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Drilling predation on spatangoid echinoids from the Miocene
of Sardinia: a taphonomic and paleoecological perspective

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Abstract:	Spatangoid echinoids appeared in the Early Cretaceous and became highly diversified in the Cainozoic colonizing a wide spectrum of marine environments and showing a high morphological variability. Predation is considered of primary importance in driving morphological adaptations and thus the ecological and evolutionary dynamic of spatangoids as well as affecting their preservation potentials. Herein, the spatangoid-dominated Miocene carbonate succession of Punta Foghe (Montiferru area, central-western Sardinia, Italy) is studied with the aim of reconstructing the paleoenvironmental conditions and investigating abiotic and biotic factors, including predation, influencing the

	<p>paleoecology and preservation potential of spatangoid echinoids. The echinoid fauna is dominated by the spatangoid <i>Agassizia</i> and, subordinately, the clypeasteroid <i>Clypeaster</i>, and includes also both regular (undetermined diadematoids and camarodonts), and irregular (<i>Plagiobrissus</i>, <i>Echinocyamus</i> and <i>Koehleraster</i>) forms. Accompanying fauna and flora consist of bivalves, including large ostreids, <i>Spondylus</i> and pectinids, larger benthic foraminifera (<i>Heterostegina</i> and <i>Amphistegina</i>) and coralline algae. Echinoids and associated fauna and flora, along with taphonomic and sedimentological signatures, indicate an inner sublittoral environment with moderate energy conditions affected by high energy events. <i>Agassizia</i> remains, which mainly consist of complete and well-preserved tests, commonly bear subcircular drill holes that are interpreted as the result of cassid gastropod predation and investigated with respect to size selectivity and stereotypy of attack siting. Potential biases by drilling predation and biostratinomy on the preservation potential of spatangoid tests is discussed. Antipredator behavior adopted by the shallow infaunal spatangoid <i>Agassizia</i> are interpreted to rely on gregarious life-history strategies, rather than defense mechanisms and deep burial depths.</p>

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Manuscripts

1 **Drilling predation on spatangoid echinoids from the Miocene of**
2 **Sardinia: a taphonomic and paleoecological perspective**

3

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10

11 **Running Header:** Drilling predation in spatangoid echinoids

12

13 **Abstract.**—Spatangoid echinoids appeared in the Early Cretaceous and became highly diversified in
14 the Cainozoic colonizing a wide spectrum of marine environments and showing a high morphological
15 variability. Predation is considered of primary importance in driving morphological adaptations and
16 thus the ecological and evolutionary dynamic of spatangoids as well as affecting their preservation
17 potentials. Herein, the spatangoid-dominated Miocene carbonate succession of Punta Foghe
18 (Montiferru area, central-western Sardinia, Italy) is studied with the aim of reconstructing the
19 paleoenvironmental conditions and investigating abiotic and biotic factors, including predation,
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21 The echinoid fauna is dominated by the spatangoid *Agassizia* and, subordinately, the
22 clypeasteroid *Clypeaster*, and includes also both regular (undetermined diadematoïds and
23 camarodonts), and irregular (*Plagiobrissus*, *Echinocyamus* and *Koehleraster*) forms. Accompanying

24 fauna and flora consist of bivalves, including large ostreids, *Spondylus* and pectinids, larger benthic
25 foraminifera (*Heterostegina* and *Amphistegina*) and coralline algae. Echinoids and associated fauna
26 and flora, along with taphonomic and sedimentological signatures, indicate an inner sublittoral
27 environment with moderate energy conditions affected by high energy events. *Agassizia* remains,
28 which mainly consist of complete and well-preserved tests, commonly bear subcircular drill holes
29 that are interpreted as the result of gastropod predation and investigated with respect to size
30 selectively and stereotypy of attack siting. Potential biases by drilling predation and biostratigraphy on
31 the preservation potential of spatangoid tests is discussed. Antipredator behavior adopted by the
32 shallow infaunal spatangoid *Agassizia* are interpreted to rely on gregarious life-history strategies,
33 rather than defense mechanisms and deep burial depths.

34

35 **Introduction**

36

37 Spatangoids constitute a successful group of irregular echinoids which appeared in the Early
38 Cretaceous (Barremian) (Villier and Navarro, 2004; Villier et al., 2004; Stockley et al., 2005; Kroh
39 and Smith, 2010), leaving a rich fossil record (Villier et al., 2004; David et al., 2009). Fossil
40 spatangoid-dominated assemblages are well documented and show a wide distribution (e.g.,
41 Néraudeau, 1991; Radwański and Wysocka, 2001; Kroh, 2003; Kroh and Nebelsick, 2003; Zamora et
42 al., 2008; Smith and Gale, 2009; Stara et al., 2012; Mancosu and Nebelsick, 2017a, 2019; Martínez
43 and Del Rio, 2017; Caron et al., 2019; Palópolo et al., 2021 and references therein).

44 Spatangoids highly diversified in the Cainozoic, with the majority of extant families dating
45 back to the Eocene (Smith and Kroh, 2011). They colonized a wide spectrum of marine environments
46 from littoral to abyssal depths (Stockley et al., 2005) and display a wide variety of test shapes and
47 morphological features related to their mode of life and environmental conditions (e.g., Saitoh and

48 Kanazawa, 2012, 2019). Spatangoids predominantly have a burrowing habit which is considered as
49 the key innovation explaining their success (Kier, 1974), allowing access to unexploited food
50 resources and escape from predators (Smith, 1984). Their rich fossil record is the result of a
51 combination of factors including their wide distribution in different habitats, related energy and
52 sedimentological conditions as well as varying taphonomic pathways (see discussion in Mancosu and
53 Nebelsick, 2017a).

54 Spatangoids in general have fragile tests that make them prone to breakage and disarticulation
55 when subjected to transportation or reworking. Their burrowing habit prevents or minimizes
56 destructive biostratinomic processes (Schäfer, 1972; Kier, 1977; Néraudeau, 1991) if the echinoid
57 succumbs in their burrows. Additionally, these echinoids live within unconsolidated, mobile
58 substrates in areas of active sedimentation, where rapid final burial under thick layers of sediments
59 prevents the remains to be reworked and destroyed, leading to a high fossilization potential (Ernst et
60 al., 1973; Smith, 1984; Greenstein, 1993; Radwański and Wysocka, 2001; Mancosu et al., 2015;
61 Mancosu and Nebelsick, 2017a).

62 Oxygen deficiency can play a role in preservation potential of spatangoid echinoids inducing
63 emergence on the sediment surface and subsequent death of infaunal forms, as documented for
64 *Echinocardium cordatum* (Nilsson and Rosenberg, 1994) and *Ova canalifera*, tests of which can
65 serve as substratum for epigrowth (Stachowitsch, 1991; Nebelsick et al., 1997). Bioinfestation by
66 encrusting organisms can also increase their chance for preservation on the sea floor (see Ernst et al.,
67 1973; Nebelsick, 2004; Zamora et al., 2008). In addition, dysoxic or anoxic conditions and low water
68 temperature can enhance their preservation potential, delaying soft tissue decay and test
69 disarticulation (see Nebelsick et al., 1997; Banno, 2008; Mancosu et al., 2015; Palópolo et al., 2021).

70 Predation is also considered to be of primary importance in affecting the preservation potential
71 of spatangoids (see discussion in Tyler et al., 2018) and shaping their ecological and evolutionary
72 dynamic (McNamara, 1994; Kanazawa, 2004, 2010), thus influencing the nature of their fossil record.

73 Many different organisms, such as turtles, birds, fishes, sea stars and gastropods prey spatangoid
74 echinoids today (e.g., Chesher, 1969; Hughes, 1986; Nebelsick, 1999; Scheibling, 2013; Sievers et
75 al., 2014; Grun, 2016; Tyler et al., 2018 and references cited therein). Despite these investigations,
76 spatangoids have been poorly studied with respect to predator-prey interaction from a paleoecological
77 and taphonomic perspective. Durophagus predation can destroy the echinoid test while feeding,
78 leaving few recognizable fragments of the prey and may be difficult to distinguish from damage
79 caused by post mortem breakage. By contrast, gastropod predation producing discrete, small holes in
80 the echinoid test which can not only be common, but also allow for detailed investigations on size
81 and site selectively, distribution among different facies within sedimentary environments, defense
82 mechanisms and the co-evolution of predator and prey (e.g., Nebelsick, 1999; Kowalewski and
83 Nebelsick, 2003; Farrar et al., 2020; Petsios et al., 2021).

84 Drilling predation is documented on a number of spatangoids, including *Plagiobrissus*,
85 *Meoma*, *Echinocardium*, *Lovenia*, *Brissus* and *Spatangus* (Moore, 1956; Chesher, 1969; Hendler,
86 1977; Hughes and Hughes, 1981; Hughes, 1986; Gerace and Lindsay, 1992; Lindsay, 1996; Dexter,
87 2011; Tewfik, 2014; Tyler et al., 2018; personal observations) and is attributed by present-day cassid
88 gastropods (Tonnacea), such as *Cassis tuberosa*, *C. madagascarensis* and *C. cornuta*, *Cypreacassis*
89 *testiculus* and *Galeodea echinophora*. Evidence of drilling predation attributes to gastropods has also
90 been recognized in fossil spatangoids, including *Hemiaster*, *Micraster*, *Pericosmus*, *Lovenia*,
91 *Eupatagus*, *Brissopsis*, and various schizasterid echinoids (e.g., Beu et al., 1972; Kier, 1981; Gibson
92 and Watson, 1989; McKinney and McNamara, 1991; McNamara, 1994; Rose and Cross, 1993; Miller
93 and Walker, 2009; Mancosu and Nebelsick, 2017a).

94 Herein, a spatangoid-rich sedimentary succession from the Early-Middle Miocene of Punta
95 Foghe (central-western Sardinia; western Mediterranean) is studied with the aim of reconstructing
96 paleoecological and associated paleoenvironmental conditions, and investigating abiotic and biotic
97 factors, including predation, influencing the preservation potential of spatangoid echinoids. This is

98 accomplished by 1) detailed logging of sedimentary facies, 2) applying the functional morphological
99 reconstructions of echinoid skeletons and interpreting their behavior and life habits, 3) quantifying
100 various taphonomic features of test preservation, and 4) investigating predatory patterns, such as
101 drilling intensities, size, and site selectivity.

102

103 **Geological setting**

104

105 The Oligo-Miocene volcano-sedimentary succession of Sardinia consists of three cycles of the
106 following ages (1) Chattian to early Burdigalian; (2) a late Burdigalian to early Serravallian; and (3)
107 Serravallian to early Messinian (Assorgia et al., 1997a, c). This succession is predominately present
108 in the NNW-SSE-oriented Sardinian Basin (Fig. 1.1), a tectonic trough that extends from the Gulf of
109 Sassari in the northwest to Cagliari in the south and comprises a number of minor sub-basins, which
110 originated during Oligo-Miocene tectonic movements of the Corsica-Sardinia microplate (Cherchi
111 and Montandert, 1982; Thomas and Gennesseaux, 1986; Carmignani et al., 2001; Facenna et al.,
112 2002; Speranza et al., 2002).

113 The sedimentary succession studied herein is located in the central-western part of the
114 Montiferru area (central-western Sardinia) (Fig. 1.1-1.3) along the coast between the village of Santa
115 Caterina di Pittinuri and Punta Foghe (Cuglieri/Tresnuraghes) and pertains to the second sedimentary
116 cycle (Assorgia et al., 1997b; Carboni et al., 2010). In the Montiferru area, the Miocene volcano-
117 sedimentary sequence commences with andesitic lavas and pyroclastic deposits of rhyolitic and
118 dacitic composition (Assorgia et al., 1997b; Bottero et al., 2002 and references cited therein) dated
119 by the K–Ar method to 19–16 Ma and 17–13 Ma, respectively (Assorgia et al., 1997a,b and references
120 cited therein). These deposits are followed by heterometric conglomerates, epiclastites and
121 volcanoclastic deposits of fluvio-lacustrine origin (Assorgia et al., 1997b and references cited therein;

122 Mighela et al., 1997). The succession continues with a thick marine carbonate sedimentary sequence
123 ranging from Late Burdigalian to Early Serravallian based on their stratigraphic position and
124 macrofossil content (Comaschi Caria, 1951; Assorgia et al., 1997b; Carboni et al., 2010). This
125 succession consists of calcarenites and bioclastic limestones, passing upward to fine-grained
126 lithologies dominated by bivalves and echinoids (see Mancosu and Nebelsick, 2019).

127 Miocene sedimentary deposits are unconformably overlain by subaerial, fluvio-deltaic
128 sandstones and conglomerates intercalated with Pliocene to lower Pleistocene basanites as well as
129 trachytic and phonolitic lava flows (Beccaluva et al., 1974; Assorgia et al., 1997b; Carboni et al.,
130 2010). As noted by Mighela et al. (1997), the tectono-sedimentary development and the stratigraphic
131 framework of the Montiferru area is comparable in part to that of the well-known Logudoro and Porto
132 Torres Basins (Northern Sardinia) as described by Mazzei and Oggiano (1990) and Funedda et al.
133 (2000, 2003).

134 The Early-Middle Miocene carbonate sedimentary sequence cropping out along the coast
135 between S'Archittu-Santa Caterina di Pittinuri and Punta Foghe consists at the base of grainstones,
136 floatstone and rudstones, containing the echinoid assemblages studied herein, passing upward to fine-
137 grained lithologies (calcareous sandstones, mudstone, wackestones and packstones). Fossil content is
138 dominated by echinoid remains which occur throughout the sedimentary sequence and have been
139 described in part by Comaschi Caria (1951, 1972) and Mancosu and Nebelsick (2019).

140

141 **Material and methods**

142

143 Paleontological, taphonomic and sedimentological analyses were conducted in the field and
144 laboratory. Complete and fragmented echinoid tests were observed and can be attributed to specific
145 echinoid taxa at least at genus level due the presence of specific morphological features. Taxonomic

146 classification at and above genus level follows Smith and Kroh (2011), and Kroh (2020) and
147 Mongiardino Koch and Thompson (2021), respectively.

148 A stratigraphic section (Fig. 2) was measured in which echinoid remains are common
149 throughout. The sedimentary succession was investigated in detail with respect to diversity and
150 relative abundance of echinoids and accompanying fauna and flora, fossil orientation as well as
151 taphonomic and sedimentological features. Field determinations include the abundance, orientation,
152 preservation and packing fabric (following Kidwell and Holland, 1991). Taphonomic signatures such
153 as disarticulation, fragmentation, abrasion, encrustation and bioerosion were evaluated. Abrasion,
154 encrustation and bioerosion were evaluated on both fragments and complete specimens. Surface
155 abrasion was distinguished by noting the presence or absence of tubercles on the test surface. The
156 fabric of the assemblages was analyzed by recording the orientation of complete specimens relative
157 to the bedding plane. The study of the sedimentary succession was based on field observations and
158 microfacies analysis of thin-sections cut in samples selectively collected from different levels
159 recognized in the field, with the aim to assess facies changes across the sedimentary sequence.
160 Identification of carbonate rocks follows Lokier and Junaibi (2016).

161 Life habit of the fossil echinoids results from the functional morphological interpretation of
162 skeletal features based on Nichols (1959), Smith (1980), and Kanazawa (1992), and actualistic
163 comparisons to closely related extant taxa. Terminology of the echinoid test follows Smith and Kroh
164 (2011).

165 Spatangoid tests were obtained by surface collecting and examined for evidence of predation.
166 Drilled tests were analyzed for drilling intensity, drill hole dimension, drill hole morphology and size
167 and site selectivity. Maximum and minimum drill hole diameters were measured from photographs
168 using ImageJ software. As the diameter of drill holes made by gastropods correlates with the size of
169 the predator (Hughes and Hughes, 1981), drill holes were analyzed for their maximum length with
170 respect to the length of the drilled test in which they occur, thus testing for a possible size selectively

171 of the predator. In addition, size selectivity was examined by comparing drilled and undrilled test size
172 distribution. All linear measurements on the echinoid test were conducted using a caliper with an
173 accuracy of 0.02 mm. To assess site selectivity, the position of drill hole center was detected by
174 dividing the test of *Agassizia* into eight sectors (1-8) by three perpendicular planes, dividing the test
175 in a right/left side, aboral/oral side and anterior/posterior side, respectively (Fig. 3). Statistical
176 analyses were performed with Past 4.03 (Hammer et al., 2001). Samples are stored in the
177 Dipartimento di Scienze Chimiche e Geologiche, Università degli studi di Cagliari.

178

179 **Results**

180

181 *Facies description.*—The sedimentary succession studied herein is ca. 5 meters thick and consists of
182 carbonate lithologies with a very abundant fossiliferous content, including echinoids, bivalves,
183 coralline algae, and larger benthic foraminifera (LBF). Five facies were recognized based on lithology
184 and fossil content (Fig. 2).

185 The sedimentary succession starts with coralline algae floatstones to rudstones (Facies 1) with
186 the common occurrence of disarticulated valves of ostreids and *Spondylus*, followed by calcareous
187 sandstones (Facies 2). The fossil content in Facies 2 is dominated by the spatangoid echinoid
188 *Agassizia*, which occur very commonly, with subordinate amounts of the clypeasteroid *Clypeaster*
189 showing different morphotypes. The larger benthic foraminifera *Heterostegina* also occur commonly,
190 along with rare *Amphistegina*, and smaller benthic foraminifera including rotaliids, elphidiids and
191 miliolids. Further macrofossils also include large ostreids, *Spondylus* and small pectinid bivalve.

192 Calcareous sandstones pass gradually to floatstone/rudstone (Facies 3) composed of coralline
193 algae and the benthic foraminifera *Heterostegina* in a packstone matrix. Echinoid remains are
194 common and consist mainly of *Clypeaster* with rare *Agassizia*.

195 Coralline algae gradually decrease upward passing to a rudstone with densely packed coquinas
196 (Facies 4), which consist of densely packed, variously oriented and imbricated and mostly fragmented
197 shell remains of *Heterostegina*, with rare *Amphistegina* and miliolids. *Clypeaster* remains (Fig. 4) are
198 very common with the sporadic occurrence of small complete regular echinoids (possibly small
199 *Schizechinus*). A single test remain of the echinoneoid *Koehleraster* was also found.

200 The sedimentary succession ends with floatstones to rudstones (Facies 5) in a bioclastic
201 packstone matrix. The fossil content is dominated by echinoid remains (Fig. 5) and larger benthic
202 foraminifera, including *Heterostegina* and rare *Amphistegina*, which can be present as complete and
203 fragmented shell remains. Very rare small benthic foraminifera (rotaliids and miliolids) are also
204 present. The echinoid fauna is dominated by *Agassizia*, which occur abundantly, reaching density of
205 60 individual/m². *Clypeaster* remnants also occur very commonly. Test fragments of a large
206 spatangoid, possibly *Plagiobrissus* (Fig. 6A), and regular echinoid remains, including a single
207 fragmented diadematoïd spine, a rotula and isolated interambulacral plates are also present.
208 Specimens of the minute clypeasteroid *Echinocyamus* (Fig. 6B) are also present. Pectinid bivalves
209 are represented by disarticulated and fragmented remains.

210

211 *Echinoid taphonomy*.—The echinoid remains occur abundantly throughout the succession and range
212 from loosely packed to dispersed (sensu Kidwell and Holland, 1991). The echinoid fauna shows a
213 low diversity, being mainly dominated by *Agassizia* and *Clypeaster*.

214 Remnants of the spatangoid *Agassizia*, in facies 2 and 5 consist of both complete specimens
215 lacking spines (Fig. 5) as well as large test fragments, which occur sporadically. The orientation of
216 complete tests ranges from concordant to perpendicular (specimens lying on their sides) to the
217 bedding plane. Evidence for abrasion is lacking as echinoid tests and their fragments are very well
218 preserved with respect to surface details. Tests commonly bear subcircular to slightly elongated holes
219 (Fig. 7).

220 *Clypeaster* remains are present predominantly as test fragments (Fig. 4.1) ranging from those
221 representing up to half test size to pie-shaped portions and smaller fragments. Both inter- and
222 intraplate fragmentation are present. Complete specimens are also present, though rare. Both
223 complete specimens and fragments show orientations ranging from concordant to perpendicular to
224 the bedding plane. Small fragments can be readily recognized due to the small evenly distributed
225 sunken tubercles on the surface as well as presence of internal support structure in the interior of the
226 test. Complete specimens are well-preserved displaying surface details, while the preservation of
227 fragments ranges from well preserved to abraded. Encrustation by coralline algae occurs on test
228 fragments. Bioerosion is present on *Clypeaster* test fragments as multiple closely spaced, circular to
229 sub-circular holes, affecting both oral and aboral side (Fig. 4.2).

230 Minute undetermined regular echinoids, and the irregulars *Koehleraster* and *Echinocyamus*
231 are present as complete tests. By contrast, the remains of diadematid echinoids and large spatangoids
232 (possibly *Plagiobrissus*) occur exclusively as spine and test fragments, respectively. The sediment
233 infilling the echinoid tests is identical to that of the embedding rock.

234
235 *Drill holes in Agassizia*.—The spatangoid *Agassizia*, which ranges in test length from 7.12 to 25.3
236 mm with a mean of 16.12 mm (Fig. 8.1), is affected by drill holes on 35 out of 78 complete (44.87%)
237 specimens selected for this study. Undrilled tests have a mean in length of 15.53 mm (Fig. 8.2). The
238 drilled tests range from 10 to 24 mm in length with a mean of 16.83 mm (Fig. 8.3). The drill holes
239 range from 0.94 to 3.8 mm in maximum length, with a mean of 2.24 mm (Fig. 8.4). These holes are
240 subcircular to slightly elongated in outline with smooth to fairly irregular margins and can be
241 attributed to the trace fossil *Oichnus simplex*. A strong correlation ($r = 0.92$) between the maximum
242 and minimum diameter of the drill hole is present (Fig. 8.5). There is a weak positive correlation ($r =$
243 0.11) between test length and maximum drill hole length (Fig. 8.6). All bored specimens bear single
244 drill holes which completely penetrate the test. The drill holes are predominantly (74.28%) located

245 on the aboral side (Fig. 9.1) with a slight difference in test length between aborally (mean 17.21 mm)
246 and orally (mean 15.73 mm) drilled specimens (Fig. 9.2). There is no apparent preference of drill hole
247 location on either the anterior (51.42%) or the posterior side of the test (Fig. 9.3).

248

249 **Discussion**

250

251 *Paleoenvironment and paleoecological interpretation.*—Based on facies analysis and fossil contents,
252 the Early-Middle Miocene sedimentary succession of Punta Foghe was deposited in a shallow inner
253 sublittoral environment. Taphonomic and sedimentological signatures suggest moderate energy
254 conditions affected by high energy events.

255 *Agassiza* is well represented in facies 2 and 5 indicating shallow settings with sandy
256 sediments. Currently, this genus includes two extant species, both of which are restricted to tropical
257 seas, *A. scobiculata* having a bathymetric distribution from littoral to shallow sublittoral depths, while
258 *A. excentrica* is more common at greater depths, from sublittoral to bathyal zones (Mortensen, 1951;
259 Chesher, 1972; Serafy, 1979; Kier, 1984; Lessios, 2005; Alvarado et al., 2010; Galván-Villa et al.,
260 2018; Gondim et al., 2018). Species of *Agassizia* are deposit feeders living infaunally in fine sands
261 and sandy-muddy sediments (Mortensen, 1951; Chesher, 1972; Serafy, 1979; Galvan-Villa et al.,
262 2018; Gondim et al., 2018). *Agassizia* from the Miocene of Punta Foghe is morphologically very
263 similar to *A. scrobiculata*, the type species of the genus, which has a small to medium globular test
264 with no anterior sulcus, an anterior ambulacrum (III) narrow and weakly depressed adapically with
265 uniseriably arranged small pore-pairs bearing small penicillate tube-feet. The other ambulacra are
266 petaloid and weakly sunken. Pores in the anterior column of the anterior petals are entirely
267 rudimentary. Peripetalous and lateroanal fascioles are present.

268 *Agassizia* from the Miocene deposits studied herein is interpreted as a shallow infaunal form.
269 Since this echinoid lacks respiratory tube-feet in the distal half of the anterior column of the anterior
270 paired petals, it did not have the ability to develop a long respiratory funnel through the sediments to
271 the surface and could thus not burrow deeply. *Agassizia* is not common in the Miocene sedimentary
272 sequences of Sardinia. It is reported to occur in association with the scutellid *Amphiope* within coarse-
273 grained (conglomeratic) levels of the Mores Formation (Lower Miocene) which represents littoral
274 environments with moderate energy conditions (Mancosu and Nebelsick, 2013). A single test was
275 also found in fine-grained sandstones of Porto Torres (Lower-Middle Miocene) associated to a
276 spatangoid-dominated fauna reflecting deeper sublittoral environments (Mancosu and Nebelsick,
277 2017a).

278 *Clypeaster* is also common in the examined deposit of Punta Foghe (from facies 2 to 5). Extant
279 representatives of the genus *Clypeaster* mostly inhabit soft-bottom areas of shallow continental
280 shelves (e.g., Nebelsick, 2020 and references therein). In the succession studied herein, *Clypeaster* is
281 represented by different morphotypes, including *C. calabrus*, *C. latirostris* and *C. marginatus*. Based
282 on morphological features and comparison with recent analogues (see discussion in Mancosu and
283 Nebelsick, 2015, 2016 and 2017b), *Clypeaster calabrus* morphotype, with its highly-domed test with
284 thick and tumid margins and flat oral surface, and *Clypeaster latirostris* morphotype, with a lower
285 test and relatively thin margin, are interpreted as epibenthic and semi- to shallow infaunal forms,
286 respectively. These morphotypes occur frequently in the Miocene sedimentary deposits of shallow
287 water settings (see Mancosu and Nebelsick, 2015, 2016, 2017b and discussion therein). *Clypeaster*
288 *marginatus* morphotype with a low, flattened test and thin margins is interpreted as shallowly buried
289 to partially burrowed form. It rarely occurs in association of other *Clypeaster* morphotypes in shallow
290 sublittoral environments and more commonly as a minor component in spatangoid-dominated
291 assemblages of moderately deep sublittoral environments (Mancosu and Nebelsick, 2015, 2017b,
292 2019).

293 In the Facies 5, the echinoid assemblage also includes the brissid spatangoid *Plagiobrissus*,
294 *Echinocyamus* and *Koehleraster*. Modern representatives of *Plagiobrissus*, such as *P. grandis*, are
295 mainly shallow water forms although it has been recorded at depth of 200 m and more (Mortensen,
296 1951; Serafy, 1979). *Plagiobrissus grandis* lives buried in shallow water sandy areas (Chesher, 1969;
297 Serafy, 1979; Hendler et al., 1995; Gondim et al., 2018 and references cited therein) and is typically
298 found buried at a depth of 50 mm (Kier and Grant, 1965). Cassid gastropods, including *Cassis*
299 *tuberosa* and *C. madagascariensis* are the main predators of *Plagiobrissus* (Moore, 1956) that when
300 buried, exposes its long aboral spines, possibly as a defense against predators (Hendler et al., 1995).
301 *Plagiobrissus* is very rare in the sedimentary succession of Punta Foghe as well as in other Miocene
302 fossil deposits of Sardinia. In the Montiferru area, it is found associated with *Clypeaster marginatus*
303 in fine-grained sandstones.

304 Extant representatives of the genus *Echinocyamus*, including *E. pusillus* from the
305 Mediterranean and Atlantic Ocean, show a wide ecological distribution ranging from shallow waters
306 down to 1250 m depth (Mortensen, 1948b; Ghiold, 1982; Grun et al., 2014). *Echinocyamus pusillus*
307 commonly occurs nearshore at depth from 2 to 50 m (Tortonese, 1965; Zavodnik, 2003). It inhabits
308 coarse sandy to pebbly substrates in areas exposed to extensive wave and tidal current activity, but
309 also in medium sands bordering seagrass meadows (Telford et al., 1983; Telford, 1985; Grun et al.,
310 2014). Another species, *Echinocyamus crispus*, lives in poorly sorted fine sands with seagrass in
311 depths between 20 to 30 m in the Red Sea (Nebelsick, 1992a, b; Nebelsick and Kowalewski, 1999).
312 *Echinocyamus* is common if not locally abundant in the Miocene of Sardinia and occurs in littoral,
313 shallow and deep sublittoral settings, commonly co-occurring with spatangoid echinoids (Mancosu
314 and Nebelsick, 2016, 2017a, 2019).

315 The single specimen of *Koehleraster* recognized herein shows a strict morphological affinity
316 to the recent echinoneoid *Koehleraster abnormalis* (see Smith and Kroh, 2011), the ecology of which
317 is poorly known. *Koehleraster* (previously attributed to the genus *Echinoneus*) occurs in the Indo-
318 Pacific (Ghiold, 1989; Arachchige et al., 2019) from the intertidal to 85 m (Mortensen, 1948a; Lane

319 et al., 2000). It is reported to inhabit sands under coral heads in lagoon grass flats and under boulders
320 in shallow sublittoral environments (Sloan et al., 1979; Lane et al., 2000). *Koehleraster* occurs rarely
321 within the Miocene sequences of Sardinia in shallow and moderately deep sublittoral settings (see
322 Mancosu and Nebelsick, 2017a,b).

323 The remains of large oysters and *Spondylus*, which are commonly associated to clypeasteroid
324 echinoids, are consistent with other Miocene shallow water depositional settings of Sardinia
325 (Mancosu and Nebelsick, 2017b). Throughout the section, the presence of coralline algae points to
326 the photic zone, as does the presence of the larger benthic foraminifera *Heterostegina* and
327 *Amphistegina* which are symbiotrophs and today occur in tropical and warm-temperate seas (e.g.,
328 Reiss and Hottinger, 1984; Betzler et al., 1997; Langer and Hottinger, 2000; Eder et al., 2016).
329 *Heterostegina* is found to prefer living on hard substrates (Reiss and Hottinger, 1984), in clear water,
330 it may reach >100 m depth with the optimal range between 40 and 70 m (Hottinger, 1983, 1997;
331 Hohenegger, 1994). In the Oligo-Miocene, it is reported to inhabit high energy forereef environments
332 (BouDagher-Fadel et al., 2000) of 20–30 m depth (Banner and Hodgkinson, 1991). Living
333 *Amphistegina* is adapted to high-energy conditions although this species also occurs in mud-free
334 sands in areas of seagrass or coralline algae and in reefal areas down to depths of 35m (McKee et al.,
335 1959). *Amphistegina* is found in water depths not exceeding 130 m (Hallock, 1999) but its main depth
336 range is reported at 5–20 m (Murray, 1973).

337 The taphonomic and sedimentary signatures are consistent with a shallow water setting with
338 moderate energy conditions, with sporadic high energy events and related episodes of rapid
339 sedimentation. Differences in the state of preservation between the spatangoid *Agassizia* and the
340 clypeasteroid *Clypeaster* can be recognized. *Agassizia* remains occur almost exclusively as complete
341 pristine tests, though lacking spines. In contrast, *Clypeaster* is present in a spectrum of preservation
342 states ranging from well-preserved specimens to highly fragmented remains with evidence of
343 encrustation and bioerosion, with multiple circular holes (*Entobia*) representing post-mortem
344 colonization by endolithic organisms.

345 During high-energy events, spatangoids living within their shallow burrows and their freshly
346 dead fragmented remnants, could be scoured out, and then after limited transport be smothered by a
347 thick layer of sediment. This led to excellently preserved surface preservation of both complete tests
348 and larger fragments. *Agassizia* remains lying on the surface for a prolonged amount of time were
349 readily fragmented and destroyed being thin and fragile. By contrast, *Clypeaster*, with their thick and
350 robust tests, experienced longer surface residence times, and were exposed to biostratinomic
351 processes including fragmentation and bioinfestation. This resulted in the preservation of small
352 abraded, encrusted and bioeroded fragments along with well-preserved, complete test remains. The
353 accumulation of larger benthic foraminifera, with densely packed complete and fragmented shells
354 showing imbrication, is consistent with episodes of high energy conditions.

355 The carbonate succession studied herein pertains to the lower portion of the thick sedimentary
356 succession cropping out along the coast of the Montiferru area (see Mancosu and Nebelsick, 2019).
357 The echinoid fauna represents somewhat shallower sublittoral environments than those described by
358 Mancosu and Nebelsick (2019), which are characterised by a more diversified echinoid fauna,
359 including regular forms, such as the diadematoid *Diadema* and the camarodonts *Tripneustes* and
360 *Schizechinus*, and irregular echinoids, with the clypeasteroids *Clypeaster marginatus* and
361 *Echinocyamus* and different spatangoid taxa, including *Brissopsis*, *Hemipatagus*, *Echinocardium* and
362 various (diverse) schizasterids, typical of the fine-grained facies of outer sublittoral environments.

363
364 *Predation in spatangoid taphonomy and paleoecology.*—The drill holes on *Agassizia* tests are
365 interpreted herein as the result of predation by cassid gastropods. The attribution is supported by the
366 general shape and size of the bore holes and the well documented gastropod–echinoid interactions as
367 found in living populations of both regular and irregular echinoids, including spatangoids (e.g.,
368 Moore, 1956; Hughes and Hughes, 1971; Hughes, 1986; Gerace and Lindsay, 1992; Lindsay, 1996;
369 Grun, 2017; Tewfik and Scheuer, 2013; Tyler et al., 2018).

370 Moore (1956) observed *Cassid madagascarensis* preying during the day upon the shallow
371 infaunal spatangoid *Plagiobrissus grandis*. The cassid gastropod ploughs and burrows into the sand
372 substrate at a sharp angle in pursuit of the prey which is then removed from the sediment. After the
373 predatory attack, the urchin is left with an area of the test devoid of spines within which a circular
374 drill hole is found. Hughes (1986) described in detail the hunting technique used by the cassid
375 *Galeodea echinophora* to prey upon the infaunal spatangoid *Echinocardium cordatum*. After
376 detecting a buried *Echinocardium* by olfaction, the gastropod attacks the infaunal prey, extending its
377 proboscis down through the sediments. Although in some occasions, the prey remains buried
378 throughout the attack, more often *Echinocardium*, by vigorously moving their spines and tube feet,
379 rises to the sediment surface. A few prey specimens were, however, attacked and consumed entirely
380 within the sediment. The predator crawls upon its prey, engulfing the echinoid with its foot, partly
381 removing the echinoid spines, and drilling into the test using its radula and sulfuric acid, whereby a
382 circular puncturing wound is produced. The remaining central disc is then pushed into the test's cavity
383 producing the bore hole. The gastropod extends its long proboscis throughout the interior of the test
384 thereby consuming the internal tissues (Hughes and Hughes, 1981; Hughes, 1986). Cassids generally
385 bore a single hole into the urchin test, although in some cases more than one gastropod individual
386 attack the same prey object, either simultaneously or sequentially, thus producing several bore holes
387 (Hughes, 1986). The cassid *Phalium granulatum* uses a mode of attack while foraging upon buried
388 spatangoids (see Hughes and Hughes, 1981).

389 The measured drilling frequency in *Agassizia* (45.33%) is comparable to levels of gastropod
390 predation on spatangoid echinoids from the Miocene of South Australia as documented for *Lovenia*
391 *forbesi* (32%) and *Eupatagus* ssp. (46-48%) (McNamara, 1994). Higher drilling intensities (96.8%)
392 were documented for the extant *Meoma ventricosa* by Dexter (2011) and Tyler et al. (2018).

393 Statistical analyses performed herein indicate no evidence of size selectivity by predators. As
394 discussed by Grun (2017), cassid predators rarely exhibit size selectivity on their echinoid prey.

395 Nebelsick and Kowalewski (1999) noted that where size selectivity is present, a statistically
396 distinguishable distributions of drilled and undrilled echinoid specimens is expected.

397 Comparison of test length distributions between drilled (mean 16.83 mm; median 17.06 mm)
398 and undrilled tests (mean 15.53 mm; median 15.12 mm) of *Agassizia* indicates a slight, non-
399 significant difference, which suggests that predators did not hunt a distinct size class of prey.
400 Furthermore, predator size, as indicated by drill hole dimensions, is only slightly correlated with prey
401 test size (Fig. 8.6), indicating that distinct size range of cassid predators did not select certain range
402 size of prey. *Agassizia* lived shallowly burrowed within the sediment and occurred in large numbers.
403 It is thus likely that the cassid predator preyed upon randomly encountered echinoids.

404 In contrast to prey size, a clear drilling stereotypy is recognized, with the prey mainly attacked
405 from on the upper, aboral surface (Fig. 9.3). Handling by the predator in a preferred anterior-posterior
406 orientation is, however, not present. The random distribution of drill holes over the aboral surface of
407 *Agassizia*, with fewer incidences occurring on the oral side of the test, is consistent with observations
408 of the distribution of drill holes in the test of extant *Echinocardium* (Hughes, 1986), which also
409 mainly affects the aboral side of the test. This is in contrast with observations on the Caribbean
410 spatangoid *Meoma ventricosa* (Dexter, 2011; Tyler et al., 2018) with the majority of drill holes
411 occurring on the oral side of the test.

412 Drilling predation by cassid gastropods may be an important factor influencing the
413 preservation of spatangoid echinoid tests (see Tyler et al., 2018). Potential predation-related biases
414 should be considered in estimating drilling frequency in relation to predation intensity and size and
415 site selectivity. Cassid predators can enhance the preservation of echinoid tests, preying upon the
416 spatangoids within the sediment. Additionally, they create an enlarged opening and remove internal
417 soft tissue, including the peristomal and periproctal membranes, thus accelerating sediment infill and
418 burial of the test (Tyler et al., 2018). This indicates that echinoid tests preyed by drilling gastropods

419 might have a greater chance of preservation than echinoids killed by durophagous predator, which
420 extensively damage the echinoid test (see Grun, 2016).

421 By contrast, if echinoid tests are weakened by drill holes, they would be more easily destroyed
422 by mechanical, chemical, and biological processes, leading to the underestimation of drilling
423 frequencies. In the case of *Meoma ventricosa*, the high percentage of drilled tests suggests that drill
424 holes did not weaken the test sufficiently to lead to preferential breakage of drilled specimens (Tyler
425 et al., 2018). This was also observed by Nebelsick and Kowalewski (1999) for *Echinocyamus* and
426 *Fibularia* from the Red Sea. Drilling predation may also introduce a size bias when large holes occur
427 on small tests (Grun and Nebelsick, 2015) which become more prone to be destroyed, and when large
428 predators totally destroy the test of a much smaller prey during the hunting process (Grun et al., 2014).

429 The random orientation of complete drilled tests of *Agassizia*, with respect to the bedding
430 plane, and their state of preservation, indicate that predated spatangoids suffered exhumation and
431 limited reworking. The rapid infilling of small-medium tests by fine-grained sediments, which
432 entered through the peristome and periproct, both of which will have lost their membranes through
433 decay, as by the newly produced bore hole, after all internal soft tissues were fed upon by the
434 gastropod predators, possible enhanced the preservation potential. The subsequent overturning and
435 redeposition by high energy events and final burial under thick layer of sediments then led to the
436 preservation of otherwise thin and fragile spatangoid tests.

437 Predation is considered one of the major selective force in the evolution of morphological and
438 behavioral characteristics in marine invertebrates, including species distributions, life habits and
439 population densities (Vermeij, 1977; Bardhan and Chattopadhyay, 2003). Morphological innovations
440 and diversification in spatangoids have been related to the increasing predator pressure by cassid
441 gastropods (Smith, 1984; McNamara, 1994; Kanazawa, 2004, 2010; Saitoh and Kanazawa, 2019),
442 which diversified during the Eocene (Farrar et al., 2020; Petsios et al., 2021). Specialized
443 morphology, refuge by increasing in size and test thickness, infaunalisation, habitat selection,

444 colonization of fine-grained sediments in both deeper water settings or gravelly substrates in shallow
445 unstable environments, and related functional and morphological adaptations, are interpreted as anti-
446 predatory strategies adopted by spatangoids (McNamara, 1994; McKinney and McNamara, 1991;
447 Kanazawa, 2004, 2010; Saitho and Kanazawa, 2019).

448 An antipredator adaptation is suggested for *Agassizia* that depends on high-density
449 populations. *Agassizia* does not appear to possess any specific morphological adaptations to
450 minimizing predation risk, as it lacks the long and robust aboral defensive spines as present, for
451 example, in *Lovenia elongata*, which inhabits shallow water, coarse grained environments (Lawrence
452 and Ferber, 1971; Ferber and Lawrence, 1976). *Agassizia* also lacks the functional adaptation to
453 burrow deeply into the sediment. The gregarious behavior in *Agassizia*, as suggested by the high
454 number of preserved tests, allowed a defensive response against predation by providing safety in
455 numbers in reducing the per capita frequency of attack by predators.

456 Aggregating behavior has been documented in spatangoid echinoids both in shallow and
457 deeper water settings (e.g., Ursin, 1960; Buchanan, 1966; Chesher, 1969; Ferber and Lawrence, 1976;
458 Scheibling, 1982; Norris, 1991; Young et al., 1992; Poulin and Féral, 1995; Hollertz et al., 1998;
459 Nakamura, 2001; Keesing and Irvine, 2013; Pawson and Pawson, 2013). In some cases, aggregation
460 is related to substrate preferences and feeding (Chesher, 1969; Norris, 1991; Poulin and Féral, 1995)
461 and reproduction (Buchanan, 1966); in other, no obvious explanations are provided.

462 Safety in numbers, including the dilution effect of living in dense assemblages, is seen relevant
463 for influencing the possibility of being preyed, as the larger the group of prey animals, the smaller
464 the chance that any given individual will be the prey (e.g., Foster and Treherne, 1981; Lehtonen and
465 Jaatinen, 2016). Defensive aggregating behavior in the regular sea urchins *Strongylocentrotus* and
466 *Echinometra* reducing the intensity of predation by crabs and lobsters and sea stars, respectively, has
467 been discussed by Bernstein et al. (1983) and Morishita and Barreto (2011).

468

469 **Conclusions**

470

471 A spatangoid-dominated sedimentary succession from the Early-Middle Miocene of Sardinia was
472 investigated with respect to abiotic and biotic aspects, including predation, with a paleoecological
473 and taphonomic perspective.

474 The sedimentary succession consists of carbonate lithologies including (containing) a
475 diversified echinoid fauna with the dominance of the spatangoid *Agassizia* and, subordinately, the
476 clypeasteroid *Clypeaster*. Minor components include the irregular echinoids *Koehleraster*,
477 *Plagiobrissus* and *Echinocyamus* and remains of regular echinoids, namely diadematoids and small
478 camarodont echinoids.

479 Echinoid diversity and accompanying fauna (including large ostreids and *Spondylus* and
480 larger benthic foraminifera) and flora (coralline algae), along with taphonomic and sedimentological
481 signatures, support the interpretation of an inner sublittoral environment with moderate energy
482 conditions affected by high energy events.

483 *Agassizia* remains consist predominantly of intact and well-preserved tests which commonly
484 bear subcircular drill holes that are interpreted as cassid gastropod predation. Frequency of drilling
485 predation (44.87%) and behavior of predatory gastropods, with no echinoids featuring multiple drill
486 holes, indicate a high drilling success for the cassids on these infaunal spatangoids. A slight statistical
487 difference in test length between drilled and undrilled specimens along with a weak correlation
488 between predator-prey dimension indicate no size selectivity by cassid predators. Site selectivity is
489 observed with attack sites favoring the aboral side of spatangoid test (74.28%). Drilled spatangoid
490 tests undergone exhumation and rapid infilling by fine-grained sediments, trough the periproct and
491 peristome, along with the bore holes produced by gastropod predators. Subsequent overturning and
492 re-sedimentation of the tests by high energy events, with final burial under thick layer of sediments,
493 promote the preservation of thin and fragile spatangoid tests.

494 Potential biases related to drilling predation and biostratinomy are considered for a more
495 thorough understanding of the relationship between drilling frequency and predation intensity.

496 Antipredator behavior adopted by the shallow infaunal spatangoid *Agassizia* in inner
497 sublittoral environments with high predation rates by cassid gastropods possibly rely on gregarious
498 life-history strategies, rather than defense mechanisms and deep burial depths.

499

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501

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892

893 **Figure captions**

894

895 **Figure 1.** (1) Distribution of Miocene sedimentary rocks in Sardinia and location of the study area;
896 (2) Simplified geological map of the study area (modified from Carboni et al., 2010) with the
897 location of the stratigraphic section measured herein; (3) Panoramic view of the volcano-
898 sedimentary succession.

899 **Figure 2.** Stratigraphic section with distribution and relative abundance of echinoids and associated
900 fauna and flora. Und. = Undetermined. F1-F5 = Facies 1 to 5.

901 **Figure 3.** *Agassizia* test (in aboral, oral, lateral and posterior view) divided into 8 sectors by three
902 perpendicular planes.

903 **Figure 4.** (1) *Clypeaster* test affected by fragmentation (Facies 3); (2) Test fragment of *Clypeaster*
904 affected by multiple circular drill holes. Scale bar = 1 cm.

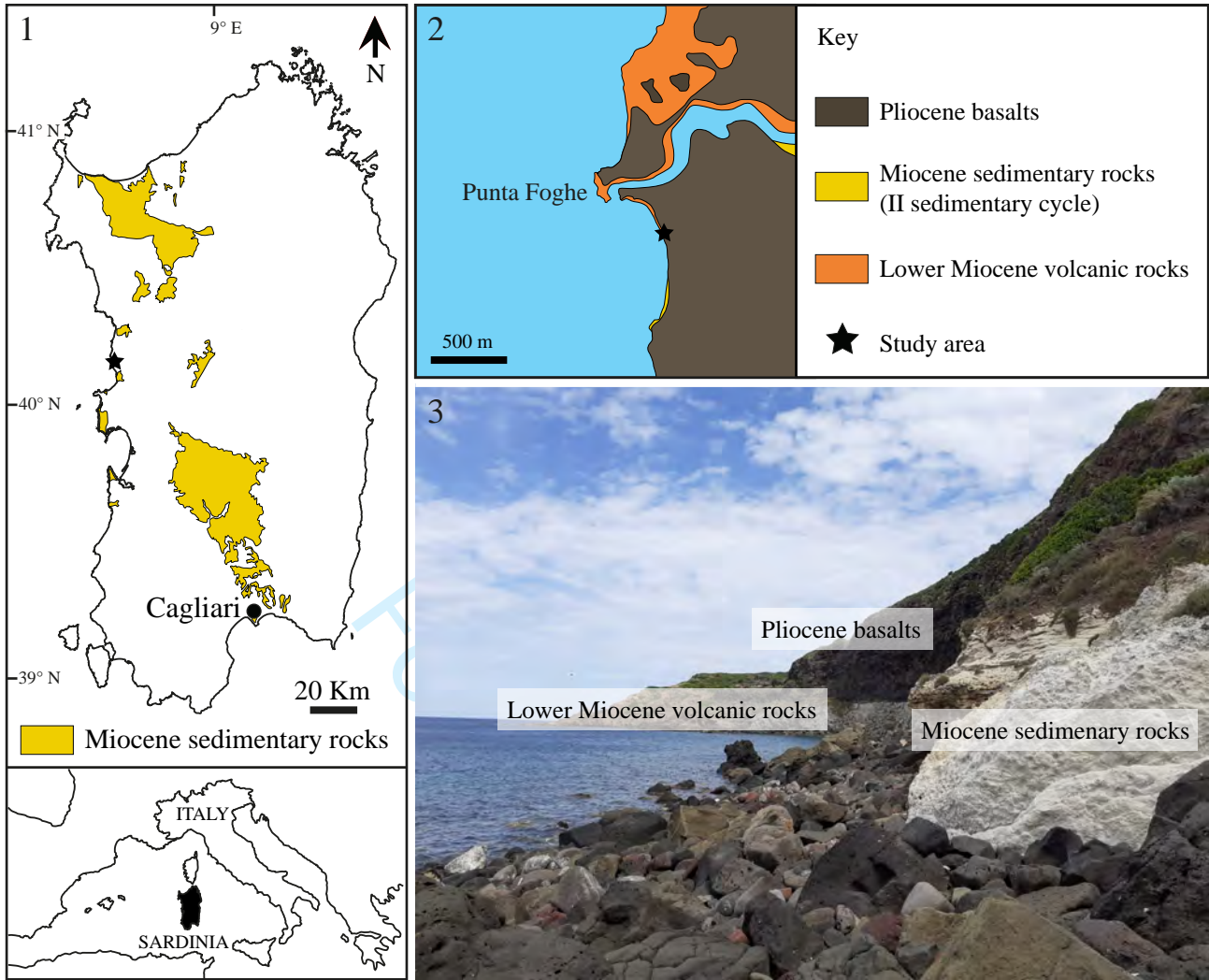
905 **Figure 5.** (1) Plan view of floatstone to rudstone composed of foraminifera (*Heterostegina*) in a
906 bioclast packstone matrix (Facies 5) with abundant echinoid remains; (2, 3) Details showing
907 accumulation of complete tests of *Agassizia* (A), test fragments of *Clypeaster* (B), regular
908 echinoid interambulacral plates (C) and pectinid remains (D).

909 **Figure 6.** Remains of the spatangoid *Plagiobrissus* (A), the clypeasteroid *Echinocyamus* (B) and the
910 benthic foraminifera *Heterostegina* (C) (Facies 5). Scale bar = 1 cm.

911 **Figure 7.** (1) Drilled specimen of *Agassizia* in aboral view; (2) Close up of the drill hole; (3) Drilled
912 specimen of *Agassizia* in lateral view; (4) Close up of the drill hole; (1, 3) Scale bars = 1 cm;
913 (2, 4) Scale bars = 0.5 cm.

914 **Figure 8.** Size selectively analysis: (1) Test size (Length) distribution of *Agassizia*; (2) Test length
915 distribution of undrilled specimens; (3) Test length distribution of drilled specimens; (4) Drill
916 hole size distribution; (5) Drill hole length and width plot; (6) Test length and drill hole length
917 plot; r = Pearson's correlation coefficient.

918 **Figure 9.** Site selectivity analysis: (1) Drill hole site distribution; (2) Difference in test length between
919 aborally and orally drilled specimens; (3) Drill hole location on anterior/posterior side of the
920 test.





Punta Foghe Section

Latitude 40°10'23"N
Longitude 8°27'40"E



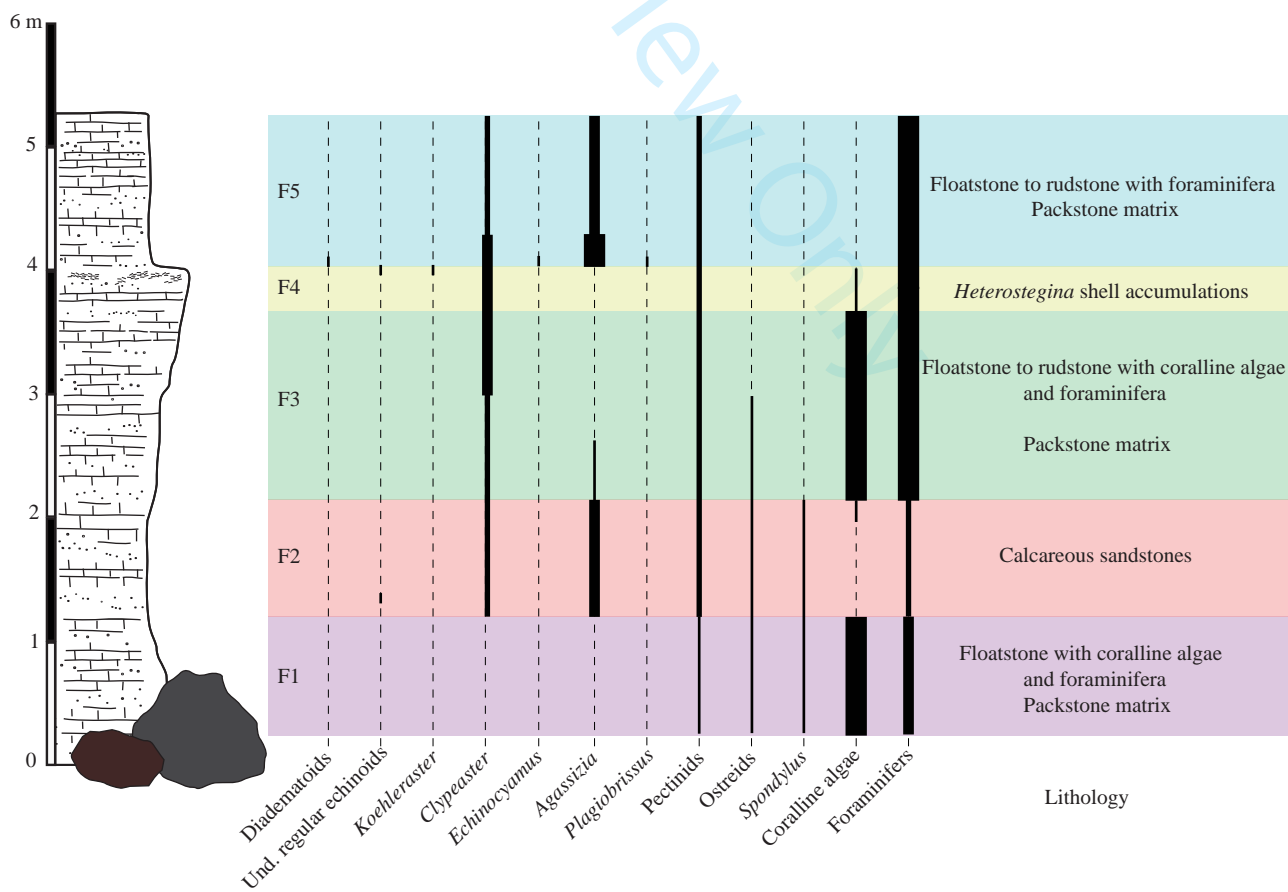
Carbonate rocks

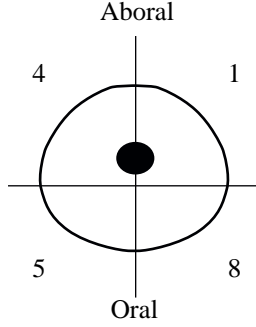
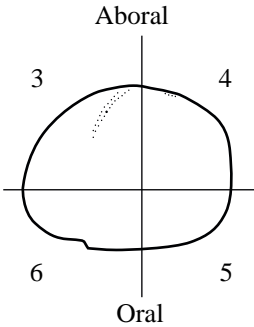
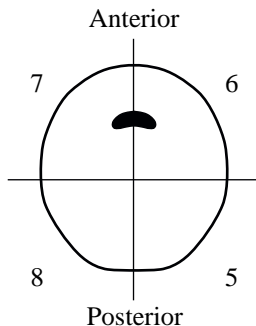
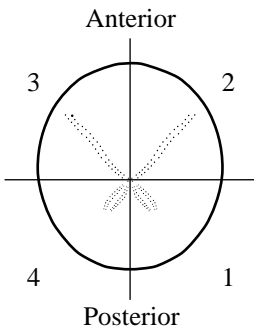


Basalt boulders

Relative abundance of taxa

- | Rare < 10
- | Common 10-50
- | Very common 50-150
- | Abundant > 150

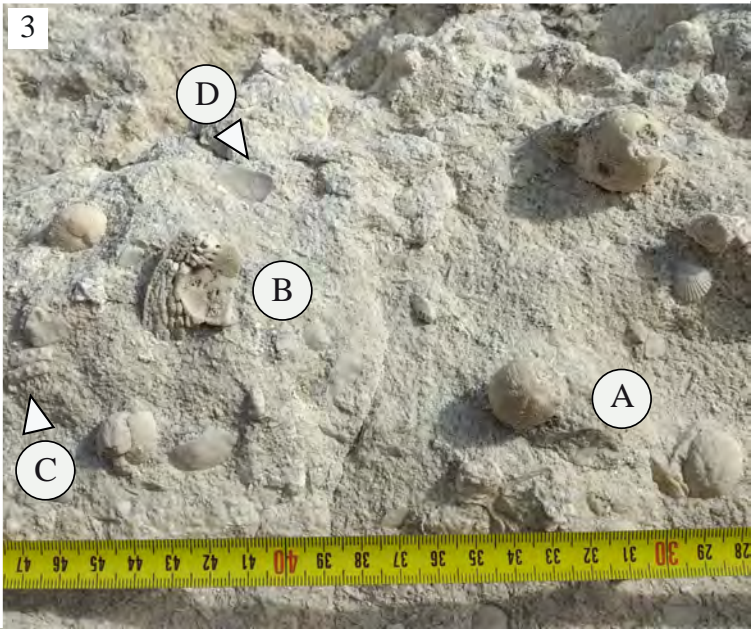
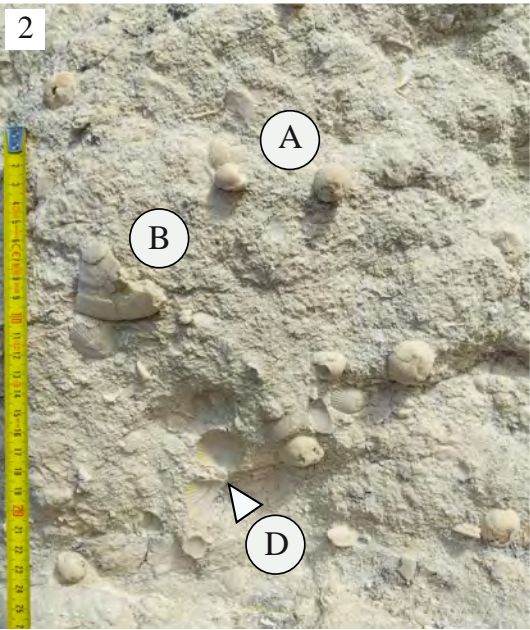
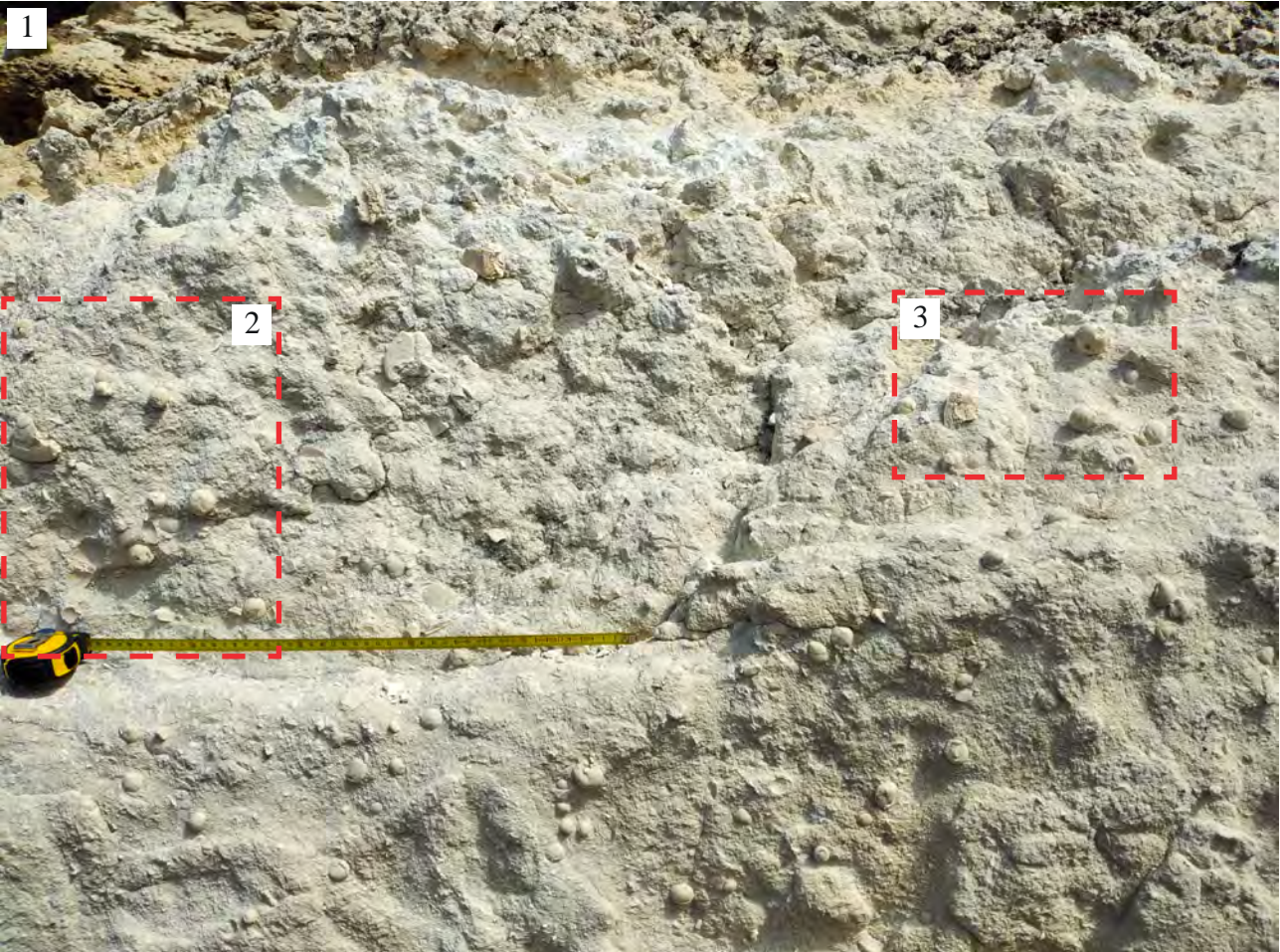


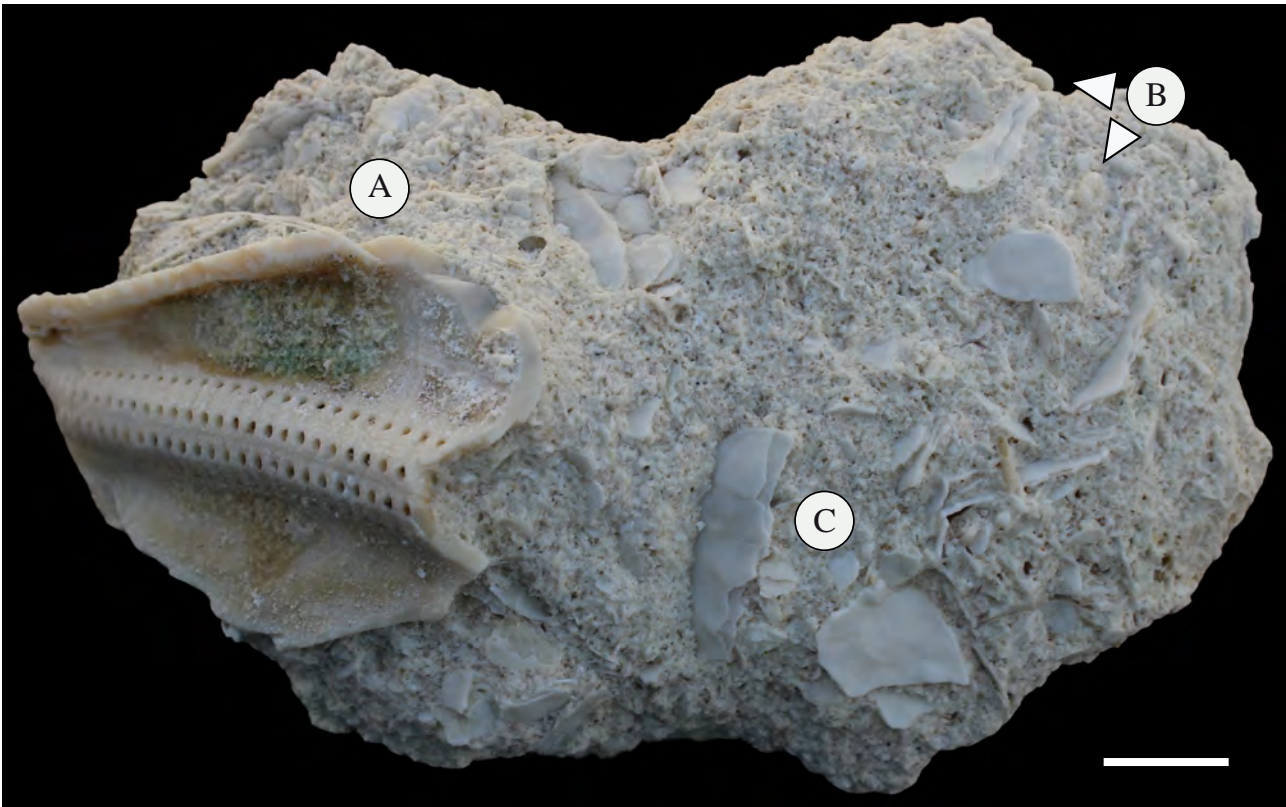


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