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1 **Skeletal elements controlled soft-tissue preservation in echinoderms from**
2 **the Early Ordovician Fezouata Biota**

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20 **Abstract**

21 Exceptional fossils preserve non-biomineralized tissues in the geological record and provide
22 crucial information on the evolution of life on Earth. Exceptionally preserved fossils are
23 rarely discovered complete, challenging their morphological description and their
24 palaeontological interpretation. Although decay experiments reconstructing degradation
25 sequences in modern animals are necessary to better understand taphonomic processes
26 involved in exceptional preservation, their applicability to some enigmatic and/or extinct
27 fossil taxa is limited. Here, based on a representative sample of 423 specimens collected from
28 a single stratigraphic level from the Early Ordovician Fezouata Biota, we reconstruct the
29 degradation sequence of both skeletal remains and soft tissues of stylophorans, an extinct
30 clade of echinoderms. The rare preservation of the water vascular system can be explained by
31 the rapid post-mortem opening of cover plates resulting from the fast decay of associated
32 muscles and the action of ligaments. In contrast, the proximal aulacophore and associated
33 stylocone formed a particularly decay-resistant closed module, thus favouring the preferential
34 preservation of included soft parts (fore-gut). The non-random location and frequency of
35 pyritized intra-skeletal structures strongly suggest that skeletal elements dictated the
36 preservation of underlying soft parts. As such, taphonomic investigations should not only
37 focus on the environment surrounding a decaying animal, but also on the different
38 environments created within a particular carcass.

39

40 *Keywords:* Echinodermata, Fezouata Shale, Morocco, Ordovician, Stylophora, taphonomy

41

42

43 **1. Introduction**

44 Since their first appearance in the fossil record in Cambrian Series 2, echinoderms are
45 characterized by the possession of a multi-element calcite endoskeleton consisting of
46 numerous, highly distinctive (e.g. three-dimensional stereom microstructure) skeletal
47 elements (plates) more or less tightly bound together in life by mesodermal connective soft
48 tissues (Ubaghs, 1968; Kouchinsky et al., 2012; Brusca et al., 2016). A corollary of this
49 constructional pattern is that, within the weeks following the death of an echinoderm, once
50 connective tissues (muscles, then ligaments) have decayed, its skeleton disarticulates into
51 hundreds to thousands of individual elements (Donovan, 1991; Nebelsick, 1995, 2004;
52 Ausich, 2001, 2021). Consequently, the preservation of intact, fully articulated echinoderm
53 skeletons requires very specific taphonomic conditions, generally associated with obrution
54 deposits (e.g. tempestites, turbidites; Brett et al., 1997; Ausich, 2021). The term 'echinoderm
55 Lagerstätten' was coined by Smith (1988) to designate localities yielding such exceptionally
56 preserved, fully articulated skeletal remains of fossil echinoderms (Brett et al., 1997;
57 Nebelsick, 2004; Lefebvre, 2007; Thuy et al., 2011; Rousseau and Nakrem, 2012; Zamora et
58 al., 2013; Cole et al., 2018). Although echinoderm Lagerstätten are known throughout the
59 whole Phanerozoic, they are particularly abundant in the Palaeozoic, bringing invaluable
60 information on the morphology, ontogeny, and/or palaeoecology of the first echinoderms,
61 including those belonging to extinct clades (Durham and Caster, 1963; Sprinkle, 1973; Zhao
62 et al., 2007; Parsley, 2009, 2012). Localities yielding fully articulated echinoderms are often
63 also either Konzentrat-Lagerstätten (i.e. deposits characterized by very dense, packed
64 accumulations of skeletal remains) or Konservat-Lagerstätten (i.e. sites where non-
65 mineralized, soft or lightly sclerotized tissues can be exceptionally preserved) (Seilacher et
66 al., 1985; Brett et al., 1997).

67 In recent years, the fossil record of exceptionally preserved soft parts in echinoderms (e.g.
68 ambulacral system, gonads, gut) has increased markedly with the development of CT-scan
69 imagery (Sutton et al., 2005; Rahman et al., 2015, 2019; Briggs et al., 2017) and new
70 techniques for fossil preparation (Glass and Blake, 2004). However, in sharp contrast with
71 some other metazoan phyla (e.g. arthropods), fossil evidence of soft tissues remains extremely
72 scarce in echinoderms and restricted to a handful of Palaeozoic Konservat-Lagerstätten:
73 primarily the Fezouata Shale (Lower Ordovician, Morocco; Lefebvre et al., 2019; Saleh et al.,
74 2020a, 2021a), the upper part of the Wenlock Series (Silurian, UK; Sutton et al. 2005; Briggs
75 et al., 2017; Rahman et al., 2019) and the Hunsrück Slate (Lower Devonian, Germany; Glass
76 and Blake, 2004). Whereas plated ambulacral tube feet are relatively common in both
77 bothriocidaroid echinoids (Männil, 1962; Thompson et al., 2022) and ophiocistioids (Rahman
78 et al., 2019), soft parts belonging to the water-vascular system (podia, ambulacral rays, ring
79 canal) are seldom preserved. They have only been reported in a dozen of specimens belonging
80 to six distinct classes: asteroids (Gale, 1987; Sutton et al., 2005), edrioasteroids (Briggs et al.,
81 2017), ophiocistioids (Rahman et al., 2019), ophiuroids (Glass and Blake, 2004; Glass, 2006),
82 stylophorans (Lefebvre et al. 2019), and possibly solutans (Daley, 1996). The occurrence of
83 putative tube feet was also repeatedly mentioned in some crinoids (Schmidt, 1934; Südkamp,
84 1997; Ausich et al., 2013) and holothurians (Lehman, 1958) from the Hunsrück Slate, but
85 these reports were debated (Seilacher, 1961; Glass and Blake, 2004; Südkamp, 2011; Smith
86 and Reich, 2013). With the exception of the Burlington and Harrodsburg formations
87 (Mississippian, USA), which yielded abundant remains of camerate crinoids with three-
88 dimensionally silicified guts in their calyx (Haugh, 1975), the digestive system was only
89 reported in a handful of specimens belonging to four classes of Palaeozoic echinoderms:
90 blastoids (Rahman et al., 2015), crinoids (Kammer and Ausich, 2007), solutans (Lefebvre et
91 al., 2013; Saleh et al., 2021a), and stylophorans (Lefebvre et al., 2019). Finally, gonads (and

92 eggs) were so far described in a single female specimen of the blastoid *Pentremites rusticus*
93 (Pennsylvanian, USA; Katz and Sprinkle, 1976; Sevastopulo, 2005). Exceptionally preserved
94 soft parts are crucial for reconstructing the anatomy of extinct organisms and elucidating their
95 phylogenetic affinities (Briggs, 1992; Vinther et al., 2008, 2017; Moysiuk et al., 2017). The
96 nature of the stylophoran appendage (crinoid-like stem, chordate-like tail, hemichordate-like
97 stalk or echinoderm feeding appendage) is a good example of a long-standing, hotly debated
98 palaeontological conundrum (see e.g. Bather 1930; Ubaghs 1961; Jefferies, 1968; Smith,
99 2005), which could be clarified with the description of exceptionally preserved soft parts
100 (ambulacral tube feet) in a specimen from the Fezouata Shale Lagerstätte (Lefebvre et al.,
101 2019).

102 So as to better understand the taphonomic processes involved in exceptional preservation
103 in fossil echinoderms, it is thus essential to investigate the successive stages occurring
104 between the death of the organism and the decay of mesodermal connective soft parts,
105 generally leading to the collapse and disarticulation of the skeleton. Field and laboratory
106 decay experiments aiming at reconstructing degradation sequences of extant echinoderms
107 demonstrated that soft parts are entirely decayed within two to three weeks (Meyer, 1971;
108 Kidwell and Baumiller, 1990; Kerr and Twitchett, 2004). The timing of this process can be
109 modulated by temperature, oxygenation, and/or turbulence (Meyer, 1971; Kidwell and
110 Baumiller, 1990; Donovan, 1991; Nebelsick, 1995; Brett et al., 1997; Kerr and Twitchett,
111 2004). However, studies constraining decay sequences in extinct echinoderms are extremely
112 rare, because they require a large-sized sample corresponding to an 'ecological snapshot'
113 *sensu* Taylor and Brett (1996) (see also Ausich, 2021). Even if a given taxon is exceptionally
114 preserved in several sites, it would be inaccurate to reconstruct its degradation sequence by
115 the combination of data from different localities (and stratigraphic levels), very likely
116 characterized by originally distinct environmental conditions (e.g. turbulence, oxygenation,

117 pH, temperature). In this study, we aim at reconstructing the degradation sequence of extinct
118 echinoderms (cornute stylophorans), based on a large number of specimens illustrating
119 different stages of decay, and all recovered from a single fossiliferous horizon within the
120 Lower Ordovician Fezouata Shale Lagerstätte (Morocco).

121

122 **2. Geological context**

123 In the Zagora area (Central Anti-Atlas, Morocco), the Fezouata Shale (Tremadocian–
124 Floian) consists of a ~900 m thick succession of blue-green to yellow-green sandy mudstones
125 and siltstones that coarsen upwards (Fig. 1; Destombes et al., 1985; Martin et al., 2016).

126 Sediments in this formation were deposited on a shallow, storm-dominated environment
127 slightly deepening towards the northwest (in present-day orientation) and originally situated
128 at high southern latitudes on the Gondwanan margin (Vaucher et al., 2016, 2017; Saleh et al.,
129 2018, 2020b, 2021a). Two distinct, narrow intervals of the Fezouata Shale yielded abundant
130 remains of organisms with both skeletal and soft tissue preservation (Van Roy et al., 2010;
131 Martin et al. 2016; Vaucher et al., 2016, 2017; Lefebvre et al., 2018; Saleh et al., 2020b,
132 2021a).

133 The study material was collected at Bou Izargane (Fig. 1), along the slopes of a small hill
134 located about 18 km north of Zagora (Lefebvre et al., 2019; Saleh et al., 2020a). All fossils
135 were collected from a single, lenticular level (~2.25 m² wide and 3 cm thick) of fine, dark
136 blue mudstones occurring ~270 m above the base of the Ordovician succession, within the
137 lower interval with exceptional preservation (*Sagenograptus murrayi* Zone, late Tremadocian;
138 Lefebvre et al., 2016, 2019; Martin, 2016). The Z-F4(15) fossiliferous lens yielded more than
139 500 specimens belonging to a low diversity assemblage, largely dominated by cornute
140 stylophorans (*Bohemiaecystis* sp., *Chauvelicystis* sp. and *Hanusia* sp.), associated with
141 relatively common trilobites (*Anacheirurus* sp., Asaphidae indet. and *Bavarilla* sp.) and rare

142 other taxa (brachiopods, graptolites, marrellomorphs, worms) (Fig. 2). Field observations
143 suggest that the Z-F4(15) lens corresponds to three successive, superimposed assemblages
144 (Lefebvre et al., 2019). The stratigraphically lower and less extensive one yielded several
145 specimens of marrellomorphs associated with few trilobites and echinoderms. The
146 intermediate assemblage is dominated by the two trilobites *Anacheirurus* and *Bavarilla*,
147 whereas the upper and most extensive one comprises abundant cornute remains
148 (*Bohemiaecystis*, *Hanusia* and *Chauvelicystis*).

149 Detailed sedimentological analysis of the Bou Izargane section suggests that the Z-F4(15)
150 lens preserves autochthonous assemblages associated with quiet environmental conditions,
151 right below Storm Wave Base (SWB). These assemblages were occasionally smothered by
152 thin blankets of distal storm deposits, resulting from big storms in proximal settings, that
153 could sometimes transport a little amount of sediment below the SWB (Vaucher et al., 2016;
154 Saleh et al., 2020b). It is very likely that living members of the vagile benthos could escape
155 from burial and are thus not preserved at Bou Izargane (Saleh et al., 2020b, 2021b). This
156 interpretation is supported by the absence (or extreme rarity) of external soft parts and soft-
157 bodied organisms and the occurrence of numerous escape traces across the storm deposits
158 (Saleh et al., 2020b, 2021b). Consequently, it is very likely that fossils from the Bou Izargane
159 Z-F4(15) lens correspond almost exclusively to decaying carcasses, sealed, and protected by a
160 thin layer of sediments providing favourable conditions for exceptional preservation (Saleh et
161 al., 2020b, 2021a). Thus, this locality offers a unique snapshot documenting almost all
162 possible taphonomic grades for both cornute stylophorans and trilobites, ranging from
163 disarticulated individuals to fully articulated ones with exceptionally preserved soft parts
164 (Martin, 2016; Lefebvre et al., 2019; Saleh et al., 2020b).

165

166 **3. Palaeobiology of cornute stylophorans**

167 The class Stylophora is an extinct clade of echinoderms (Miaolingian–Pennsylvanian),
168 which was particularly abundant, morphologically diverse, and palaeobiogeographically
169 widespread during the late Cambrian (Furongian) – Early Ordovician (Tremadocian and
170 Floian) time interval (Lefebvre et al., 2006, 2013, 2022; Lefebvre, 2007). This class is
171 traditionally subdivided into the two orders Cornuta and Mitrata, with mitrates deriving from
172 paraphyletic cornutes (Jefferies and Prokop, 1972; Derstler, 1979; Cripps, 1991; Parsley,
173 1997; Lefebvre et al., 2022). The systematics of cornutes (~30 genera ranging from the early
174 Wuliuan to the late Katian) was recently reevaluated by Lefebvre et al. (2022), who identified
175 seven main clades (families). The main palaeobiological features of cornutes are summarized
176 below, with a special emphasis on the three clades (Chauvelicystidae, Hanusiidae and
177 Scotiaecystidae) occurring in the Z-F4(15) stylophoran-dominated lens.

178

179 *3.1. Skeletal morphology*

180 Descriptive terms used below follow Ubaghs (1963, 1968, 1970) and Lefebvre et al.
181 (2022). Cornutes are characterized by a fundamentally bipartite organization, consisting of a
182 single, delicate, articulated appendage ('aulacophore') inserted into a massive, flattened, and
183 asymmetrical body ('theca') (Fig. 3). The aulacophore (housing the mouth) is considered as
184 anterior, and the theca (bearing the periproct), is posterior (Fig. 3). By convention, the contact
185 between the appendage and the theca is considered as a landmark for orientation: structures
186 close to it are designated 'proximal', and those away from it, 'distal'.

187 The cornute appendage consists of two distinct, bilaterally symmetrical parts. The first one
188 ('proximal aulacophore') forms a relatively wide, moderately elongate cylindrical structure,
189 posteriorly in contact with the theca (Figs 3, 4). It is made of several imbricate rings
190 ('proximal rings'), each formed by four tightly sutured plates: one upper pair of 'tectals', and
191 one lower pair of more extensive 'inferolaterals'. The proximal aulacophore formed during life

192 a particularly flexible, telescopic structure, which could be flexed in almost any direction,
193 laterally and vertically (Ubaghs, 1968; Lefebvre, 2003; Clark et al., 2020). The proximal rings
194 were enclosing a wide lumen ('proximal cavity'), which was communicating posteriorly with
195 the main body cavity ('intrathecal cavity') (Fig. 4(B)).

196 In marked contrast, the second region of the appendage ('distal aulacophore') is particularly
197 long, narrow, and formed a stiff structure. The distal appendage comprises a single lower
198 series of relatively stout, semi-cylindrical 'ossicles' and, articulated to them, two (left and
199 right) upper sets of delicate, fan-shaped 'cover plates' (Fig. 4(A)). The morphology of the
200 proximal-most ossicle ('stylocone') is funnel-shaped, so as to accommodate the transition
201 between proximal rings (posteriorly) and narrower, more distal ossicles (anteriorly). The large
202 posterior region of the stylocone was partly overlapped by distal-most proximal rings and
203 housed the anterior-most extremity of the proximal cavity (Fig. 4(B)). Ossicles are abutting
204 against each other along almost flat interossicular surfaces, thus supporting the view that the
205 distal aulacophore formed a relatively rigid structure (Ubaghs, 1968, 1970; Lefebvre, 2003;
206 Clark et al., 2020; Lefebvre et al., 2022). The lower surface of ossicles is typically smooth
207 and rounded (e.g. *Bohemiaecystis*, *Chauvelicystis*, *Hanusia*; Ubaghs, 1968, 1970; Cripps,
208 1989; Lefebvre et al., 2022), but a spike can be present in some taxa (e.g. *Nanocarpus*,
209 *Reticulocarpus*; Jefferies and Prokop, 1972; Ubaghs, 1991).

210 A well-defined, deep 'median longitudinal groove' occurs on the upper (internal) surface of
211 all ossicles. This groove extends from the distal tip of the appendage (anteriorly) to the
212 'proximal notch' on the stylocone (posteriorly), where it plunges into the proximal cavity
213 (Ubaghs, 1968, 1970; Lefebvre et al., 2019, 2022). On both sides of the longitudinal median
214 groove, the upper surface of each ossicle bears two opposite (left and right) shallow lateral
215 depressions. In most taxa, each lateral depression is connected to the longitudinal median
216 groove by a deep, narrow 'transverse channel'. Left and right cover plates were articulated to

217 the lateral edges of the upper surface of underlying ossicles (Fig. 4(A)). In cornutes, cover
218 plates are thin, fan-shaped elements, frequently ornamented with delicate radiating ridges.
219 Their movements (opening, closure) were controlled by muscles (internally) and ligament
220 (externally) (Ubaghs, 1970; Lefebvre et al., 2022). However, all cover plates belonging to the
221 same lateral set were partly overlapping each other distally, so that individual movement was
222 not possible.

223 The theca is strongly flattened and comprises two opposite sides: a flat to slightly concave
224 lower surface, originally in contact with the substrate and a gently convex upper surface,
225 facing the water column. In most cornutes (e.g. *Bohemiaecystis*, *Chauvelicystis*, *Hanusia*), the
226 theca is well-delimited by a series of relatively massive plates ('marginals') forming a delicate
227 but rigid 'marginal frame' (Fig. 4(A)). The two most anterior marginals are always associated
228 to two (e.g. *Bohemiaecystis*, *Hanusia*) or three (e.g. *Chauvelicystis*) additional overlying
229 skeletal elements (the 'adorals'): all together these four (or five) plates are framing the
230 aulacophore insertion. The communication between the proximal lumen and the intrathecal
231 cavity was partly occluded by two vertical walls (the left and right 'apophyses') emitted by the
232 two anterior-most marginals (Fig. 4(B)). In cornutes, the right adoral plate generally bears a
233 distinct orifice ('right adoral orifice'), which is connected to a cavity ('infundibulum') borne by
234 the underlying marginal (Ubaghs, 1968, 1970; Lefebvre et al., 2022). Two grooves radiating
235 from the infundibulum suggest that this cavity was originally communicating with both the
236 proximal lumen (through the 'anterior oblique groove') and the intrathecal cavity (through the
237 'anterior transverse groove').

238 Anterior marginals are typically high, thick, and massive. Their lower surface commonly
239 bears protuberances and/or spikes directed downwards and laterally (e.g. *Bohemiaecystis*,
240 *Hanusia*), which probably helped anchoring the organism into the substrate (Ubaghs, 1968,
241 1970; Parsley, 1988; Lefebvre, 2003). Some other cornutes (e.g. *Chauvelicystis*) are lacking

242 protuberances but are displaying a fringe of articulated spines along the lateral and/or
243 posterior edges of their marginal frame (Chauvel, 1966; Ubaghs, 1970, 1983; Lefebvre et al.,
244 2022). Posteriorly, the marginal frame regularly decreases in height, with its distal-most
245 elements frequently modified into thin, elongate blade-like processes ('digital', 'glossal' and
246 'spinal'; Fig. 4(A)), which probably helped maintain the organism on the surface of soft
247 substrates ('snowshoe strategy'; Jefferies and Prokop, 1972; Woods and Jefferies, 1992;
248 Lefebvre, 2003; Lefebvre et al., 2006; Noailles, 2016).

249 Most of the lower and upper thecal surfaces are paved by numerous, unorganized,
250 adjoining platelets forming two thin, delicate, and flexible integumentary membranes: the
251 'infracentral' and 'supracentral' areas, respectively (Ubaghs, 1963, 1968; Lefebvre and
252 Vizcaïno, 1999). In cornutes, the lower side of the theca is generally divided into two unequal
253 fields (the 'left and right infracentral areas') by an oblique strut (the 'zygal bar') emitted by two
254 opposite plates of the marginal frame (Fig. 3). On its upper (internal) side, the zygal bar bears
255 a well-defined ridge (the 'zygal crest'), which extends from the posterior wall of the left
256 apophysis (anteriorly) and regularly decreases in height posteriorly, towards the anal opening
257 (Ubaghs, 1968, 1970; Lefebvre et al., 1998, 2022). In hanusiids (e.g. *Hanusia*), a second strut
258 is also present on the upper thecal surface, which is then subdivided into two unequal 'anterior
259 and posterior supracentral areas' (Ubaghs, 1970; Jefferies and Prokop, 1972; Cripps, 1989;
260 Lefebvre et al., 2022). In cornutes, the anal pyramid corresponds to a well-defined, cone-
261 shaped structure occurring either at the posterior extremity of the supracentral area on the
262 upper thecal surface (e.g. *Bohemiaecystis*; Fig. 4(A)) or in a more terminal position at the
263 distal end of the left infracentral and supracentral areas (e.g. *Chauvelicystis*) (Ubaghs, 1968,
264 1970; Parsley, 1988; Lefebvre et al., 2022).

265 Respiratory structures also occur within the supracentral area of many cornutes (Ubaghs,
266 1968, 1970; Lefebvre and Vizcaïno, 1999; Lefebvre et al. 2022). They can consist of

267 numerous orifices shared by two large adjoining plates and morphologically similar to the
268 'sutural pores' (or 'epispores') of other echinoderms (e.g. cinctans, edrioasteroids, eocrinoids).
269 Such sutural pores can be distributed everywhere within the supracentral area (e.g.
270 *Nevadaecystis*; Ubaghs, 1963), but they are generally restricted to the right anterior corner of
271 the upper thecal surface (e.g. *Ceratocystis*, *Protocystites*; Ubaghs, 1968; Jefferies, 1969;
272 Jefferies et al., 1987). In several taxa, sutural pores correspond to small-sized, cone-shaped
273 chimneys elaborated at the junction between several adjoining supracentrals. Such pores can
274 be more or less randomly distributed in the right anterior corner of the upper thecal surface
275 (e.g. *Phyllocystis crassimarginata*) or grouped within small clusters ('cothurnopores')
276 protected by two opposite U-shaped elements (e.g. *Chauvelicystis*) (Ubaghs, 1968, 1970;
277 Lefebvre and Vizcaïno, 1999). In some other taxa (e.g. *Bohemiaecystis*; Fig. 4(A)), small
278 chimney-like sutural pores are totally lacking, and respiratory structures correspond to thin,
279 slit-like openings ('lamellipores') between numerous, tightly packed U-shaped plates forming
280 together an elongate, oblique structure ('lamellate organ') in the right anterior corner of the
281 supracentral area (Ubaghs, 1968, 1970; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022).
282 Finally, respiratory structures are totally absent in several cornute taxa (e.g. *Hanusia*).

283

284 3.2. *Soft anatomy*

285 Several specimens of the cornutes *Bohemiaecystis* and *Hanusia* extracted from the Z-
286 F4(15) lens at Bou Izargane provided the first evidence of exceptionally preserved soft parts
287 in the stylophoran appendage and theca (Lefebvre et al., 2019). All specimens are preserved
288 in a siliciclastic matrix (argillaceous silts). Structures found within the skeleton are preserved
289 as iron oxides (Figs 5, 6; Lefebvre et al., 2019). Iron oxides are in the shape of small euhedral
290 crystals, and rarely framboids, indicating that intra-skeletal structures were pyritized (Gabbott
291 et al., 2004). Thus, these structures represent real anatomical features that were replaced by

292 authigenic minerals early on during the fossilization process (Gabbott et al., 2004), and they
293 are not preservational artefacts (Saleh et al., 2020a). Authigenic mineralization through
294 pyritization was shown to play a major role in the preservation of soft tissues in the Fezouata
295 Shale (Saleh et al., 2020b, 2020c, 2021a). Pyrite replicates in this formation replaced the
296 original organic matter of certain tissues that could have been otherwise lost during decay
297 (Saleh et al., 2019, 2020c, 2021a). Pyrite was then weathered by water circulations at outcrop,
298 and S was lost, resulting in the transformation of pyrite crystals in iron oxides (Saleh et al.,
299 2020b, 2021a). An accessory product of this reaction is sulfuric acid (i.e., $2\text{FeS}_2 + 19\text{H}_2\text{O} \rightarrow$
300 $\text{Fe}_2\text{O}_3 + 15\text{H}_2 + 4\text{H}_2\text{SO}_4$) (Saleh et al., 2020c, 2021a). The formation of H_2SO_4 leads to the
301 dissolution of nearby carbonate in the skeletal parts of calcified taxa, which can explain why
302 skeletal elements of stylophorans are preserved as imprints having the same chemical signal
303 as the matrix (Saleh et al., 2021a).

304 In Bou Izargane cornutes, exceptionally preserved, pyritized intra-skeletal structures were
305 evidenced in three distinct parts of their body (Lefebvre et al., 2019). In the distal
306 aulacophore, the most obvious 'soft' parts correspond to a well-defined longitudinal canal
307 running within the longitudinal median groove, on the upper surface of the stylocone and all
308 more distal ossicles (Lefebvre et al., 2019). Laterally, this canal gives rise to regularly spaced,
309 narrow, delicate, and elongate tube-like extensions, protruding beyond the cover plates (Figs
310 4, 5(A)). Proximally, this canal stops at the deep 'proximal notch' of the stylocone. The soft
311 anatomical structures preserved in the Bou Izargane cornutes confirmed previous
312 interpretations of the stylophoran distal aulacophore as a feeding appendage carrying a single
313 ambulacral canal of the water-vascular system (longitudinal canal) and its associated tube feet
314 (lateral extensions) (Ubaghs, 1963, 1968, 1970; Nichols, 1972; Parsley, 1988; David et al.,
315 2000; Lefebvre, 2003). In this context, the proximal notch on the upper surface of the

316 stylocone very likely corresponds to the mouth (Fig. 4(B)) and the right adoral orifice, to the
317 hydropore (Ubaghs, 1968; Nichols, 1972; David et al., 2000; Lefebvre et al., 2022).

318 A second, fainter and less regular longitudinal structure was also evidenced, running inside
319 the stylocone and other ossicles, below the ambulacral canal (Fig. 4(B); Lefebvre et al.,
320 2019). No intra-ossicular canal was previously detected in cornutes (no evidence on inter-
321 ossicular facets), but its presence is well-known in mitrates (Jefferies, 1968). This structure
322 was tentatively interpreted as a possible coelomic canal by Lefebvre et al. (2019). However,
323 this seems unlikely because of its irregular aspect and the absence of a clear connection with
324 the proximal cavity. Comparison with other Palaeozoic echinoderms rather suggests that this
325 structure is more likely equivalent to the 'median canal' occurring inside the flooring plates of
326 brachioles in many blastozoans (see Sprinkle, 1973; Clausen et al., 2009; Sheffield and
327 Sumrall, 2019). This median canal probably housed nerves.

328 A large, elongate, spindle-shaped, intra-skeletal pyritized structure was also documented
329 for the first time within the proximal cavity of Bou Izargane cornutes (Figs 4–6; Lefebvre et
330 al., 2019). Anteriorly, this internal structure extends into the enlarged posterior region of the
331 stylocone, where it tapers upwards into the proximal notch. Posteriorly, this structure is
332 similarly narrowing upwards, along the anterior wall of the apophyses. This internal structure,
333 which is connected to the intrathecal cavity (posteriorly), the mouth, and the water-vascular
334 system (anteriorly), was interpreted as the fore-gut (oesophagus) by Lefebvre et al. (2019).

335 Additional skeletal evidence (labyrinthic stereom meshwork within the posterior region of the
336 stylocone and on the anterior wall of the apophyses) suggests that proximal rings were also
337 housing powerful muscles, which could be flexed to move the whole appendage laterally
338 (Ubaghs, 1968; Clausen and Smith, 2005; Lefebvre et al., 2019; Clark et al., 2020).

339 Finally, an elongate, relatively complex internal pyritized structure was also evidenced
340 within the intrathecal cavity (Figs 4, 5). Its connection with both the spindle-shaped structure

341 housed within proximal rings (anteriorly) and the anal pyramid (posteriorly) supports its
342 interpretation as the posterior part of the gut (Lefebvre et al., 2019). This identification is in
343 good accordance with previous hypotheses suggesting that the digestive system of
344 stylophorans was closely associated to the zygial crest (Chauvel, 1941; Caster, 1954;
345 Lefebvre, 1999).

346

347 3.3. Mode of life

348 The wide, flattened, lightly built theca of asymmetrical cornutes (e.g. *Bohemiaecystis*,
349 *Chauvelicystis*, *Hanusia*), along with the frequent occurrence of elongate posterior spine-
350 shaped plates represent adaptations for an epibenthic mode of life on soft substrates (Jefferies
351 and Prokop, 1972; Woods and Jefferies, 1992; Lefebvre, 2003; Lefebvre et al., 2006, 2022;
352 Noailles, 2016). With the exception of some heavily plated Cambrian taxa (e.g. *Ceratocystis*),
353 most cornutes were generally living in quiet, low-energy settings (below storm-wave base),
354 where they could locally form particularly dense, gregarious communities (Lefebvre, 2007;
355 Botting et al., 2013; Lefebvre et al., 2016). However, recent reports of abundant cornute
356 remains in Ordovician storm deposits indicate that they could also occur massively in more
357 proximal settings (Lefebvre et al., 2022). By analogy with extant echinoderms (Warner, 1971;
358 Fujita, 1992; Aronson and Blake, 1997), it is possible that such a gregarious mode of life
359 provided several advantages, e.g. for feeding, reproduction, stability and/or protection against
360 slow-moving predators (Lefebvre, 2007). Cornutes were free-living (unattached) mobile
361 organisms, which were very likely capable of active reorientation and limited movements by
362 wagging their aulacophore from side to side. However, the frequent presence of strong
363 protuberances on the lower surface of anterior marginals probably largely hindered any
364 efficient forward movement in most taxa (e.g. *Bohemiaecystis*; Ubaghs, 1968; Parsley, 1988;
365 Lefebvre, 2003; Clark et al., 2020). This interpretation is also supported by the lack (or

366 extreme reduction) of sediment-gripping devices (e.g. spikes) on the lower surface of ossicles,
367 and the absence of any differentiated interossicular articulations (Lefebvre, 2003).

368 A low-level suspension-feeding or a detritus-feeding mode of life is generally inferred for
369 cornutes (Ubaghs, 1968; Parsley, 1988; Guensburg and Sprinkle, 2000; Lefebvre, 2007).

370 Minute food particles were probably collected from the sea water and/or from the surrounding
371 sediment by the tube feet. Cornutes were very likely feeding with their appendage lying over
372 the substrate and facing the current (Parsley, 1988; Lefebvre, 2003, 2007). The frequent
373 preservation of distal aulacophores with widely open cover plates was often interpreted as the
374 original feeding posture of cornutes (Ubaghs, 1968; Parsley, 1988; Lefebvre, 2003; Martin et
375 al., 2015). However, this interpretation was recently questioned by the observation of
376 numerous fully articulated specimens preserved in life position with ajar cover plates
377 (Lefebvre et al., 2022). This rather suggests that, in life, cover plates were probably
378 maintained in a nearly closed position by (internal) muscles, with tube feet protruding in
379 between them (Fig. 4). This implies that the opening of the two lateral sets of cover plates was
380 probably post-mortem and resulted both from the decay of muscles and the antagonistic
381 action of (external) ligaments (Ubaghs, 1970; Lefebvre et al., 2022). The resulting mechanical
382 opening of cover plates in cornutes would then be relatively similar to the post-mortem,
383 ligamentary-induced 'butterfly position' observed in bivalves (Polechová, 2016). Although
384 specialized respiratory structures (sutural pores, cothurnopores, lamellipores) are present in
385 some cornutes, it is very likely that, similarly to the situation in extant echinoderms,
386 ambulacral tube feet were also involved in respiration (Ubaghs, 1968).

387

388 **4. Material and methods**

389 The study material comprises 423 specimens of cornutes (Fig. 2(B)) from the lower part of
390 the Fezouata Formation (late Tremadocian). They were all extracted during the same field

391 campaign (January–February 2014) from the Z-F4(15) lenticular level at Bou Izargane
392 (Zagora Province, Morocco; Fig. 1). Sampling during field work tried to be as exhaustive as
393 possible, but it cannot be excluded that small isolated skeletal elements were possibly under-
394 sampled compared to more eye-catching, complete, articulated individuals. All specimens
395 belong to the palaeontological collections of Cadi-Ayyad University, Marrakesh (Morocco).
396 Thecal width (TW) was estimated perpendicularly to the main body axis (Fig. 3), following
397 the same procedure as in Lefebvre et al. (2022).

398 All specimens were observed with a Zeiss SteREO Discovery.V8 stereoscopic binocular.
399 For each individual specimen, the quality of preservation of its skeletal remains was estimated
400 based on the taphonomic classification proposed by Martin et al. (2015) for cornute
401 stylophorans. This classification was slightly amended to better describe the diversity of
402 observed taphonomic grades (Fig. 7). For example, taphonomic group 1 was subdivided into
403 the two subgroups (1a) for individuals with closed or ajar cover plates, and (1b) for those with
404 widely open sets of cover plates on both sides of the aulacophore. Similarly, taphonomic
405 group 3 was split into two subsets, corresponding to more or less articulated thecae associated
406 with (3a) proximal rings and the stylocone, or (3b) only the proximal appendage. Moreover,
407 each incomplete individual was coded so as to specify if the missing parts were originally
408 absent or if they could not be observed because of sampling (e.g. specimen broken during
409 extraction in the field) or observational limitations (e.g. only parts of the specimen exposed
410 on the rock surface). Finally, when pyritized intra-skeletal structures were observed, they
411 were coded into three categories related to the region where they were occurring: (A) in the
412 distal appendage (ambulacral canal, ambulacral tube feet, median canal); (B) in proximal
413 rings (fore-gut); and (C) within the theca (mid- and hind-gut).

414 Specimens were photographed in the palaeontological collections of Lyon 1 University,
415 Villeurbanne (France) with a Canon 5DSR camera, equipped with a MP-E 65 mm macro lens.

416

417 **5. Results**

418 *5.1. Taphonomy*

419 On large slabs displaying several co-occurring cornutes, individuals are randomly
420 distributed (no obvious orientation) and generally preserved on the same (lower or upper) side
421 (Fig. 8(A)). Rarely, some thecae are twisted, and a few specimens are exposed in lateral
422 position (Fig. 5). Stylophoran skeletal elements are generally relatively poorly preserved, as
423 faint, flattened imprints in the rock, whereas pyritized intra-skeletal remains correspond to
424 colourful (white, yellow, red or purple), three-dimensionally preserved structures (Figs 5, 6).
425 The most abundant cornute, *Bohemiaecystis* sp., displays a wide range of thecal sizes, from
426 relatively small (TW = 7 mm) to very large individuals (TW = 21 mm).

427

428 *5.2. Skeletal elements*

429 Cornute stylophorans from Z-F4(15) can be assigned to two main taphonomic grades.
430 About 30 percent of individuals are characterized by a fully preserved appendage inserted into
431 a more or less complete and articulated theca (Figs 6(C), 9). Most of them display widely
432 open cover plates on both sides of the stylocone and more distal ossicles (taphonomic grade
433 1b). However, due to the poor preservation of skeletal elements, the imprint left by cover
434 plates is sometimes very faint and hardly visible. For the same reason, it is likely that cover
435 plates are closed or ajar in the rare individuals preserved in lateral position (see below, Fig. 5;
436 taphonomic grade 1a). The theca is sometimes fully articulated, but very often, the two
437 particularly elongate posterior spine-shaped marginals (glossal and spinal) are displaced or
438 missing. Rare individuals display a twisted, fully articulated theca, i.e. with its right, spinal-
439 bearing side superimposed over its left, glossal-bearing margin. With the exception of the
440 single specimen of *Chauvelicystis*, which displays a fully articulated supracentral area (Fig.

441 10), very little information on the preservation of these thin, delicate membranes is available
442 for individuals belonging to the two other genera. In some individuals, their presence is
443 suggested by numerous faint, tiny, polygonal imprints probably corresponding to poorly
444 preserved integumentary platelets. In specimens of *Bohemiaecystis*, lamellipores are generally
445 clearly visible and fully articulated in the right anterior corner of the upper thecal surface (Fig.
446 9(B)). In Z-F4(15), the proportion of cornutes belonging to taphonomic grade 1b is probably
447 slightly underestimated, because several fully articulated thecae are located on slab edges,
448 making it impossible to document if the distal appendage was originally present or not.

449 Around 66 percent of cornute specimens correspond to more or less articulated thecae
450 closely associated to intact proximal rings and stylocone (taphonomic grade 3a; Figs 6(A, B),
451 8(B–D, G)). Cover plates and more distal ossicles are absent. Posterior spines (glossal, spinal)
452 are seldom present. The marginal frame is sometimes intact, but generally more or less
453 disarticulated, with marginals no longer tightly sutured to each other and frequently slightly
454 displaced. No clear evidence of supracentral or infracentral areas could be observed in these
455 specimens.

456 Finally, the remaining 4 percent of cornutes correspond mainly to more or less
457 disarticulated thecae, with no associated aulacophore (taphonomic grade 4; Fig. 8(E)) and
458 rare, isolated skeletal elements (taphonomic grade 5). However, the latter are generally well-
459 preserved, intact posterior spine-shaped marginals (glossal, spinal), probably dissociated from
460 nearby individuals belonging to taphonomic grades 1b or 3a (Fig. 8(F)).

461

462 5.3. *Soft parts*

463 Clear evidence of pyritized structures corresponding to originally 'soft' parts could be
464 unambiguously observed in five specimens (i.e. about 1.2 percent of the total sample). A
465 single individual (AA.BIZ15.OI.259; Fig. 5(A)) exhibits widespread exceptional preservation

466 (A+B+C), with pyritized intra-skeletal structures occurring within the distal aulacophore
467 (ambulacral canal and associated tube feet, median canal), proximal rings (oesophagus), and
468 the theca (mid- and hind-gut). This cornute is a fully articulated specimen of *Bohemiaecystis*
469 sp. exposed in lateral position, with its distal aulacophore and posterior thecal spine (spinal)
470 almost parallel to each other and unusually bent upwards. In this specimen, the observation of
471 regularly arranged imbricate cover plates articulated to underlying ossicles strongly suggests
472 that cover plates were either closed or ajar. In lateral view, widely open cover plates would be
473 hardly visible, because they would be almost perpendicular to ossicles.

474 In specimen AA.BIZ15.OI.110 (Fig. 5(B)), exceptional preservation is restricted to
475 proximal rings (oesophagus) and the intrathecal cavity (mid- and hind-gut) (B+C). In this
476 individual, the spindle-shaped morphology of the elongate fore-gut is remarkably preserved in
477 three dimensions. This specimen of *Hanusia* sp. is exposed in lateral view, with its
478 aulacophore in a straight to gently curved forward position. Similarly to AA.BIZ15.OI.259,
479 the observed arrangement of cover plates in AA.BIZ15.OI.110 indicates that they were not
480 horizontal and widely open on both sides of the distal appendage but vertical and either closed
481 or ajar.

482 In the last three specimens, exceptional preservation is restricted to proximal rings (B). The
483 spindle-shaped morphology of the fore-gut is particularly obvious in AA.BIZ15.OI.80 (Fig.
484 6(A)). In this incomplete specimen of *Hanusia* sp. exposed in life position (taphonomic grade
485 3a), the oesophagus corresponds to a well-defined intra-skeletal reddish structure extending
486 longitudinally across proximal rings, and tapering both anteriorly (into the proximal notch of
487 the stylocone) and posteriorly (towards the apophyses and the intrathecal cavity). A similar
488 spindle-shaped pyritized intra-skeletal structure occurs in two other individuals:
489 AA.BIZ15.OI.58 (Fig. 6(C)) is a specimen of *Bohemiaecystis* sp. consisting of a well-
490 preserved appendage (including widely open cover plates) and a partly disarticulated theca

491 (taphonomic grade 1b), whereas AA.BIZ.OI.132 (Fig. 6(B)) is a more incomplete cornute
492 (distal appendage restricted to the stylocone), which can be also assigned to *B. sp.* based on
493 the presence of poorly preserved lamellipores (taphonomic grade 3a).

494 Finally, very faint evidence of putative pyritized intra-skeletal structures restricted to the
495 proximal aulacophore (B) can be documented, though less convincingly, in five additional
496 cornutes belonging to taphonomic grades 1b (AA.BIZ15.OI.30, 41 and 67; Fig. 9(D, E)) and
497 3a (AA.BIZ15.OI.116, 156).

498

499 **6. Discussion**

500 The occurrence of more than 400 cornutes collected from a same horizon (the Z-F4(15)
501 lens, at Bou Izargane) provides a rare opportunity to document their biostratinomy, and to
502 compare it to the few other studies devoted to stylophoran taphonomy (e.g. Lefebvre, 2007;
503 Martin et al., 2015; Reid et al., 2015; Lefebvre et al., 2016, 2022). In Z-F4(15), the random
504 orientation of cornutes, their preservation in life position (very few individuals upside-down
505 or in lateral aspect), as well as the occurrence of a significant proportion (~30 percent) of
506 fully articulated specimens with even their very delicate sets of cover plates preserved in open
507 position on both sides of the distal aulacophore (taphonomic grade 1b), are all indications
508 suggesting relatively distal, quiet environmental conditions. More incomplete specimens
509 (taphonomic grades 3 to 5) result from the *in situ* collapse of carcasses on the sea floor, and
510 the action of very limited bottom currents (or infaunal organisms?) slightly displacing some
511 skeletal elements. These biostratinomic characteristics are comparable to those reported by
512 Martin et al. (2015) in their third cornute taphofacies, at Jbel Tizagzaouine. They are also in
513 good agreement with sedimentological data suggesting distal, low turbulence (below storm
514 wave base) environmental conditions at Bou Izargane (Vaucher et al., 2016; Saleh et al.,
515 2020b).

516 Moreover, with the possible exception of the two specimens preserved in lateral position
517 with their cover plates very likely closed or ajar (taphonomic grade 1a; see below), all other
518 cornutes collected in Z-F4(15) correspond to various stages of decaying carcasses
519 (taphonomic grades 1b–5). This result confirms previous biostratigraphic interpretations of
520 Bou Izargane assemblages as resulting from the burial of already dead, more or less decayed
521 organisms by a thin blanket of distal storm deposits (Vaucher et al., 2016, 2017; Saleh et al.,
522 2020a, 2020d). The observation of escape traces in Bou Izargane suggests that obrution
523 deposits were not enough to kill most benthic animals in this locality (Saleh et al., 2021c),
524 corroborating why preservation is often solely associated with exposed carcasses decaying on
525 the seafloor . This is the case for most sites preserving soft tissues from this Lagerstätte,
526 except the recently discovered one in Taichoute, in which carcasses were transported by
527 sedimentary flows to a setting well below storm wave, where they got dominantly preserved
528 in concretions (Saleh et al., 2022). The very unusual lateral position of the two specimens
529 AA.BIZ15.OI.110 (Fig. 5(B)) and 259 (Fig. 5(A)) possibly results from their desperate and
530 unsuccessful efforts to escape from obrution deposits: the preservation of their cover plates in
531 closed or ajar position implies that these two cornutes were either alive or recently dead when
532 burial occurred (Lefebvre et al., 2022). If this interpretation is correct, the distal aulacophore
533 of AA.BIZ15.OI.110 then appears surprisingly much shorter (stylocone and seven ossicles,
534 with their associated cover plates) and apparently distally truncated, compared to that of
535 AA.BIZ15.OI.259 (stylocone and over 25 ossicles, and associated cover plates). It is possible
536 that the absence of a significant part of the distal aulacophore of AA.BIZ15.OI.110 results
537 from its autotomy, which is widespread in extant echinoderms submitted to stressful
538 conditions (Ausich, 2021).

539 The relatively wide range of skeletal disarticulation exhibited by the Z-F4(15) cornutes
540 makes it possible to document that this process did not occur randomly but always following

541 the same order, with some parts of their skeleton forming more resistant modules than others.
542 The resulting taphonomic sequence of skeletal disarticulation documented in Bou Izargane
543 (Fig. 7) largely confirms the preliminary results of Martin et al. (2015) and their identification
544 of successive taphonomic grades in cornutes (see also Lefebvre et al., 2022). Experimental
545 studies on extant echinoderms indicate that muscles decay faster than ligaments (Ausich,
546 2021). This probably explains the ligament-induced opening of the cover plates (taphonomic
547 grade 1b; Fig. 7(B)), as a consequence of the decay of the muscles maintaining them in ajar
548 position in life (Fig. 7(A); Lefebvre et al., 2022). In cornutes, the next biostratinomic stage
549 (Fig. 7(C)) corresponds to the loss of the cover plates, the disarticulation of the long posterior
550 thecal spines (glossal and digital), and the collapse of integumentary areas (taphonomic grade
551 2). This stage is followed by the loss of the distal appendage ossicles and the progressive
552 disarticulation and collapse of most marginals (taphonomic grade 3a). At this stage, the
553 stylocone, the proximal rings and the anterior-most thecal plates framing the aulacophore
554 insertion are still tightly articulated to each other and constitute a relatively decay-resistant
555 module (Fig. 7(D)). The subsequent loss of the stylocone and increased disarticulation of
556 thecal plates are generally associated to the collapse (taphonomic grade 3b; Fig. 7(E)),
557 disarticulation, and loss of proximal rings (taphonomic grade 4; Fig. 7(F)). The last
558 biostratinomic stage (Fig. 7(G)) corresponds to totally dissociated, scattered skeletal elements
559 (taphonomic grade 5).

560 Soft tissue preservation in stylophorans from the Z-F4(15) lens was limited to a very low
561 number of specimens. The same phenomenon occurs also in the Hunsrück Slate (Emsian,
562 Germany). Although this Lagerstätte yielded hundreds of fully articulated ophiuroids
563 pyritized soft parts (ambulacral tube feet) have only been reported in six specimens of
564 protasterids (Glass and Blake, 2004). Similarly, although trilobites are abundant in the Z-
565 F4(15) lens, lightly sclerotized appendages are exceptionally preserved only in a minority of

566 individuals (Martin, 2016). Moreover, although pyritization played a major role in soft tissue
567 preservation in Bou Izargane cornutes, not all specimens were equally pyritized. The most
568 complete specimen in terms of exceptional preservation is AA.BIZ15.OI.259 (Fig. 5(A)), in
569 which both the water-vascular and digestive systems are entirely pyritized. Pyritization is less
570 complete in AA.BIZ15.OI.110 (Fig. 5(B)), as only the digestive system is preserved. Finally,
571 in AA.BIZ15.OI.58, 80 and 132 (and less convincingly in five additional specimens; see
572 above), pyritization is restricted to the fore-gut (Figs 6, 9(D, E)). These observations indicate
573 that in most cases, soft parts decayed and disappeared prior to the establishment of permissive
574 conditions suitable for their pyritization.

575 As skeletal remains of Bou Izargane cornutes document a wide biostratigraphic range from
576 alive or recently dead organisms (taphonomic grade 1a) to totally disarticulated individuals
577 (taphonomic grade 5), it can be postulated that the different degrees of pyritization are also
578 the result of varying pre-burial decay of soft parts (Fig. 7). This implies that, when burial
579 occurred, a freshly killed organism had a greater chance of retaining soft parts, that
580 could be eventually pyritized than another individual decaying on the sea floor for several
581 days or weeks (Parry et al., 2018; Saleh et al., 2020a, 2021a). This pre-burial decay of soft
582 parts is not random in Z-F4(15) cornutes, as the oesophagus is the most frequently preserved
583 organ, whereas the water vascular system occurs only in one specimen. This preservational
584 heterogeneity of soft-tissues can be correlated to skeletal element disposition and
585 disarticulation in stylophorans (Fig. 7; Martin et al., 2015).

586 The progressive disarticulation of the cornute skeleton certainly played a key role during
587 decay by creating different and separate microenvironments within the carcass, thus,
588 controlling the access of scavengers, sea water, and decaying bacteria. In this context, cover
589 plates are the most delicate skeletal elements and the first parts to disarticulate, thus directly
590 exposing the water vascular system (taphonomic grade 1b; Fig. 7(B)). Concomitantly, the

591 collapse of integumentary areas and the progressive disarticulation of marginals certainly
592 result in the disappearance of the intrathecal cavity (taphonomic grade 1b; Fig. 7(B)). Until
593 their final disarticulation, the stylocone, the proximal aulacophore and associated anterior-
594 most thecal plates together formed the most resistant skeletal module in cornutes (taphonomic
595 grade 3a; Fig. 7(B–D)). In life, this module was housing powerful muscles and the
596 oesophagus. This remarkable correlation between skeletal disarticulation, and the distribution
597 and frequency of exceptionally preserved soft parts within the body are in good accordance
598 with results from probabilistic modelling highlighting that the presence of solid mineralized
599 skeletal parts favoured the preservation of underlying soft-tissues within the Fezouata Shale
600 (Saleh et al., 2020d, 2021c). The role of proximal rings in preserving the oesophagus might
601 not have been limited to slowing down pre-burial decay by isolating the tissue from its
602 surrounding environmental conditions. It is most likely that the relatively closed environment
603 within proximal rings also created more permissive conditions for pyrite precipitation than in
604 the rest of the carcass. All these suggestions do not exclude that the favourable
605 preservation/loss of some tissues might be controlled as well, at least partially, by their own
606 chemical compositions, enzymes, and bacterial communities (Lerosey-Aubril et al., 2012;
607 Hancy and Antcliffe, 2020).

608

609 **7. Conclusions**

610 A single upper Tremadocian level of the Fezouata Shale (i.e. the Z-F4(15) lens at Bou
611 Izargane, Zagora area, Morocco) yielded a low diversity assemblage dominated by cornutes
612 (more than 400 specimens belonging to three distinct taxa), associated with arthropods
613 (marrellomorphs, trilobites), brachiopods, graptolites, and worm-like organisms. The detailed
614 biostratinomic analysis of this stylophoran dense bed made it possible to reconstruct with
615 unprecedented detail the sequence of skeletal disarticulation in cornutes originally proposed

616 by Martin et al. (2015). Moreover, structures preserved within the skeleton of several cornutes
617 from Z-F4(15) represent replicates of original tissues in pyrite crystals (Lefebvre et al., 2019;
618 Saleh et al., 2020a). Here, we suggest that the frequency and distribution of exceptionally
619 preserved soft parts in cornutes is not random but directly controlled by their heterogenous
620 exoskeleton. Their water vascular system is only partially protected by moveable cover plates.
621 These plates are the first skeletal elements to disarticulate after death, thus exposing the water
622 vascular system to water chemistry, external bacteria, and scavengers. In contrast, the
623 oesophagus is the last organ to decay, because it is fully protected by resistant proximal rings.
624 The correlation between skeletal element disarticulation and soft tissue degradation in
625 stylophorans highlights that non-random decay pathways exist within echinoderms. However,
626 generalization on different animal groups, and other fossiliferous localities should be made
627 carefully, due to differences in biotic and abiotic conditions.

628

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646

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965 **Figure captions**

966

967 **Fig. 1.** Geographical and geological context of the Bou Izargane locality. **A.** Location of B in
968 Africa. **B.** Location of C and main areas of Ordovician outcrops in northwestern Africa; scale
969 bar: 200 km. **C.** Location of Bou Izargane hill and main areas of Ordovician outcrops in the
970 Zagora area, Central Anti-Atlas (Morocco); scale bar: 50 km. **D.** Sedimentary succession at
971 Bou Izargane hill showing the location of the Z-F4(15) stylophoran dense bed, lower part of
972 the Fezouata Formation (*S. murrayi* Zone; upper Tremadocian); adapted from Martin (2016),
973 Lefebvre et al. (2019), and Saleh et al. (2020b).

974

975 **Fig. 2.** Taxonomic composition and relative abundance of taxa within the Z-F4(15) level at
976 Bou Izargane (Zagora area, Morocco), lower part of the Fezouata Formation (*S. murrayi*
977 Zone; upper Tremadocian); n: number of specimens. **A.** Global composition and relative
978 abundance of main taxonomic groups occurring within the Z-F4(15) low diversity
979 echinoderm dense bed; other taxa include brachiopods, graptolites, marrellomorphs, and
980 worm-like organisms. **B.** Taxonomic composition and relative abundance of the echinoderm
981 component of the Z-F4(15) assemblage. **C.** Taxonomic composition and relative abundance
982 of trilobites within the stylophoran dense bed. Redrawn and modified from Martin (2016).

983

984 **Fig. 3.** Skeletal morphology, orientation and measurement of thecal width (TW) in the
985 cornute stylophoran *Bohemiaecystis* sp. from the lower part of the Fezouata Formation (upper
986 Tremadocian), Zagora area, Central Anti-Atlas (Morocco). Reconstruction of lower side, with
987 cover plates in open, post-mortem position.

988

989 **Fig. 4.** Skeletal morphology and associated soft parts of the cornute stylophoran
990 *Bohemiaecystis* sp. from the lower part of the Fezouata Formation (upper Tremadocian),
991 Zagora area, Central Anti-Atlas (Morocco). **A.** Reconstruction of upper side, with ambulacral
992 tube feet protruding in between ajar cover plates. Some skeletal elements are removed or
993 sectioned, so as to illustrate the internal anatomy. **B.** Longitudinal cross section along A-A' in
994 A.

995
996 **Fig. 5.** Cornutes with exceptionally preserved soft parts, level Z-F4(15), Bou Izargane,
997 Zagora Province, Morocco, lower part of the Fezouata Formation (*S. murrayi* Biozone, upper
998 Tremadocian). All scale bars: 5 mm. **A.** *Bohemiaecystis* sp. (AA.BIZ15.OI.259): complete,
999 fully articulated specimen in lateral aspect (taphonomic grade 1a); pyritized, dark intra-
1000 skeletal structures are preserved in the distal aulacophore (longitudinal ambulacral canal and
1001 regularly spaced tube feet), in proximal rings (fore-gut) and within the theca (mid- and hind-
1002 gut). **B.** *Hanusia* sp. (AA.BIZ15.OI.100): fully articulated individual in lateral view; anterior
1003 truncature of distal aulacophore, possibly resulting from autotomy (taphonomic grade 1a);
1004 pyritized, dark intra-skeletal structures are preserved in proximal rings (spindle-shaped fore-
1005 gut) and also within the theca (mid- and hind-gut).

1006
1007 **Fig. 6.** Cornutes with exceptionally preserved soft parts, level Z-F4(15), Bou Izargane,
1008 Zagora Province, Morocco, lower part of the Fezouata Formation (*S. murrayi* Biozone, upper
1009 Tremadocian). All scale bars: 2 mm. **A.** *Hanusia* sp. (AA.BIZ15.OI.80): complete, slightly
1010 disarticulated theca (in upper aspect), with proximal aulacophore and stylocone (taphonomic
1011 grade 3a); the red, elongate intra-skeletal structure extending longitudinally within the
1012 proximal appendage corresponds to the oesophagus; the fore-gut is tapering both anteriorly
1013 (into the stylocone notch) and posteriorly (towards the thecal apophyses). **B.** *Bohemiaecystis*

1014 sp. (AA.BIZ15.OI.132): incomplete, disarticulated theca, with poorly preserved lamellipores,
1015 and appendage restricted to proximal rings and stylocone (taphonomic grade 3a); the red,
1016 elongate intra-skeletal structure extending longitudinally within the proximal appendage
1017 probably corresponds to the oesophagus. **C.** *Bohemiaecystis* sp. (AA.BIZ15.OI.58): partly
1018 disarticulated, incomplete theca (broken during sampling) and complete, fully articulated
1019 aulacophore, with cover plates in open position (taphonomic grade 1b); the yellow, elongate
1020 intra-skeletal structure extending longitudinally within the proximal appendage probably
1021 corresponds to the oesophagus.

1022

1023 **Fig. 7.** Degradation sequence of the cornute stylophoran *Bohemiaecystis* sp., based on the
1024 observation of 410 individuals from level Z-F4(15), Bou Izargane (Zagora area, Morocco),
1025 lower part of the Fezouata Formation (*S. murrayi* Zone, upper Tremadocian). **A.** Taphonomic
1026 grade 1a. **B.** Taphonomic grade 1b. **C.** Taphonomic grade 2. **D.** Taphonomic grade 3a. **E.**
1027 Taphonomic grade 3b. **F.** Taphonomic grade 4. **G.** Taphonomic grade 5.

1028

1029 **Fig. 8.** Cornutes from level Z-F4(15), Bou Izargane, Zagora Province, Morocco, lower part of
1030 the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian). All scale bars: 2 mm. **A.**
1031 *Bohemiaecystis* sp. (AA.BIZ15.OI.69): three side by side, differently oriented, slightly
1032 disarticulated individuals in upper aspect. **B.** *Bohemiaecystis* sp. (AA.BIZ15.OI.109): slightly
1033 disarticulated theca (with well-preserved lamellipores) in upper aspect, proximal rings and
1034 stylocone; more distal ossicles and cover plates missing (taphonomic grade 3a). **C.** *Hanusia*
1035 sp. (AA.BIZ15.OI.30): slightly disarticulated theca in upper aspect, proximal rings and
1036 stylocone (taphonomic grade 3a). **D.** *Bohemiaecystis* sp. (AA.BIZ15.OI.101): slightly
1037 disarticulated theca in lower aspect, with long spinal blade, proximal aulacophore and
1038 stylocone. **E.** *Bohemiaecystis* sp. (AA.BIZ15.OI.94): poorly preserved, partly disarticulated,

1039 with elongate spinal blade; aulacophore entirely missing (taphonomic grade 4). **F.**
1040 *Bohemiaecystis* sp. (AA.BIZ15.OI.136): on the left, isolated spinal blade (taphonomic grade
1041 5); on the right, stump of fully articulated distal aulacophore consisting of nine ossicles and
1042 associated cover plates in closed position (taphonomic grade 1a), and possibly corresponding
1043 to an autotomized portion of appendage. **G.** *Bohemiaecystis* sp. (AA.BIZ15.OI.202):
1044 incomplete, slightly disarticulated theca in upper view, with distinct lamellipores;
1045 aulacophore consisting of proximal rings and stylocone (taphonomic grade 3a).
1046

1047 **Fig. 9.** Well-preserved cornutes, level Z-F4(15), Bou Izargane, Zagora Province, Morocco,
1048 lower part of the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian). All scale
1049 bars: 2 mm. **A.** *Bohemiaecystis* sp. (AA.BIZ15.OI.249): slightly disarticulated theca in lower
1050 aspect, with well-preserved left posterior spine (digital), and complete aulacophore, with
1051 widely open cover plates (taphonomic grade 1b). **B.** *Bohemiaecystis* sp. (AA.BIZ15.OI.289):
1052 slightly disarticulated theca in lower aspect, with elongate isolated glossal lying posteriorly to
1053 it; proximal rings well-preserved, but more putative more distal parts of aulacophore not
1054 visible (unexposed). **C.** *Bohemiaecystis* sp. (AA.BIZ15.OI.227): fully articulated, complete
1055 theca and aulacophore (in upper aspect), with widely open cover plates (taphonomic grade
1056 1b). **D.** *Hanusia* sp. (AA.BIZ15.OI.67): complete, slightly disarticulated theca in lower
1057 aspect; well-preserved aulacophore with widely open cover plates (taphonomic grade 1b); the
1058 white, elongate intra-skeletal structure extending longitudinally within proximal rings
1059 possibly represents a poorly preserved oesophagus. **E.** *Bohemiaecystis* sp. (AA.BIZ15.OI.41):
1060 slightly disarticulated theca, posteriorly broken during sampling; well-preserved aulacophore,
1061 with widely open cover plates; the white, elongate intra-skeletal structure extending
1062 longitudinally within the proximal aulacophore probably corresponds to the fore-gut. **F.**

1063 *Bohemiaecystis* sp. (AA.BIZ15.OI.235): well-preserved, fully articulated distal aulacophore,
1064 with wide open cover plates, still attached to underlying ossicles.

1065

1066 **Fig. 10.** *Chauvelicystis* sp. (AA.BIZ15.OI.121), Bou Izargane, Zagora Province, Morocco,
1067 lower part of the Fezouata Formation (*S. murrayi* Biozone, upper Tremadocian); scale bar: 2
1068 mm. Fully articulated theca (including very well-preserved supracentral area) and proximal
1069 rings in upper aspect; right thecal side unexposed; distal aulacophore broken during sampling.

1070



















