 In order to evaluate competing hypotheses of cinctan feeding mode, we quantitatively
73 analysed the functional performance of a Cambrian fossil cinctan. Using three-dimensional
74 computational fluid dynamics (CFD), we simulated flow past a digital reconstruction of the
75 fossil in a range of different positions relative to the current direction and the sediment–water
76 interface, approximating both hypothesized feeding scenarios. The results provide new
77 insights into the hydrodynamics of feeding in cinctans, with implications for the
78 plesiomorphic mode of feeding in deuterostomes.

79

80

81 **2. Material and methods**

82

83 **(a) Fossil specimen**

84 The holotype of the cinctan *Protocinctus mansillaensis* (MPZ 2004/170; Museo
85 Paleontológico de la Universidad de Zaragoza, Spain) was selected for use in CFD
86 simulations owing to its exceptional three-dimensional preservation as recrystallized calcite.
87 This species comes from the Mansilla Formation of Purujosa, north-east Spain, which is early
88 middle Cambrian (Cambrian Series 3, Stage 5) in age (~510 Ma) and is characterized by
89 purple to reddish nodular limestones and shales, indicative of a shoreface to offshore
90 depositional setting. Like all cinctans, *Protocinctus* has a flattened, asymmetrical body

91 (theca) and a rigid posterior appendage. A circular mouth is located on the anterior right side
92 of the theca; a larger exhalant aperture (the porta) is situated at the anterior midline of the
93 theca, covered by a movable plate (the operculum). *Protocinctus* is also characterized by an
94 elongate, oval-shaped theca, a single left marginal groove and a weakly-developed ventral
95 swelling at the anterior (figure 1a).

96

97 **(b) X-ray micro-tomography**

98 The fossil was scanned with a Phoenix v|tome|x s system and digitally reconstructed using
99 the SPIERS software suite [22]. See Rahman and Zamora [23] for details. A ZIP archive
100 containing the digital reconstruction in VAXML format can be downloaded from Dryad
101 (doi:10.5061/dryad.g4n5m).

102

103 **(c) Digital restoration**

104 In order to restore the poorly-preserved upper surface of the studied specimen, the dorsal
105 integument and the operculum were virtually extrapolated in SPIERS with a closed spline
106 (using other specimens in which the upper surface is better preserved as a reference). The
107 operculum was restored in two hypothetical life positions: (1) ‘closed’, with the porta entirely
108 covered by the operculum (figure 1b) and (2) ‘open’, with the operculum raised above the
109 porta (figure 1c). These reconstructions were then optimized with a low smoothing value to
110 remove noise, and converted into NURBS surfaces using Geomagic Studio
111 (www.geomagic.com) (models can be downloaded from Dryad: doi:10.5061/dryad.g4n5m).

112

113 **(d) Computational fluid dynamics simulations**

114 CFD simulations of water flow around *Protocinctus* were performed using COMSOL
115 Multiphysics (www.uk.comsol.com). The computational domain consisted of a three-

116 dimensional volume above a flat solid boundary (85 mm in length and 17.5 mm in diameter),
117 on which the *Protocinctus* reconstruction (23 mm in length and 10 mm in width) was
118 centrally fixed (electronic supplementary material, figure S1a). Flow was simulated through
119 this domain with an initially uniform inflow velocity at the upstream end and an outflow
120 boundary condition (zero pressure gradient across the boundary) at the downstream end. Slip
121 conditions (zero stress across the boundary) were used for the domain sides and top, with no-
122 slip conditions (zero velocity relative to the boundary) for the solid surfaces of the
123 reconstruction and the underlying base. The flow domain was a semi-cylinder and was
124 sufficiently large that the boundary conditions did not influence the flow. The domain was
125 meshed using free tetrahedral elements (electronic supplementary material, figure S1b), with
126 mesh resolution fully tested to ensure grid scale independence for the simulation results
127 (electronic supplementary material, sensitivity analyses).

128

129 A total of 100 simulations were undertaken, using a range of input parameters (electronic
130 supplementary material, table S1). In all cases, three-dimensional, incompressible (constant
131 density) flow of water was simulated, with the *Protocinctus* reconstruction held stationary.
132 Ambient flow velocities of 0.05, 0.1 or 0.2 m/s (Reynolds numbers of 525–925, 1050–1850
133 and 2100–3700, respectively; width of the specimen in the flow taken as the characteristic
134 dimension) were simulated to approximate typical near-bottom currents in modern shoreface
135 to offshore environments [24]. A stationary solver was used to compute the steady-state flow
136 patterns and a laminar flow model was used to solve the Navier-Stokes equations for
137 conservation of momentum and the continuity equation for conservation of mass. The effects
138 of varying the solver type and flow model were examined for the higher Reynolds number
139 flows (electronic supplementary material, sensitivity analyses). In addition, experimental
140 studies of flow around a 3-D printed model of *Protocinctus* were carried out in a flume tank

141 for comparison with the computer simulations (electronic supplementary material, flume tank
142 experiments, figure S2).

143

144 Three different feeding scenarios were simulated. (1) Passive tentacular feeding using the
145 closed *Protocinctus* reconstruction with the mouth cross-section allowing flow to pass
146 through (outflow boundary). (2) The inhalant current of active pharyngeal filter feeding using
147 the closed *Protocinctus* reconstruction with flow velocity through the mouth cross-section
148 given a normal outflow velocity of 0.015 m/s. (3) The exhalant current of active pharyngeal
149 filter feeding using the open *Protocinctus* reconstruction with flow velocity through the
150 operculum cross-section given a normal inflow velocity of 0.04 m/s. The inhalant and
151 exhalant velocities of pharyngeal filter feeding were based on analogy with the extant
152 urochordate *Styela clava* [25].

153

154 To explore the hydrodynamic consequences of different life positions, all of the above
155 simulations were performed with the *Protocinctus* reconstruction oriented at 0°, 45°, 90°,
156 135° and 180° to the current, and with the ventral swelling positioned either below
157 (equivalent to burial within the sediment) or on top of (equivalent to resting on the sediment)
158 the lower boundary of the computational domain. The results were visualized as two-
159 dimensional cross-sections of flow velocity magnitude with flow vectors (arrows) and
160 streamlines. Drag and lift forces and their coefficients (projected frontal area taken as the
161 reference area) were calculated to quantify flow around the digital reconstructions.

162

163

164 **3. Results**

165

166 The results of the CFD simulations show that the overall characteristics of the flow around
167 the *Protocinctus* reconstruction conformed to expectations for boundary layer and wake
168 development. In all cases, the velocity decreased rapidly immediately upstream of the
169 *Protocinctus* reconstruction (figure 2; electronic supplementary material, figures S3–S8) and
170 a distinctive wake (elongate, low-velocity flow region, typically with an asymmetrical
171 vortex) was formed immediately downstream. The size and shape of the wake varied
172 depending on the orientation of the reconstruction to the current, but were not significantly
173 affected by the simulated feeding scenario, or the placement of the reconstruction in relation
174 to the lower boundary of the domain (figure 2; electronic supplementary material, figures S3–
175 S8). A characteristic boundary layer, shown by a rapid drop in velocity as the flow
176 approached the bottom of the domain, was well developed in all the simulations. The
177 thickness of the boundary layer was roughly equal to the height of the *Protocinctus*
178 reconstruction in both positions relative to the underlying base (figure 2).

179

180 Distinctly different flow patterns were associated with different feeding scenarios. Flow
181 vectors and streamlines indicate that the velocity of the flow into the mouth was greatest in
182 the simulations of the inhalant current generated by pharyngeal filter feeding (figure 2*g–l*;
183 electronic supplementary material, figures S5 and S6). This was most pronounced when the
184 *Protocinctus* reconstruction was oriented at 180° to the current. Conversely, in the
185 simulations where there was no inhalant current, flow into the mouth was generally much
186 weaker (figure 2*a–f, m–r*; electronic supplementary material, figures S3, S4, S7 and S8).
187 Flow to the marginal groove was very low for all the simulated feeding modes (electronic
188 supplementary material, figure S9).

189

190 In the simulations of the exhalant current produced by pharyngeal filter feeding, a jet of high-
191 velocity flow passed out of the porta, intruding into the ambient flow or the wake, depending
192 on the orientation of the reconstruction (figure 2*m-r*; electronic supplementary material,
193 figures S7 and S8). When the *Protocinctus* reconstruction was oriented at 0° to the current,
194 this jet directly opposed the ambient flow direction (electronic supplementary material,
195 figures S7*a-c* and S8*a-c*), whereas with the reconstruction oriented at 180° to the current, it
196 flowed in the same direction as the ambient flow, contributing to the wake (figure 2*m-r*).
197

198 Consistent with theoretical expectations, the drag force exerted by the reconstruction on the
199 fluid flow increased as the ambient velocity increased, whereas the drag coefficient
200 decreased. The lift force also increased with increasing ambient velocity. The orientation of
201 the reconstruction strongly influenced both the drag and lift forces and the lift coefficient,
202 which were greatest when the reconstructions were oriented at 45°, 90° or 135° to the current.
203 The reconstruction position relative to the domain bottom was likewise important, with the
204 drag and lift forces and the drag coefficient higher when the ventral swelling was positioned
205 on top of the lower boundary of the domain (figure 3; electronic supplementary material,
206 figures S10 and S11, tables S2 and S3).
207

208 The results of the simulations were not greatly influenced by varying the mesh size, solver or
209 flow type, with all these analyses producing very similar flow structures, drag and lift
210 (electronic supplementary material, figures S12–S14, table S4). Moreover, comparisons
211 between the experimental studies and the computer simulations showed that both approaches
212 obtained similar downstream current velocities (electronic supplementary material, figure
213 S15).
214

215

216 **4. Discussion**

217

218 CFD simulations indicate that orientation had a marked effect on the amount of drag
219 generated by *Protocinctus*, with the largest wake size and highest drag force occurring when
220 the reconstruction was oriented at 45°, 90° or 135° to the current (figure 3; electronic
221 supplementary material, figures S3–S8, table S2). The lift force and coefficient were also
222 greatest when the reconstruction was non-parallel to the current (figure 3; electronic
223 supplementary material, figure S11, table S3). Drag and lift can be detrimental to epibenthic
224 organisms, making it harder to maintain posture and even dislodging or injuring animals
225 [26,27]. While some suspension feeders seek to increase drag to aid feeding [26], this was
226 almost certainly not the case for *Protocinctus*, which exhibits a streamlined profile (figure 1)
227 that is clearly adapted to reduce drag parallel to the flow direction. Therefore, it seems most
228 probable (on functional grounds) that *Protocinctus* was preferentially oriented parallel to the
229 current in life, minimizing both drag and lift. Simulations with the reconstruction facing
230 upstream and downstream produced similar amounts of drag (figure 3; electronic
231 supplementary material, figure S10, table S2). However, the lift was substantially greater
232 when the reconstruction faced upstream (figure 3; electronic supplementary material, figure
233 S11, table S3). Moreover, the simulations of the exhalant current clearly show that the jet of
234 exhalant flow out of the porta would have been transported to the mouth by the ambient flow
235 if the reconstruction faced into the current (electronic supplementary material, figures S7a–c
236 and S8a–c). Because the porta is interpreted as an exhalant opening under both passive
237 [19,20] and active [14,21] feeding scenarios, an upstream orientation would have led to
238 fouling of the mouth and associated marginal groove in either mode of feeding.
239 Consequently, it can be inferred that cinctans were oriented downstream in life, and this

240 agrees with previous interpretations of cinctan functional morphology [7,19,21] and a
241 qualitative flume study [18], which suggested that an orientation with the mouth facing away
242 from the prevailing current would have enhanced feeding and/or stability.

243

244 The flow structure did not vary appreciably according to the position of *Protocinctus* relative
245 to the sediment–water interface, but the drag and lift forces were higher in the simulations of
246 the ventral swelling resting on top of the sediment surface (figure 3; electronic supplementary
247 material, tables S2 and S3). This suggests that a position with the ventral swelling buried was
248 optimal for reducing drag and lift, and might also have been beneficial for anchoring the
249 animal to the seafloor [17,28]. Regardless of the placement of the ventral swelling, however,
250 *Protocinctus* would always have been situated in the low-velocity boundary layer, with the
251 mouth and marginal groove close to the sediment surface (figure 2). This position has
252 implications for the interpretation of the animal’s mode of feeding. The simulations of
253 passive feeding with *Protocinctus* in a downstream orientation demonstrate that there was
254 almost no flow to the mouth and adjacent marginal groove (figure 2*a–f*; electronic
255 supplementary material, figure S9), indicating that the transport of suspended particles to the
256 animal would have been extremely limited. Nutrient flux is known to be very low within the
257 boundary layer [29], and modern passive suspension feeders typically possess specialized
258 food-capturing structures, such as fans, nets or tentacles, which are elevated above this zone,
259 where there are higher rates of flow and nutrient flux, to facilitate feeding [26,30]. There is
260 no evidence of such morphological adaptations in cinctans, which are characterized by a
261 flattened body with recumbent feeding structures (mouth and marginal groove). Thus, if
262 cinctans faced downstream (as argued above) and relied on external flows alone, they would
263 have had access to a very limited supply of nutrients, which was likely insufficient for
264 passive tentaculate feeding.

265

266 CFD simulations provide better support for an active pharyngeal filter feeding mode of life.
267 The inhalant current generated by *Protocinctus* channelled considerable flow towards the
268 animal (figure 2g–l), which would have enhanced the transport of suspended particles into the
269 mouth. Furthermore, simulations of active feeding with *Protocinctus* facing downstream
270 show that the exhalant jet ejected from the porta travelled above any recirculating flow in the
271 wake close to the mouth and marginal groove, avoiding potential contamination of feeding
272 currents (figure 2m–r). The same pattern is documented in extant pharyngeal filter feeders,
273 such as urochordates, which are capable of generating powerful exhalant flows that carry
274 wastewater beyond the mouth [25,26]. Consequently, simulations of both inhalant (figure 2g–
275 l) and exhalant (figure 2m–r) currents are compatible with pharyngeal filter feeding, and this
276 agrees with studies of cinctans that suggested such a feeding mode based on the functional
277 morphology of the porta–operculum complex and detailed comparisons with urochordates
278 [14,18,21].

279

280 Our findings are broadly in agreement with previous interpretations of the earliest fossil
281 stem-group echinoderms (*Ctenoimbricata*, ctenocystoids and cinctans) as pharyngeal filter
282 feeders [14–16], and argue against their interpretation as passive tentaculate feeders [19,20].
283 Among modern deuterostomes, active suspension feeding with pharyngeal gill slits is
284 documented in enteropneust hemichordates, urochordates, cephalochordates and larval
285 lampreys, while suspension feeding with tentacles characterizes crinoids and pterobranch
286 hemichordates. Owing to their position close to the base of echinoderm phylogeny, the
287 inference of pharyngeal filter feeding in cinctans allows us to extend this feeding mode back
288 to the latest common ancestor of all deuterostomes (figure 4). This provides strong support
289 for the hypothesis that the ancestral deuterostome fed through pharyngeal filtering [8–10],

290 indicating that a pharynx with gill slits is in all likelihood a deuterostome symplesiomorphy
291 and that the tentacular feeding systems of echinoderms and pterobranchs are most probably
292 not homologous.

293

294

295 **Data accessibility.** Digital models of *Protocinctus* and a video file can be downloaded from
296 Dryad (doi:10.5061/dryad.g4n5m).

297

298 **Competing interests.** We have no competing interests.

299

300 **Authors' contributions.** IAR and PLF conceived the study. IAR and JCP carried out CFD
301 simulations. IAR wrote the paper and prepared figures/tables. All authors analysed the data,
302 reviewed drafts of the paper and gave final approval for publication.

303

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314

315

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317

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396

397

398 **Figure captions**

399

400 **Figure 1.** *Protocinctus mansillaensis*. (a) Original fossil specimen (ventral view). (b) Digital
401 restoration with the operculum closed (anterolateral view). (c) Digital restoration with the
402 operculum open (anterolateral view). (d) Digital restoration with the operculum closed
403 (lateral view).

404

405 **Figure 2.** Results of the CFD simulations with *Protocinctus* oriented at 180° to the current,
406 visualized as two-dimensional plots (horizontal and vertical cross-sections) of flow velocity
407 magnitude (false-colour scale different for each ambient flow velocity) with flow vectors
408 (arrows; length of arrows proportional to the natural logarithm of the flow velocity
409 magnitude) and streamlines. (a–f) Simulations of passive tentacular feeding. (g–l)
410 Simulations of the inhalant current of pharyngeal filter feeding. (m–r) Simulations of the

411 exhalant current of pharyngeal filter feeding. The mouth is indicated by a *, the porta is
412 indicated by a +. The ambient flow is from left to right.

413

414 **Figure 3.** Drag and lift forces for the CFD simulations. (*a–c*) Simulations of passive
415 tentacular feeding. (*d–f*) Simulations of the inhalant current of pharyngeal filter feeding. (*g–i*)
416 Simulations of the exhalant current of pharyngeal filter feeding. Red symbols indicate drag
417 force, blue symbols indicate lift force. Triangles indicate results of simulations of the ventral
418 swelling resting on top of the sediment surface, circles indicate results of simulations of the
419 ventral swelling buried in the sediment.

420

421 **Figure 4.** Phylogeny showing feeding modes of extant and extinct deuterostomes (cinctans
422 marked with a †). Blue boxes indicate tentaculate suspension feeding, red boxes indicate
423 pharyngeal filter feeding, green boxes indicate multiple feeding modes.

424

425

426 **Electronic supplementary material**

427

428 **Supplementary Information.** Supplementary methods and figures.

429

430 **Table S1.** Input parameters for the CFD simulations.

431

432 **Table S2.** Drag force and coefficient for the CFD simulations.

433

434 **Table S3.** Lift force and coefficient for the CFD simulations.

435

436 **Table S4.** Drag and lift forces and their coefficients for the sensitivity analyses of mesh size,
437 solver and flow type.

438

439

440 **Data available on Dryad**

441

442 **Model S1.** Digital reconstruction of *Protocinctus* in VAXML format, compressed in a ZIP
443 archive. To view, unzip the .zip file and open the unpacked .vaxml file with SPIERSview
444 (program and documentation available from www.spiers-software.org).

445

446 **Model S2.** Digitally restored model of *Protocinctus* (operculum in ‘closed’ position) in IGES
447 format, compressed in a ZIP archive. To view, unzip the .zip file and open the unpacked .igs
448 file with FreeCAD (program and documentation available from www.freecadweb.org).

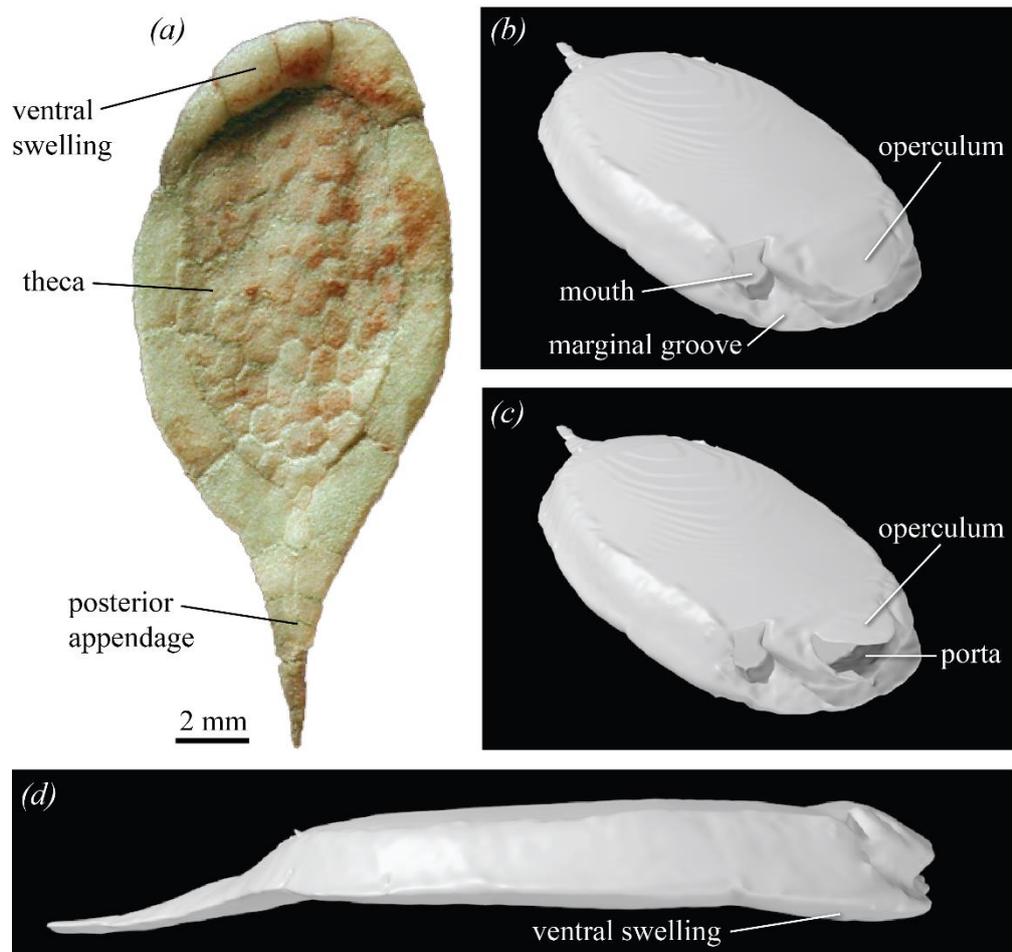
449

450 **Model S3.** Digitally restored model of *Protocinctus* (operculum in ‘open’ position) in IGES
451 format, compressed in a ZIP archive. To view, unzip the .zip file and open the unpacked .igs
452 file with FreeCAD (program and documentation available from www.freecadweb.org).

453

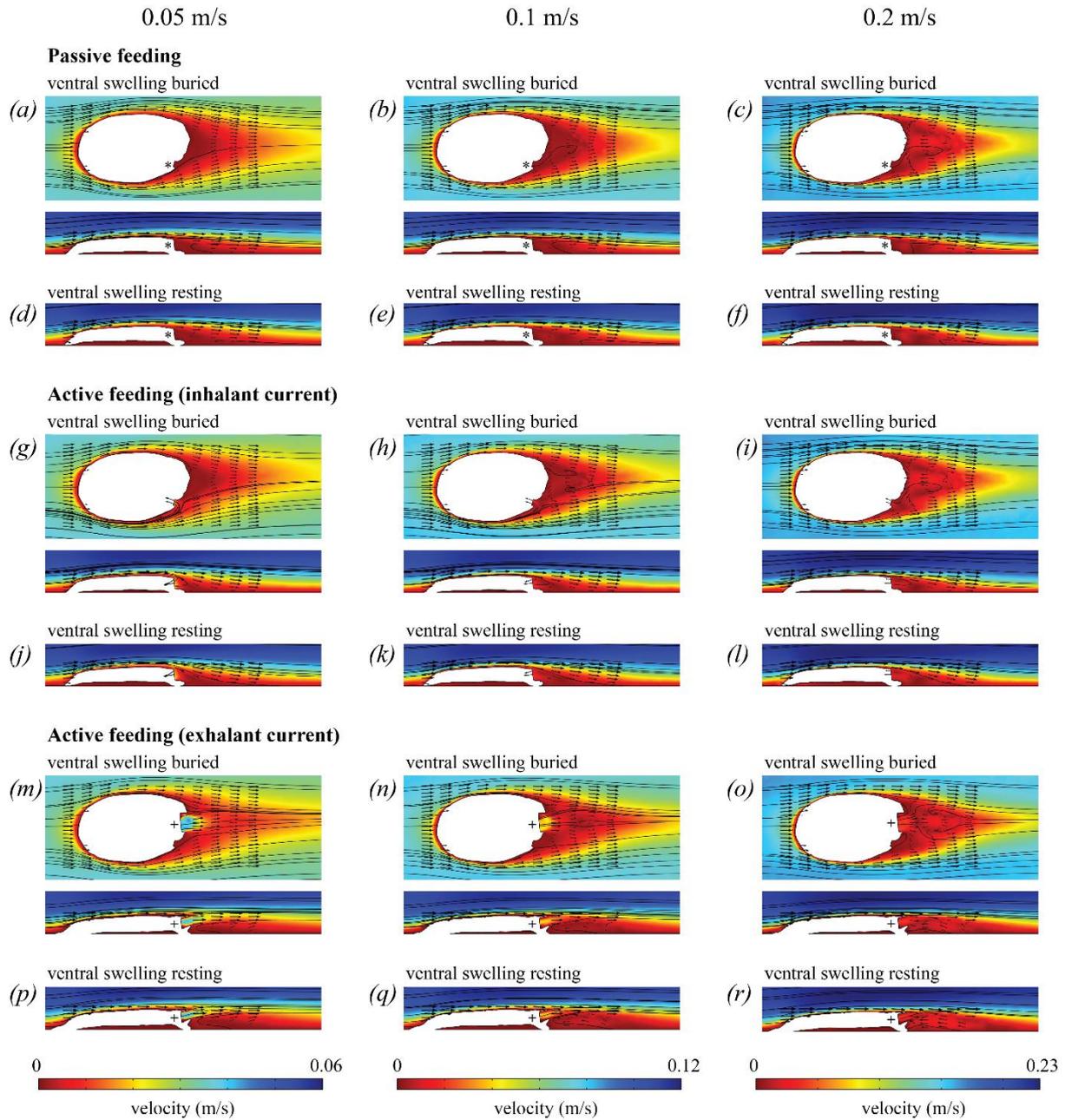
454 **Video S1.** Results of a CFD simulation using a time-dependent solver to show flow time-
455 evolution. Simulation of passive tentacular feeding with *Protocinctus* oriented at 180° to the
456 current (ambient velocity of 0.2 m/s) and with the ventral swelling buried within the
457 sediment, visualized as two-dimensional plots (horizontal cross-sections) of flow velocity
458 magnitude (false-colour scale different for each ambient flow velocity) with streamlines over
459 the first 10 s with a time step size of 0.01 s.

460



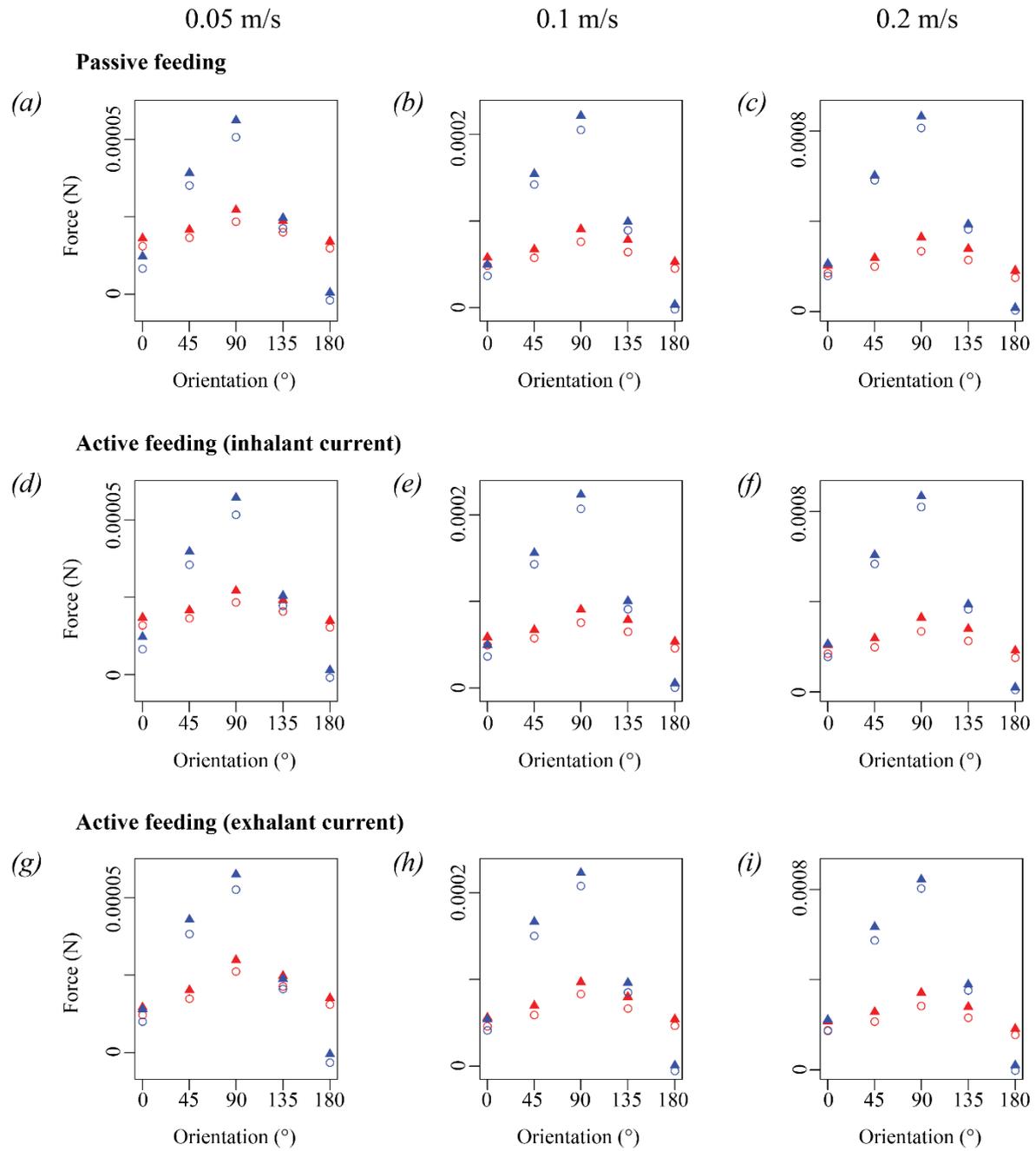
461

462 **Figure 1.**



463

464 **Figure 2.**



465

466 **Figure 3.**

