

1 **Testing an indirect palaeo-seagrass indicator: benthic foraminifera from the lower**
2 **Pleistocene *Posidonia* meadow of Fauglia (Tuscany, Italy)**

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18
19 **Abstract**

20 Well-preserved remains of a *Posidonia oceanica* meadow have been found in a lower
21 Pleistocene (Calabrian) succession cropping out near Fauglia (Tuscany, Italy). This paper
22 analyses and describes the benthic foraminiferal community associated with this well-
23 preserved Pleistocene *P. oceanica* meadow, with the purpose of testing the usefulness of
24 foraminifera as an Indirect Palaeo-Seagrass Indicator (IPSI), providing both qualitative and
25 quantitative parameters to recognize other meadow-related environments where fossil
26 remains of seagrasses are not preserved. Despite being influenced by some diagenetic
27 processes that might have affected the foraminiferal assemblage, the Fauglia succession

28 represents a suitable setting for testing benthic foraminifera as IPSI in a temperate
29 environment. Considering this limitation, together with other ecological constraints such as
30 seawater temperature, this study provides evidence of the high potential of benthic
31 foraminifera as IPSI. Several parameters such as the modified Foraminifera Index (FI'), the
32 "long vs. short life-span index" (I_{LS}), and the presence of permanently attached, encrusting
33 foraminifera were tested. New indexes were also developed, namely the K/R ratio,
34 consisting of the ratio between keeled *Elphidium* and the sum of rounded elphidiids (e.g.,
35 *Elphidium translucens*, *Criboelphidium*, *Porosononion*) and *Haynesina*, and the K/R_{EXT}
36 ratio, consisting of the ratio between keeled *Elphidium* and the sum of rounded elphidiids,
37 *Haynesina* and other related genera that display a rounded periphery (i.e., *Astrononion*,
38 *Melonis*, *Nonion*, *Nonionella*, *Valvulineria*). All these indexes were examined, suggesting
39 their potential use for recognizing seagrass-related palaeoenvironments. The K/R_{EXT} ratio
40 (and K/R) in association with the presence of permanently attached foraminifera revealed
41 to be the most reliable palaeo-seagrass indicators, suggesting that this combination could
42 be very useful also in other case studies where diagenesis altered the foraminiferal
43 association.

44
45 **Keywords:** *Posidonia oceanica*; *Elphidium*; Quaternary; IPSI; paleoenvironmental
46 reconstructions; taphonomic biases

54 **1. Introduction**

55 *Posidonia oceanica* is a seagrass species endemic of the Mediterranean Sea. It dominates
56 infralittoral soft bottoms, developing one of the most biologically diverse and ecologically
57 relevant marine ecosystems of the Mediterranean Sea (Duarte & Chiscano, 1999; Short et
58 al., 2007). Within the benthic zonation of the Mediterranean Sea (Pérès & Picard, 1964), *P.*
59 *oceanica* meadows constitute the climax stage of the soft-bottom ecosystem succession of
60 the infralittoral zone. *Posidonia oceanica* is an ecosystem engineer that stabilizes the
61 seafloor with its dense rhizome-meshwork, while the leaves favour local sedimentation by
62 baffling floating particles (Boudouresque & Jeudy de Grissac, 1983; Moriarty & Boon,
63 1989; De Falco et al., 2000; Gacia & Duarte, 2001; Sanchez-Vidal et al., 2021). By
64 creating a complex three-dimensional structure with separate foliar and rhizomatic strata, it
65 provides the microhabitat for a wide variety of organisms, many of them with epiphytic
66 living modes, such as encrusting red algae, bryozoans, molluscs, hydrozoans, and
67 foraminifera (Chimenz et al., 1989; Langer, 1993; Murray, 2006; Pardi et al., 2006; Frezza
68 et al., 2011; Mateu-Vicens et al., 2014). Many of these epiphytes are characterized by a
69 mineralized skeleton, contributing to carbonate production within the meadow (Mazzella et
70 al., 1989; Langer, 1993; De Falco et al., 2008; Mateu-Vicens et al., 2014; Brandano et al.,
71 2016). In addition to the epiphytic taxa, *P. oceanica* meadows also host abundant infaunal
72 foraminifera that can proliferate in the sediment trapped among the rhizomes (Den Hartog,
73 1979; Langer, 1993). Indeed, the main carbonate-producing biota associated with the
74 meadow are calcareous algae and foraminifera, which allows to name the carbonate
75 factories typical of seagrass meadows as GA-Foralgal (characterized by green calcareous
76 algae) and RA-Foralgal (characterized by red calcareous algae) (Brandano et al., 2019).
77 Whereas the epiphytic foraminiferal communities, meadow-related carbonate factories, and
78 other indirect evidence of fossil meadows, have been widely reported from the geological
79 record (e.g., Beavington-Penney et al., 2004; Reich, 2014; Vélez-Juarbe, 2014; Reich et

80 al., 2015; Forsey, 2016), the preservation of fossil seagrasses is an exceedingly rare event.
81 Seagrass leaves, roots and pollens decompose easily, making their preservation into the
82 geological record very rare, though not impossible (e.g., Brasier, 1975; Ivany et al., 1990;
83 Hesse et al., 1999; Moissette et al., 2007). Fossils of marine plants have been reported by
84 different authors, the oldest of which is a stem of *Thalassocharis muelleri* from the lower
85 Campanian of the Netherlands (Debey, 1848, 1851; Pomel, 1849). Other Upper Cretaceous
86 well-preserved seagrass remains were described from the Izumi Stone, in Japan (Koriba &
87 Miki, 1931; Oishi, 1931); from Westphalia, in Germany (Hosius & Von der Marck, 1880);
88 from the Coon Creek Formation of Tennessee, USA (Dilcher, 2016); and from the
89 Netherlands (Voigt & Domke, 1955; Voigt, 1981). An upper Paleocene fossil seagrass was
90 reported from Belgium (Da Saporta & Marion, 1878), while *Posidonia* and *Cymodocea*
91 remains are described from the lower Eocene of France (Den Hartog, 1970) and the middle
92 and upper Eocene of Southern England (Selsey Formation; Chandler, 1961; Curry, 1965;
93 Wright & Murray, 1972; Collinson, 1996). Other Eocene seagrasses are known from the
94 London Clay Formation (Herne Bay, England; Chandler, 1961; Collinson, 1983); from the
95 Brussels Sands Formation (Belgium; Stockmans, 1936); from the Avon Park Formation
96 (Florida, USA; Lumbert et al., 1984; Brack-Hanes & Greco, 1988; Ivany et al., 1990;
97 Benzecry & Brack-Hanes, 2008); and from the Birket Qarum and Qasr El Sagha
98 formations (Egypt; Zalmout & Gingerich, 2012). Additional Eocene fossil seagrasses were
99 found in France (Phillips & Meñez, 1988), northern Italy (Gregor, 1991) and southern
100 Germany (Gregor, 2003). Oligocene fossil seagrasses were described from the Isle of
101 Wight (UK; Chesters et al., 1967) and from the Guayanilla Formation of southwestern
102 Puerto Rico (Vélez-Juarbe & Santos, 2008). Several *Cymodocea* remains have been
103 reported from the Miocene of Sulawesi, Indonesia (Laurent & Laurent, 1926) and from the
104 Messinian of Guadalquivir Basin, in southern Spain (Braga et al., 2021). The most recent
105 examples of fossilized seagrass-meadows have been described by 1) Moissette et al. (2007),

106 who reported *Posidonia* leaves and rhizomes in the lower Pleistocene deposits of the
107 Kritika Member of the Rhodes Formation in Greece; 2) Brunetti and Vecchi (2005, 2012),
108 who reported well-preserved *Posidonia oceanica* specimens from the Pleistocene of the
109 Arda River (Emilia-Romagna, Italy); and 3) Raffi and Serpagli (2003), who reported
110 examples of seagrass rhizomes from the Pleistocene of the Stirone River (Parma, Italy). In
111 addition to these examples, the lower Pleistocene seagrass of *Posidonia oceanica* exposed
112 at the Fauglia Quarry has been recently reported by Bosio et al. (2021).

113 Therefore, excluding the aforementioned examples, the recognition of paleo-seagrass
114 meadows generally relies on indirect lines of evidence (Brasier, 1975; Eva, 1980;
115 Domming, 2001; Beavington-Penney et al., 2004; Leonard-Pingel, 2005; Reuter et al.,
116 2010; Vélez-Juarbe, 2014; Reich, 2014; Reich et al., 2015; Forsey, 2016). These indirect
117 palaeo-seagrass indicators (or IPSIs) have been recently reviewed by Reich et al. (2015),
118 who summarized different criteria for recognizing ancient seagrass occurrences: 1) the
119 fossil assemblages including benthic foraminiferal associations, coralline red algae,
120 hydroids, corals, bryozoans, molluscs (e.g., different bivalve taxa such as Pinnidae and
121 chemosymbiotic species, gastropods), ostracods, echinoderms, fish otoliths, dugongid
122 remains; 2) textural features such as the occurrence of unsorted sediments and fining-
123 upward sequences; 3) the abundance of “constructive” micrite envelopes and taphonomic
124 signature of skeletal remains (e.g., root etchings on shells and root casts); 4) the carbon
125 isotopic signal of mollusc shells; and 5) seagrass biomarkers.

126 While several potential IPSIs have been investigated in the literature and several works
127 analysed the foraminiferal associations related to vegetated substrates (Colom, 1942;
128 Blanc-Vernet, 1969; Mateu, 1970; Blanc-Vernet et al., 1979; Langer, 1993; Ribes et al.,
129 2000; Mateu-Vicens et al., 2010, 2012, 2014; Frezza et al., 2011), only a few of these
130 indicators have been tested directly. With the purpose of evaluating the usefulness of
131 foraminifera as IPSI, this paper analyses and describes the benthic foraminiferal

132 community associated with a well-preserved Pleistocene *Posidonia oceanica* meadow.
133 This fossil meadow is recorded within a succession dated to the Calabrian that crops out in
134 a sand quarry near the Fauglia village, Tuscany, central Italy (Bosio et al., 2021). The
135 sedimentary succession exposed herein consists of silts and sands that also host a
136 *Cladocora caespitosa* bank and an oyster reef at the top.

137 The aim of this paper is, thus, to provide a qualitative and quantitative description of the
138 foraminiferal assemblages associated with the fossil meadow through indices that might
139 prove useful for recognizing other meadow-related palaeoenvironments where seagrass
140 remains are not preserved. Furthermore, these indices can be compared with those
141 calculated for modern case studies, in order to create models that have the capability of
142 providing us with more reliable and detailed palaeoenvironmental reconstructions.

143

144 **2. Geological setting**

145 The study site consists of an active quarry located at Podere Montalto, ca. 1.3 km ESE of
146 Fauglia (Pisa Province, Tuscany, Italy), along the Eastern side of the Isola stream
147 (geographic coordinates: 43°33'52" N, 10°31'53" E) (Fig. 1). Near the study
148 site, Pleistocene strata occur atop of Pliocene marine deposits (Marroni et al., 1990; Bossio
149 et al., 1999) and include, from bottom to top, the Morrone Formation (ART), the Sabbie di
150 Nugola Vecchia Fm (NUG) and the Casa Poggio ai Lecci Fm (QPL) (Mazzanti, 2016).

151 The ART consists of lower Calabrian (i.e., Santernian according to the 'Italian Marine
152 Stages' regional scheme; Gibbard & Cohen, 2008) sands and clays. ART strata are usually
153 rich in macroscopic remains of marine molluscs (mostly bivalves and gastropods),
154 brachiopods, echinoids, corals, crustaceans and annelids. Boreal faunal elements (e.g.,
155 *Arctica islandica*) typically occurs in the ART, representing the geologically oldest
156 occurrence of such taxa in this area. These records appear to be chronostratigraphically
157 consistent with observations of the "Northern guest" *A. islandica* in other coeval deposits

158 of Italy (e.g., Crippa et al., 2019). The ART reaches a maximum thickness of about 50 m
159 (Mazzanti, 2016).

160 The NUG consists of fine, yellowish sands interbedded with lenses of conglomerates and
161 calcarenites that have been assigned by Mazzanti (2016) to the Emilian (i.e., mid-
162 Calabrian; Gibbard & Cohen, 2008). The NUG strata contain few remains of marine
163 macro-invertebrates, which are mainly represented by bivalves (mostly oysters and
164 pectinids). The maximum thickness of the NUG exceeds 100 m (Mazzanti, 2016).

165 The QPL consists of conglomerates with subordinate sands and silts, deposited in a
166 transitional environment (including riverine, deltaic and lagoonal settings; Barsotti et al.,
167 1984) during the Chibanian (middle Pleistocene). The strata of the QPL typically contain
168 very scarce remains of macro-invertebrates, including rare bivalves and gastropods. The
169 thickness of the QPL ranges between 1 and ca. 30 m (Mazzanti, 2016).

170 There is no consensus regarding the sequence stratigraphic interpretation of the ART and
171 NUG. Some authors (Bossio et al., 1993; Tani & Gaggero, 1999; Mazzanti, 2016)
172 consider these formations to represent the transgressive and regressive tracts of a single
173 depositional cycle; other authors, in turn, regard them as corresponding to two distinct
174 depositional cycles (Sarti et al., 2007, 2008). Recent geological mapping of the Fauglia
175 area at the national (Mazzanti, 2016), regional (Regione Toscana, 2006-2009), and local
176 (Marroni et al., 1990) scales, concur in indicating that deposits belonging to the NUG crop
177 out at the study site. That said, the abundant fossil content of these deposits does not match
178 the palaeontological traits of the NUG as observed elsewhere (Mazzanti, 2016), resembling
179 instead some ART outcrops some tens of kilometres farther south. So far, published works
180 on the palaeontology of the Fauglia pit have attributed the stratigraphic succession revealed
181 by the quarrying surfaces to unnamed lower Pleistocene deposits (Brunetti et al., 2008;
182 Chirli & Forli, 2017; Cresti & Forli, 2020) or to the NUG (Berta et al., 2015; Bosio et al.,
183 2021), the latter view being embraced herein.

184

185 3. Material and methods

186 The Pleistocene deposits cropping out at the Podere Montalto quarry (Fig. 2A, B) were
187 investigated in detail by describing the lithology, sedimentary structures, and macrofossil
188 distribution. A stratigraphic log was built integrating that of Bosio et al. (2021) with a
189 description of the lower portion of the outcrop (Fig. 3; Table 1). A total of 9 samples were
190 collected at different stratigraphic heights, focusing mainly on the two *Posidonia*-bearing
191 strata - namely, the lower interval (samples P2, P4, P5, P7) and the upper interval (samples
192 F4, F5, P10, P11) (Figs. 2, 3) - to investigate both vertical and lateral variations. All
193 samples were obtained by collecting at least 20 g of sediment, after slightly digging inside
194 the deposits in order to remove the weathered surface. Four samples (P2, P5, P7, F5) were
195 collected from different, very-fine-sandy to fine-silty layers featuring in situ *Posidonia*
196 *oceanica* rhizomes (Fig. 2C) and *Pinna nobilis* shells (Fig. 2D); two samples (P4, F4) from
197 two very-fine-sandy to very-coarse-silty layers occurring within the two *Posidonia*-bearing
198 strata (Fig 2E); two samples (P10, P11) from lenses of dark-coloured sediments within the
199 *Posidonia*-bearing layer in the upper interval (Fig. 2F; P11 was collected at the boundary
200 of the dark-coloured sediment lens, whereas P10 was collected from the core of the lens);
201 one sample (F7) from the *Cladocora caespitosa* bank, which lies above the meadow and
202 does not display remains of seagrass (Fig. 2G).

203 Grain size analyses were performed on each sample with a Malvern Mastersizer 2000E™
204 Laser Granulometer at the Università degli Studi di Milano-Bicocca (Table 1).

205 Subsequently, the software GRADISTAT Version 4.0 (Blott and Pye, 2001) was employed
206 to analyse the grain size distribution and to perform statistics.

207 For the analysis of microfossils, a small amount of each sample (see Table 2 for the
208 detailed quantities) was weighted, treated with 30% hydrogen peroxide to remove organic
209 matter (Dimiza et al., 2016) and wet-sieved through a 125- μ m-sized mesh, to separate the

210 fraction for the benthic foraminifera picking ($> 125 \mu\text{m}$). Samples F4 and F5 were wet-
211 sieved through 63- μm -sized mesh, in order to check for grain-size-based differences in the
212 composition of the foraminiferal assemblages (analysing the fraction $> 63 \mu\text{m}$). After
213 sieving, the samples were oven-dried and divided into equal fractions using a microsplitter,
214 thus obtaining subsets containing at least 300 specimens each (Murray, 2006).

215 The picking and the identification of the foraminifera were performed under a ZEISS
216 Olympus SZ61 stereo microscope equipped with a high-resolution camera. The taxonomic
217 determination of the foraminifera was based on Cimerman and Langer (1991), Langer and
218 Schmidt-Sinns (2006), Milker and Schmiedl (2012), the Foraminifera.eu-Project
219 (Hesemann, 2020), and World Register of Marine Species (WoRMS Editorial Board,
220 2021). SEM imaging of epiphytic foraminifera and *Posidonia oceanica* leaves and
221 rhizomes was also performed using a FEG (SEM-FEG) Gemini 500 Zeiss scanning
222 electron microscope at the Università degli Studi di Milano-Bicocca.

223 The total amount of benthic foraminifera, the standardized quantity of benthic foraminifera
224 within 100g of sediment, the species richness (i.e., number of species) and the relative
225 frequency of each species, were calculated. To analyse the taxonomic structure of the fossil
226 assemblage, biodiversity was measured using the Shannon-Weaver index H' (Shannon &
227 Weaver, 1963; Mateu-Vicens et al., 2014):

$$228 \quad H' = - \sum_{i=0}^R p_i \ln(p_i)$$

229 where p_i is the relative abundance of each species (i) and R is the species richness (i.e.,
230 number of species).

231 Since miliolid foraminifera can be easily altered, or even dissolved, due to their
232 porcelaneous test of high-Mg calcite (Budd & Hiatt, 1993), several parameters were also
233 calculated excluding miliolids to highlight the signal of the meadow while avoiding the
234 bias from miliolids dissolution.

235 The relative abundance of epiphytic foraminifera was calculated using the $Index_{EP}$ i.e., the
236 ratio between epiphytic foraminifera and the total of benthic foraminifera (Mateu-Vicens et
237 al., 2014). $Index_{EP-M}$, a variant of $Index_{EP}$ that excludes miliolids, was also calculated.
238 According to Langer (1993) and Mateu-Vicens et al. (2014), epiphytic foraminifera can be
239 divided into five different groups based on their type of motility, life span, feeding mode,
240 and test morphology and structure. The recognized ecomorphological groups are: A*)
241 long-living (> 10 months), sessile species, permanently attached to the substrate (e.g.,
242 *Nubecularia lucifuga*, *Planorbulina mediterraneensis*); SB) long-living (> 10 months),
243 symbiont-bearing taxa (e.g., *Sorites*, *Peneroplis*, *Amphistegina*); B) short-living (3-5
244 months), generally motile species that temporarily attach to the substrate using organic
245 materials (e.g., *Rosalina* spp., *Cibicides* spp., *Ammonia* spp.); C) short-living, motile,
246 suspension-feeding foraminifera (e.g., keeled elphidiids, *Astrononion*, *Criboelphidium*);
247 and D*) short-living, permanently motile, grazing foraminifera (e.g., opportunistic species
248 living within rhizomes and sediment particles). Thus, epiphytic foraminifera specimens
249 were assigned to the different morphotypes (A* to D*). Another classification was
250 developed without including miliolids. Here, we refer to the traditional classification (i.e.,
251 that from Langer, 1993 and Mateu-Vicens et al., 2014) as “Mode-1”, and to the
252 classification without miliolids as “Mode-2”. Pie-plots showing the percentage of the
253 different morphotypes were compiled for both classifications and for each sample. The
254 modified FORAM Index (FI') developed by Mateu-Vicens et al. (2014) based on Hallock
255 et al. (2003) FORAM Index (FI), and the “long vs. short life-span” index (I_{LS} ; Mateu-
256 Vicens et al., 2014) were also tested. FI' is expressed as:

$$257 \quad FI' = 10 \times (P_{A*} + P_{SB}) \times P_{D*} + 2 \times (P_B + P_C)$$

258 Values of FI' >4 indicate optimal environmental conditions, whereas values of FI' <2 are
259 indicative of stressed conditions (Mateu-Vicens et al., 2014). I_{LS} , which consists of the
260 ratio between longer-living and short-living forms, was built to highlight the differences

261 between well-preserved and stressed *P.oceanica* meadows (Mateu-Vicens et al., 2014) and
262 is expressed as:

$$263 \quad I_{LS} = (3.5 \times (P_{A^*} + P_{SB}) + 0.01) / (P_{D^*} + 0.01)$$

264 I_{LS} values range between 0 and 36. If D^* is the dominant morphotype, the index is close to
265 0; if the dominant morphotypes are A^* and SB, the index points towards 36.

266 A new index based on the ratio between keeled *Elphidium* and the sum of rounded
267 elphidiids (e.g., *Elphidium translucens*, *Criboelphidium*, *Porosononion*) and *Haynesina*
268 was elaborated and defined as K/R index. An additional index, K/R_{EXT}, consisting of the
269 ratio between keeled *Elphidium* and the sum of rounded elphidiids (e.g., *Elphidium*
270 *translucens*, *Criboelphidium*, *Porosononion*), and other related genera that display a
271 rounded periphery, such as *Haynesina*, *Astrononion*, *Melonis*, *Nonion*, *Nonionella* and
272 *Valvulineria*, was also tested.

273 Finally, a Q-mode cluster analysis, based on the similarity of species abundances across
274 the samples, was performed with the software Primer v.6. The Log (x+1) transformation
275 was applied to both indexes. Dendrograms were plotted using the Bray-Curtis similarity
276 index.

277

278 **4. Results**

279 **4.1 Field observations and stratigraphic section**

280 The measured stratigraphic section is an 8.5-m-thick mixed carbonate-siliciclastic
281 succession (Figs. 2A, B, 3) whose upper portion has been recently described by Bosio et al.
282 (2021). The base of the succession is characterized by the presence of two brownish, fine-
283 to medium-grained, silty layers, about 1 m thick each, displaying well-preserved, reddish-
284 to-brown coloured, in-situ rhizomes of *Posidonia oceanica* (lower interval; figs. 2C, 3, 4)
285 associated with *Pinna nobilis* specimens preserved in life position (Fig. 2D). These

286 *Posidonia*-bearing layers are separated by a 50-cm-thick very fine-grained sandy to coarse
287 silty horizon (Fig. 2E), lacking macrofossils.

288 Upwards, a quarry road hides about 1 m of the succession. The overlying first interval
289 consists of an 80-cm-thick layer characterized by a fine- to medium-grained sand with silt
290 intercalations, shell lenses and internal molds of the bivalve *Panopea*. This layer is
291 followed by a 10-cm-thick silty layer and by a 30-cm-thick fine-grained sandy layer with
292 scattered specimens of the zooxanthellate coral *Cladocora caespitosa*, pectinid shells and
293 clay chips. Just above, a 150-cm-thick, brownish, coarse-grained silty layer, including a
294 very fine-grained sandy to coarse-grained silty interval, occurs (upper interval; Fig. 3).
295 Inside this layer, in situ rhizomes of *P. oceanica*, molluscs and invertebrate burrows occur.
296 Laterally, these deposits pass into a large lens of dark-coloured material (Fig. 2F), with
297 leaves of *P. oceanica* preserved as peaty remains (Fig. 4) and aragonitic macrofossils, such
298 as gastropods and *P. nobilis* specimens.

299 The uppermost part of the section includes a 250-cm-thick coarse-grained silt layer. At the
300 base, the horizon displays fragments and scattered colonies of *Cladocora caespitosa* (Fig.
301 2G), together with bivalves featuring geopetal structures. At the top of this layer
302 *Cladocora caespitosa* colonies coalesce to form a decametric to metric *Cladocora* bank.
303 The bank is abruptly overlain by an oyster reef, rich in barnacles and included in a massive
304 sandy deposit.

305

306 **4.2 Foraminiferal analysis**

307 Micropalaeontological analyses reveal that the Fauglia skeletal assemblages is constituted
308 by a large variety of carbonate producers, including benthic foraminifera, planktic
309 foraminifera, ostracods, bryozoans (for the most part belonging to “erect” forms), molluscs
310 and echinoids. Among these, benthic foraminifera are the most abundant group.

311 A total of 97 benthic foraminiferal species were identified (see Table 2; Figs. 5, 6, 7, 8, 9,
312 10; Appendix 1). Foraminiferal density (i.e., the abundance of benthic foraminifera per 100
313 g of material) varies between 26 992 and 84 479 individuals throughout the samples, with
314 the exception of samples P4 and F4 in which this value is almost one order of magnitude
315 higher, between 200 810 and 258 535 individuals (Table 2; Fig. 3). The percentage of
316 broken tests displays no significant difference across the samples, exhibiting an average
317 value of 4% (Table 2). Only in sample F7 (the *Cladocora*-bearing layer; Fig. 3) broken
318 foraminiferal tests are one order of magnitude higher, displaying a value of 11.7% (Table
319 2). Species richness is relatively variable, showing the highest value in sample F4 (74) and
320 the lowest value in sample F7 (47) (Table 2). In contrast, diversity is more homogeneous in
321 all samples, as indicated by the Shannon-Weaver Index (H'), whose values are high and
322 range from 3.10 in P11 to 3.63 in P10 (Table 2). The relative abundances of the identified
323 benthic foraminifera species are presented in Appendix 1. The most common taxa (i.e.,
324 those with abundance higher than 5%) (Table 3) are: *Ammonia* group (except for F7);
325 *Aubignyna perlucida* (F7); *Bolivina* spp. (P5, F4, F7); *Lobatula lobatula* (except for F5 and
326 F7); *Cibicides refulgens* (all samples); *Criboelphidium* cf. *magellanicum* (F7); keeled
327 elphidiids group (except for F7); *Elphidium translucens* (P4, P5, F5); *Fissurina* spp. (P2,
328 P5, P11, F7); *Fursenkoina subacuta* (P10); *Haynesina* spp. (F7); *Reussella spinulosa*
329 (except for P2); *Neoconorbina terquemi* (P4, P5, F4); *Rosalina bradyi* (P2, P7, P11, F5);
330 *Rosalina globularis* (P2, P7); miliolids (P10). Well-preserved miliolid tests actually occur
331 only in samples P10 and P11, corresponding to a dark-grey lens within the upper
332 *Posidonia*-bearing layer. In the remaining samples, miliolids are rare and usually display
333 altered and corroded tests.

334 The largest differences in the associations of common benthic foraminifera can be
335 observed between the samples from the *Posidonia*-bearing layers (P2, P4, P5, P7, P10,
336 P11, F4, F5) and the sample from the *Cladocora* bank (F7) (Table 3). In particular, the

337 *Ammonia* group is less abundant in F7, whereas *Aubignyna perlucida* and *Astrononion*
338 *stelligerum* are more common. *Bolivina* spp. show higher abundances in F7, but also in P5
339 and F4 (i.e., samples that were sieved with 63 μm mesh size). On the contrary, *Bulimina*
340 spp. remain approximately constant among all the samples. Cibicididae (e.g., *Lobatula*
341 *lobatula*, *Cibicides refulgens*, *Cibicidoides pachyderma* and *Cibicidoides*
342 *pseudoungerianus*) display the lowest values in F7. Within this group, the species that
343 contributes more to the variation is *Lobatula lobatula*, whose abundance is considerably
344 lower in F7 with respect to the samples from *Posidonia*-bearing layers. *Cibicides*
345 *refulgens*, instead, is abundant also in F7. *Criboelphidium* cf. *magellanicum* and
346 *Haynesina* spp. have the highest abundance in the *Cladocora* bank (F7). Keeled *Elphidium*
347 represent one of the most abundant group within all the samples from the *Posidonia*-
348 bearing layers. Among them, the most common species are *E. aculeatum*, *E. advenum*, *E.*
349 *crispum*, and *E. fichtelianum*; these species are almost absent in F7. *Fissurina* spp. are
350 abundant in every sample. *Fursenkoina subacuta* displays large frequency variations, but
351 no significant trends. *Planorbulina mediterraneensis* exhibits almost constant values in all
352 the samples, except for F7, where it is absent. *Elphidium translucens* and *Reussella*
353 *spinulosa* do not show particular trends, being common in every sample. Rosalinidae (i.e.,
354 *Gavelinopsis praegeri*, *Neoconorbina terquemi*, *Neoconorbina* sp., *Rosalina brady*,
355 *Rosalina globularis* and *Rosalina williamsoni*) display the lowest abundance in F7,
356 whereas in the other samples they constitute one of the most populated groups.
357 Agglutinated foraminifera (the only species identified is *Sahulia conica*) are generally
358 scarce, except for P10. Miliolids occur in P10 and, to a lesser extent, in P11. In all the
359 other samples they are rare and poorly preserved. The well-preserved miliolids of P10
360 include the encrusting species *Nubecularia lucifuga*.
361 Index_{EP} displays its lowest value of 0.4 in correspondence of F7, while in the other samples
362 its average value is 0.6 (Table 2). $\text{Index}_{\text{EP-M}}$, calculated without considering miliolids,

363 shows a similar trend (Table 2). No remarkable differences in the abundances were
364 observed between samples sieved through 63- μm and 125- μm -sized meshes. The only
365 difference is the slightly higher abundance of some opportunistic species (e.g., *Bolivina*
366 spp.) in the finer fraction. The division of the epiphytic species into the different
367 morphotypes is visible in Table 4. No specimens belonging to the SB group was
368 recognized. Morphotype percentages for both study modes are shown in Table 5 and
369 Figure 11.

370

371 **4.2.1 Mode-1: classification with miliolids**

372 In this classification, morphotype A* includes *Planorbulina mediterranensis* and
373 *Nubecularia lucifuga*. The relative frequency of this morphotype is low in all the samples,
374 and no members of this group were observed in F7. The highest value, 1.5%, was recorded
375 in sample P10, which was collected from the dark-coloured sediment within a *Posidonia*-
376 bearing layer (Table 5).

377 Morphotype B includes members of *Ammonia* (i.e., *Ammonia beccarii*, *Ammonia*
378 *parkinsoniana*, *Ammonia tepida*); Cibicididae (i.e., *Lobatula lobatula*, *Cibicides refulgens*,
379 *Cibicidoides pachyderma*, *Cibicidoides pseudoumgerianus*), Rosalinidae (i.e.,
380 *Gavelinopsis praegeri*, *Neoconorbina terquemi*, *Neoconorbina* sp., *Rosalina bradyi*,
381 *Rosalina globularis*), *Asterigerinata mamilla*, *Eponides repandus*, *Discorbinella*
382 *bertheloti*, *Discorbis vilardeboanus*, *Planulina ariminensis*, *Planulina* sp., *Hanzawaia*
383 *boueana* and *Buccella* aff. *B. frigida*. Morphotype B is predominant in all samples (44.1%
384 on average) with the lowest value in sample F7 (19.5%) (Table 5).

385 Morphotype C includes keeled *Elphidium* taxa (*Elphidium aculeatum*, *Elphidium advenum*,
386 *Elphidium complanatum*, *Elphidium crispum*, *Elphidium fichtelianum*, *Elphidium*
387 *macellum*, *Elphidium maioricense*, *Elphidium* aff. *E. aculeatum*, *Elphidium* sp., *Elphidium*
388 sp.1, *Elphidium* sp. 5; Cimerman & Langer, 1991), *Criboelphidium* cf. *magellanicum* and

389 *Astrononion stelligerum*. The frequency of morphotype C does not show any particular
390 trend and its values range between 18.6% (F7) to 5.6 % (P10) (Table 5). However, even if
391 in F7 morphotype C displays its higher values, keeled *Elphidium* are almost absent,
392 whereas in the other samples they constitute the largest portion of this morphotype. Indeed,
393 in F7 the high frequency of morphotype C is related to the high abundance of
394 *Cribrroelphidium cf. magellanicum* and *Astrononion stelligerum*, which are much less
395 abundant in the other samples.

396 Morphotype D* comprises *Sahulua conica* and small miliolids. It displays the highest
397 abundance in P10 (18.5%), i.e., the sample collected inside the dark-grey lens, whereas in
398 the other samples its contribution is always lower than 2.5% (Table 5).

399 FI' values remain almost constant in all the samples from the *Posidonia*-bearing layers,
400 with an average value of 1.24 (Table 2). Its lowest value (0.78) was observed in the
401 *Cladocora* bank sample F7 (Table 2). I_{LS} is rather constant, with the lowest value (0.31) in
402 sample P10. However, on average, *Posidonia*-bearing samples display higher (0.88) values
403 than F7 (0.36), the sample from the *Cladocora* bank (Table 2).

404

405 **4.2.2 Mode-2: classification without miliolids**

406 In this case, Morphotype A* does not include *Nubecularia lucifuga*. Thus, the frequency of
407 morphotype A* is equal to the frequency of *Planorbulina mediterraneensis*. Morphotypes B
408 and C are as in Mode-1. Morphotype D* is constituted just by agglutinated foraminifera.
409 Therefore, the frequency of morphotype D* is equal to that of *Sahulua conica* and the
410 highest value (3.5%) is still found in sample P10 (Table 5).

411 FI'-_M displays the lowest value in F7 (0.78). In the other samples FI'-_M remains almost
412 constant, with an average value of 1.20 (Table 2). I_{LS-M} shows almost constant values
413 within the different samples from the *Posidonia*-bearing layers, with an average value of

414 1.47. The lowest value occurs within the *Cladocora* bank sample, F7, and corresponds to
415 0.40 (Table 2).

416

417 **4.2.3 Keeled/rounded ratio**

418 The keeled/rounded ratio (K/R) exhibits the lowest value in F7 (0.11), whereas in the other
419 samples it is higher, with an average value of 1.45 (Table 2). The K/R_{EXT} ratio shows the
420 same pattern as K/R, displaying the lowest values in F7 (0.08), whereas in all the other
421 samples it is at least one order of magnitude higher, with an average value of 0.99 (Table
422 2).

423

424 **4.2.4 Cluster analysis**

425 The Q-mode cluster analysis (Fig. 12) produced a dendrogram with two clusters separated
426 at 60% similarity. The first cluster contains only sample F7 from the *Cladocora caespitosa*
427 bank, while the second cluster includes samples from all the *Posidonia*-bearing layers,
428 although the latter show an internal variability.

429

430 **5. Discussion**

431 **5.1 The exceptional preservation of *Posidonia oceanica* and the diagenetic imprint on** 432 **the foraminiferal association**

433 Seagrass preservation within the fossil record is an exceedingly rare event (e.g., Ivany et
434 al., 1990; Moissette et al., 2007; Van der Ham et al., 2007; Reich et al., 2015; Dilcher,
435 2016; Van der Ham et al., 2017). Indeed, most of the unequivocal fossils of seagrasses are
436 clearly linked to cases of exceptional preservation (e.g., Ivany et al., 1990; Moissette et al.,
437 2007; Van der Ham et al., 2017). For instance, Maastrichtian seagrass from Belgium and
438 the Netherlands occur as silicified material or embedded in flint (Van der Ham et al.,
439 2017). The intact in situ rhizomes from the Eocene of Florida (Avon Park Formation) have

440 been related to the sudden burial by fine-grained sediments caused by a storm (Ivany et al.,
441 1990). The spectacularly preserved lower Pleistocene seagrass of Rhodes also underwent
442 these particular conditions, having experienced a limited post-mortem transport before a
443 quick burial (Moissette et al., 2007). Consistently with this peculiar mode of preservation,
444 elements of the seagrass meadow and seagrass-associated communities are often finely
445 preserved (e.g., they display cell-level structures of the plant leaves, as well as epiphytes in
446 life position), and, in the Pleistocene example, carbonate shells highly susceptible to
447 diagenesis (e.g., gastropods) were also preserved (Moissette et al., 2007). The
448 palaeoenvironmental reconstruction of the Fauglia succession indicates a shallow-water,
449 low- to moderate-energy marine environment. This is supported by the presence of
450 *Posidonia oceanica*, that usually extend from 0 to 40 m water depth, with the upper and
451 lower limits being controlled by hydrodynamic energy and light penetration, (Duarte,
452 1991; Piazzi et al., 2000; Infantes et al., 2009; Vacchi et al., 2017) and by the presence of a
453 *Cladocora* bank above (close to the top of the section). This type of bioconstruction
454 generally occurs between 5 and 35 m water depth (Kružić & Požar-Domac, 2003; Kružić
455 & Benković, 2008; Kersting & Linares, 2012; El Kateb et al., 2016; Kersting et al., 2017;
456 Mačić et al., 2019) in sheltered areas (Kružić & Benković, 2008; Kersting & Linares,
457 2012; Chefaoui et al., 2017; Coletti et al., 2018). The presence of an oyster reef at the top
458 of the succession also points towards a shallow (less than 10 m), low- to moderate-energy
459 setting as these bioconstructions usually develop along gently sloping complex coastlines
460 with hydrodynamic conditions favouring larval pooling (and thus clustering of various
461 generations of individuals) (Puffer & Emerson, 1953; Haven & Whitcomb, 1983;
462 Luckenbach et al., 1995; Boudreaux et al., 2006; La Peyre et al., 2014; Gain et al., 2017;
463 Toscano et al., 2018; Kregting et al., 2020). The common presence of *Ammonia* is also
464 supportive of a coastal, shallow-water environment, possibly influenced by river discharge
465 (and thus high sedimentation rates) and significant salinity variations (Murray, 2006). The

466 foraminifera of the *Ammonia* group are tolerant to brackish conditions and dwell in
467 organic-matter-rich and oxygen-depleted sediments (Murray, 2006). Similar conditions,
468 where seagrass meadows coexist with cladocorian corals in riverine-influenced
469 environments, have been reported from the shallow-water deposits of the middle Eocene of
470 the Western Pyrenees (Baceta & Mateu-Vicens, 2022). In the inferred coastal setting,
471 *Posidonia* leaves and rhizomes were exceptionally preserved thanks to the low-to-
472 moderate hydrodynamic energy and to sedimentation rates sufficiently high to cover the
473 organic remains and inhibiting their decomposition.

474 In the Fauglia succession, *Posidonia oceanica* specimens consist of in-situ rhizomes (Fig.
475 4) that are either reddish, possibly fossilized through permineralization within brownish
476 sediments, or blackish, with a peaty consistence as typical of coalified compressions in
477 dark-grey sediments (Bosio et al., 2021), and finely preserved leaves (Fig. 4). The reddish
478 colour is most likely the result of iron oxides formation occurred during diagenesis,
479 whereas the dark grey colour of the sediments in which blackish rhizomes are preserved is
480 probably related to local enrichment in organic material, which in turn is likely linked to
481 oxygen deficiency at or just below the seafloor (Bosio et al., 2021).

482 The *Posidonia*-associated foraminiferal assemblage is also affected by diagenetic
483 processes, which have the potential to skew fossil associations by preferentially dissolving
484 aragonitic shells and subsequently high-Mg calcite shells like those of miliolids (Budd &
485 Hiatt, 1993; Cherns & Wright, 2000; Cherns et al., 2011). Well-preserved miliolids tests
486 were in fact recognized only within the dark-coloured sediments (P10, P11), where both
487 organic matter and aragonitic fossils are well preserved (Bosio et al., 2021). The
488 destructive effect of dissolution must thus be considered when calculating morphotype
489 frequencies and related parameters (i.e., FI', I_{LS}) in fossil assemblages, differently from
490 recent environments, where diagenesis does not play a role (e.g., El Kateb et al., 2020).
491 Differing from what proposed by Reich et al. (2015), the fossilization potential of

492 miliolids, although not low, is lower than that of rotaliids. This means that, when
493 performing paleoenvironmental reconstructions, IPSIs and quantitative parameters based
494 on porcelaneous foraminifera could be biased by diagenetic processes, and as such,
495 diagenesis should be considered for reliable interpretations.

496

497 **5.2 Epiphytic foraminifera analysis**

498 The composition and diversity of the epiphytic communities are influenced by ecological
499 parameters, structural features of the meadow and temporal persistence of the phytal
500 substrates (Langer, 1993; Mateu-Vicens et al., 2014). Symbiont-bearing taxa are typically
501 reported as a major component of the epiphytic foraminifera community (e.g., Murray,
502 2006; Langer, 1993; Mateu-Vicens et al., 2014). The lack of symbiont-bearing
503 foraminifera (morphotype SB) in the Fauglia succession is most likely related to climatic
504 constraints (Hollaus & Hottinger 1997; Beavington-Penney & Racey, 2004; Murray 2006;
505 Langer 2008; El Kateb et al., 2018). Common Mediterranean symbiont-bearing taxa like
506 *Amphistegina*, *Sorites* and *Peneroplis* are in fact limited by temperature, being abundant in
507 the eastern Mediterranean and displaying a restricted distribution in the western part of the
508 basin (Mateu-Vicens et al., 2014). *Amphistegina* only occurs in the eastern Mediterranean
509 and is limited by the 14°C winter isotherm (Langer et al., 2012; El Kateb et al., 2018). It is
510 common along the eastern and southern parts of the Mediterranean (Langer et al., 2012)
511 and its current distribution reaches the south of Sicily (Caruso & Cosentino, 2014), the
512 Maltese Islands (Yokes et al., 2007) and Crete (Hollaus & Hottinger, 1997). *Sorites* and
513 *Peneroplis* are constrained by the 18°C isotherm (Beavington-Penney & Racey, 2004;
514 Murray, 2006). Currently, peneroplids and soritids are widely distributed over all the *P.*
515 *oceanica* meadows in the Mediterranean (Blanc-Vernet, 1969; Colom, 1974; Murray,
516 2006). Peneroplids, in particular, are common in the *Posidonia* meadows of northern
517 Sardinia (Benedetti & Frezza, 2016), which is located south of the study area. Soritids and

518 peneroplids are also known from Elba Island, which is located at about the same latitude as
519 the study area (Langer & Schmidt-Sinns, 2006). Although in most of the samples these
520 symbiont-bearing miliolids would have not been preserved due to diagenesis, their absence
521 from the miliolid-bearing samples P10 and P11 suggests that early Pleistocene
522 temperatures in northern-central Italy were probably lower than today. The high
523 terrigenous content of the Fauglia deposits is also consistent with low-light penetration that
524 hampers the occurrence of SB foraminifera, as also observed in modern *Posidonia*
525 *oceanica* meadows located close to river mouths, and thus influenced by sediment
526 discharge (e.g., the Santa Marinella *Posidonia oceanica* meadow, central Italy; Frezza et
527 al., 2011).

528 In general, the number of individuals and the species richness decrease with increasing
529 mesh size, but this is especially true for deep-sea environments (Schröder et al., 1987;
530 Rathburn & Corliss, 1994; Wollenburg & Mackensen, 1998a, b; Alve, 2003), in which
531 sieving through meshes larger than 63 μm could provide misleading results (Murray,
532 2006). No remarkable differences in the benthic foraminiferal associations were found
533 between the analysed $> 125 \mu\text{m}$ and $> 63 \mu\text{m}$ sediment fractions. This quite homogeneous
534 distribution of the foraminiferal assemblages, regardless of the mesh size, is related to the
535 shallow-water character of the Fauglia succession. The only detectable trend is the slightly
536 higher abundance of some opportunistic genera (i.e., *Bolivina* and *Bulimina*) in the samples
537 sieved through the 63- μm -sized mesh.

538 Index_{EP} and $\text{Index}_{\text{EP-M}}$ display a significant difference between the samples from the
539 *Posidonia*-bearing layers and the *Cladocora* bank, revealing a good potential in indicating
540 ancient seagrass meadows. FI' and $\text{FI}'_{\text{-M}}$ also display differences between the *Posidonia*-
541 bearing layers and the *Cladocora* bank, suggesting their potential usefulness as IPSIs.
542 However, a straightforward application of the FI might induce some interpretative
543 mistakes, for example when symbiont-bearing taxa are not present due to thermal

544 constraints (Mateu-Vicens et al., 2014) or when the fossil association has been altered
545 through diagenetic and/or transport processes (as in the case for the Fauglia outcrop). The
546 same applies for I_{LS} , which consists in the ratio between long and short life-span forms,
547 and whose values must be calibrated with observations on other independent variables (i.e.,
548 plant canopy, oxygen concentration, etc.) (Mateu-Vicens et al., 2014). The morphotype
549 analysis considering miliolids (Mode-1) shows that the morphotype distribution is similar
550 for all the samples except P10 (in which miliolids are abundantly present) and F7 (the
551 sample collected from the *Cladocora* bank), thus highlighting the significant difference
552 between the foraminiferal association of the *Posidonia oceanica* meadow and the
553 *Cladocora* bank (Fig. 11). The morphotype analysis excluding miliolids (Mode-2) allowed
554 to remove the bias produced by diagenesis. In Mode-2, sample P10 is more similar,
555 although not identical, to all the others from the *Posidonia*-bearing layers, whereas sample
556 F7 is still remarkably different (Fig.11). Sample P10 displays a higher frequency of
557 morphotype D* in comparison to the other samples, due to the larger abundance of
558 agglutinated foraminifera. This is probably related to dissolution processes having
559 occurred at a lesser extent within the dark-coloured sediments, in which organic matter is
560 still preserved, thus permitting a better preservation of agglutinated tests formed by
561 particles bound together by an organic or calcareous cement (Armstrong & Brasier, 2013).
562 The presence of permanently attached, encrusting foraminifera such as *Planorbulina*
563 *mediterraneensis* and *Nubecularia lucifuga* (morphotype A*) confirms as one of the most
564 decisive tools to detect ancient *Posidonia* expanses and to distinguish them from other
565 phytal substrates (e.g., macroalgae; Mateu-Vicens et al., 2010). Indeed, the foraminiferal
566 assemblage typical of these seagrass meadows, the *Planorbulinatum mediterraneense*, was
567 formally described (Colom, 1942) based upon the abundance of this species. In the studied
568 outcrop, *Planorbulina mediterraneensis* is present in all the samples from the *Posidonia*-
569 bearing layers and is absent from the *Cladocora* bank sample. The same applies for

570 *Nubecularia lucifuga*, whose occurrence as a fossil is however strongly controlled by
571 diagenetic processes (which explains why it only occurs in sample P10). However, since
572 these taxa can be rare (as in the Fauglia case), their use as a tool for detecting ancient
573 *Posidonia* meadows requires a detailed quantitative micropalaeontological analysis.
574 Furthermore, the low abundance of these taxa within the Fauglia meadow could be related
575 to the environmental stress that possibly influenced this site. Indeed, the stress produced by
576 riverine discharge (testified also by the high terrigenous content and the abundance of
577 organic matter) could deeply influence the development of seagrass leaves, which are the
578 preferred surface onto which morphotype A* taxa live.

579 The presence of other foraminifera with a curved basal surface such as Cibicididae (Fig.
580 13) indicates that these foraminifera lived attached onto a firm substrate, which in this case
581 likely consists of *Posidonia* leaves and/or rhizomes (Fig. 4). However, this observation is
582 not necessarily diagnostic of a vegetated substrate. While hooked morphologies in
583 relatively large carbonate producers, such as coralline algae and acervulinids, have been
584 used to infer the occurrence of seagrasses in the fossil record (Beavington-Penney et al.
585 2004; Tomás et al., 2016; Baceta & Mateu-Vicens, 2022), small benthic foraminifera like
586 Cibicididae could develop a curved attachment surface even when attached onto a non-
587 phytal substrate.

588 Morphotype B epiphytic foraminifera, such as Rosalinidae, *Asterigerinata mamilla* and
589 *Lobatula lobatula*, are present within the *Cladocora caespitosa* bank sediments, although
590 scarcer than in the *Posidonia*-bearing layers. That can be explained by the occurrence of a
591 phytal substrate, with life-span shorter than one year, associated to this coral-dominated
592 environment. Indeed, morphotype B taxa are not exclusively related to seagrass meadows,
593 being indeed commonly reported attached to a broad diversity of macroalgae (Langer,
594 1993).

595 Within the context of the Fauglia succession the most reliable proxies for inferring the
596 presence of ancient seagrass meadows seem to be K/R and K/R_{EXT} indexes, whose
597 variations range across at least one order of magnitude between the *Posidonia* meadow
598 samples and the *Cladocora* bank sample. This suggests that, differing from what has been
599 proposed by Reich et al. (2015), the abundance of keeled elphidiids and in particular the
600 ratio between keeled *Elphidium* and rounded elphidiids (e.g., *Elphidium translucens*,
601 *Cribrroelphidium*, *Porosonion*), combined with other related genera that display rounded
602 periphery (i.e., *Astrononion*, *Haynesina*, *Melonis*, *Nonion*, *Nonionella* and *Valvulineria*)
603 represent a useful IPSI. Keeled elphidiids are known as typically epiphytes (Langer, 1993;
604 Murray, 2006; Mateu-Vicens et al., 2014) whereas rounded ones are more commonly
605 infaunal organisms. Although elphidiids are not strictly related to seagrass, keeled
606 *Elphidium* spp. are more common in vegetated environments; thus, thanks also to their
607 high fossilization potential, they could be used as a proxy of a seagrass-related
608 palaeobiotope. The K/R ratio, being mostly based on morphology, could be calculated also
609 in more ancient successions, where species-level identification can be difficult and often
610 needs to rely on thin sections, thus providing a useful tool for palaeoenvironmental
611 reconstructions.

612 All the calculated indices were compared to those from a modern case study, the present-
613 day Santa Marinella *Posidonia* meadow, along the Tyrrhenian coast of Italy near Rome
614 (Frezza et al., 2011; Mateu-Vicens et al., 2014). This site is heavily affected by
615 anthropogenic activity and, most importantly, by river discharge. Furthermore, the Santa
616 Marinella *Posidonia oceanica* meadow is reportedly shallower than 15 m water depth. In
617 both meadows, stress-tolerant taxa, such as *Ammonia* and *Haynesina*, are abundant and
618 they are accompanied by the presence of taxa that tolerate high organic content within the
619 sediments of the seafloor (e.g., *Bolivina* and *Bulimina*). The values of the calculated
620 indices in both seagrass meadows are similar (see Mateu-Vicens et al., 2014 for the

621 detailed values of Santa Marinella). The Shannon-Weaver index (H') exhibits similar
622 values at both sites (3.12 and 3.3 on average at Santa Marinella and Fauglia, respectively).
623 FI' presents an average value of 1.88 and 1.24 at Santa Marinella and Fauglia, respectively,
624 thus evoking stressed environmental conditions. I_{LS} displays an average value of 0.24 and
625 0.89 at Santa Marinella and Fauglia, respectively, confirming the presence of
626 environmental stress that drove the development of the meadows, as highlighted also by
627 the abundance of low-oxygen tolerant, opportunistic forms, which are associated with
628 decaying seagrass in the sediment (Mateu-Vicens et al., 2014). K/R_{EXT} index was also
629 tested, including the data obtained by Frezza et al. (2011) for Santa Marinella site. Both
630 *Posidonia* meadows show similar values: 0.74 and 0.99 on average at Santa Marinella and
631 Fauglia, respectively, strengthening the similarities between the two meadows as well as
632 the potential of the K/R_{EXT} index as IPSI. Thus, excluding the anthropogenic influence, the
633 environmental characteristics of these meadows are comparable: both meadows are located
634 in shallow water and in both the influence of riverine discharge most likely implicates their
635 growth under stressed condition. Furthermore, the morphotype analysis performed at the
636 two different meadows led to very similar results (see Mateu-Vicens et al., 2014 for
637 details). In particular, the presence of morphotype A*, which is regarded by the authors
638 among the most reliable IPSIs, is very scarce in the *Posidonia* meadows, with values $\leq 1\%$
639 in both. This witnesses that the presence, rather than the abundance, of morphotype A*
640 foraminifera is the most characteristic feature of the foraminiferal assemblage of a seagrass
641 meadow (especially if the meadows grew under stressed condition).

642 Finally, the cluster analysis (Fig. 12) clearly highlights the differences between the two
643 analysed palaeoenvironments preserved at Fauglia (i.e., the *Posidonia* meadow and the
644 *Cladocora* bank). Indeed, such a clustering is mainly related to the different abundance of
645 specific taxa within the two deposits: Cibicididae, Rosalinidae and keeled *Elphidium*
646 species are more abundant within the *Posidonia*-bearing layers (Table 3; Appendix 1),

647 whereas the abundance of *Criboelphidium* and *Haynesina* (and generally that of infaunal
648 taxa that display rounded peripheries) is higher within the sample from the *Cladocora*
649 layer (Table 3; Appendix 1).

650

651 **6. Conclusions**

652 At the Fauglia quarry, two stratigraphic intervals are characterized by the occurrence of
653 remarkably well-preserved fossil remains of marine plants (leaves and in-situ rhizomes of
654 *P. oceanica*). Within this setting, we tested the potential of foraminiferal-based Indirect
655 Palaeo-Seagrass Indicators (IPSIs). The Fauglia succession formed in a shallow, low- to
656 moderate-energy, marginal-marine environment, as indicated by the presence of in situ
657 *Posidonia oceanica* rhizomes, a *Cladocora caespitosa* bank, an oyster reef and abundant
658 foraminifera of the *Ammonia* group. Even if the *Posidonia* remains at Fauglia represent a
659 case of exceptional seagrass preservation, diagenetic processes such as dissolution have
660 modified the original composition of the seagrass-related communities. Such effect is
661 reflected by the reported foraminiferal assemblage that displays differences related to
662 diagenesis, e.g., the preferential loss of miliolids whose tests consist of high-Mg calcite.
663 The fossil assemblage is also influenced by environmental parameters, such as the
664 seawater temperature. The lack of symbiont-bearing foraminifera (e.g., *Amphistegina*,
665 *Sorites*, *Peneroplis*), which are common in seagrass-related environments, indicates that
666 early Pleistocene temperatures in northern Tuscany were probably too low for their
667 development.

668 Considering these constraints, we discussed the potential of benthic foraminifera and
669 foraminifera-based indices as indirect paleo-seagrass indicators. Although highly reliable
670 for the analysis of recent seagrass environments, FI' and I_{LS} display only slight differences
671 between the *Posidonia*-bearing strata and the *Cladocora* bank. However, these indexes
672 confirmed to be reliable for the environmental analysis of seagrass meadows: at Fauglia,

673 their values point to stressed environmental condition, similar to what has been observed at
674 a modern case study (e.g., the Santa Marinella *Posidonia* meadow). Based on our data, the
675 presence of permanently attached, encrusting foraminifera (e.g., *Planorbulina*
676 *mediterraneensis*, *Nubecularia lucifuga*) is considered a highly reliable IPSI. The ratio
677 between keeled *Elphidium* and rounded elphidiids (e.g., *Elphidium translucens*,
678 *Criboelphidium*, *Porosonion*) combined with other related genera that display rounded
679 periphery (i.e., *Astrononion*, *Haynesina*, *Melonis*, *Nonion*, *Nonionella*, *Valvulineria*), also
680 displays a significant role as IPSI. Since this latter index is based on rotaliids, which are
681 resistant to diagenetic dissolution, and on the general morphology rather than on species
682 identification, when combined with the presence of permanently attached encrusting taxa,
683 it could represent a precious tool in the analysis of sedimentary successions, where
684 seagrass remains have not been preserved. Further studies, based on both fossil and recent
685 seagrass-related environments, could allow to improve those indexes and estimate
686 threshold values useful for recognizing the presence of seagrasses in the fossil record.

687

688 **Declaration of Competing Interest**

689 None.

690

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698

699 **Appendix 1. Supplementary Data**

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1220 **Figure and table captions**

1221

1222 **Figure 1.** A. Simplified geological map of Tuscany, showing the areas of Mio-Pleistocene
1223 outcrops, and the location of the study area (modified from Carnevale et al., 2008). Azure:
1224 alluvial deposits; yellow: Neogene and Quaternary marine deposits; green: Quaternary
1225 continental deposits; brown: substratum. B. Satellite image of the Fauglia quarry (Google
1226 Earth), with the location of the sampling sites.

1227

1228 **Figure 2.** Field views and photos of the lower Pleistocene deposits cropping out at the
1229 Fauglia quarry, with location of the collected samples. A, B. Overview of the outcrop. The
1230 base of the section corresponds to picture B (lower interval), whereas the top is shown in A
1231 (upper interval). C. *Posidonia*-bearing layer. The arrow indicates in situ *Posidonia*
1232 rhizomes; D. *Pinna nobilis* specimen (arrow), in-life position, within *Posidonia* bearing
1233 layer; E. Lower section of the Fauglia succession. The arrow indicates the sandy layer
1234 interbedded between two *Posidonia*-bearing layers (lower interval); F. Dark coloured

1235 sediments within the upper *Posidonia*-bearing layer (upper interval); G. Detail of the
1236 *Cladocora caespitosa* bank.

1237

1238 **Figure 3.** Stratigraphic log of the Fauglia quarry outcrop with information on the fossil
1239 content and average grain-size based on laser granulometer analyses. The stratigraphic
1240 position of the collected samples is also indicated.

1241

1242 **Figure 4.** A, B, C. Detail of the well-preserved *Posidonia oceanica* rhizomes collected
1243 within the *Posidonia*-bearing layers of the Fauglia outcrop. D. Fossil *Posidonia oceanica*
1244 rhizome surface; E. Fossil *Posidonia oceanica* leaf; F. Fossil *Posidonia oceanica* leaf,
1245 surface detail. Even if the single plant cells are not preserved, it is possible to appreciate
1246 the preferential orientation of the fibres that constitute the leaf. G. Recent *Posidonia*
1247 *oceanica* rhizome surface, with a *Planorbulina mediterranensis* specimen attached to the
1248 surface. H. Recent *Posidonia oceanica* leaf. It is possible to appreciate the single cells that
1249 constitute the leaf. I. Recent *Posidonia oceanica* leaf, surface detail. Images D, E, F, G, H,
1250 I were obtained with a scanning electron microscope (SEM).

1251

1252 **Figure 5.** LM images of selected foraminifera species. A. *Sahulina conica*; B. *Nubecularia*
1253 *lucifuga*; C. *Adelosina* sp.(juvenile specimens); D. *Quinqueloculina irregularis*; E.
1254 *Spiroloculina excavata*; F. *Cycloforina* sp.; G. *Quinqueloculina seminulum*; H.
1255 *Quinqueloculina schlumbergeri*; I *Pyrgo subsphaerica*; J. *Triloculina* sp.; K. *Dentalina*
1256 *albatrossi*; L. *Lenticulina orbicularis*; M. *Amphicoryna scalaris*; N. *Hyalinonetrion*
1257 *gracillimum*; O. *Lagena doveyensis*; P. *Lagena striata*; Q. *Globulina gibba*; R. *Globulina*
1258 *punctata*; S. *Guttulina communis*; T. *Favulina hexagona*; U, *Fissurina orbignyana*; V.
1259 *Fissurina pseudoorbignyana*; W. *Bolivina alata*; X. *Bolivina dilatata*; Y. *Bolivina*
1260 *pseudoplicata*; Z. *Bolivina spathulata*; AA. *Bolivina striatula*; AB. *Bolivina subspinescens*;
1261 AC. *Bolivina variabilis*; AD. *Cassidulina carinata*. The white bars correspond to 100 µm.

1262

1263 **Figure 6.** LM images of selected foraminifera species. A. *Globocassidulina subglobosa*;
1264 B. *Evolvocassidulina bradyi*; C. *Bulimina aculeata*; D. *Bulimina elongata*; E. *Bulimina*
1265 *marginata*; F. *Bulimina striata*; G. *Globobulimina affinis*; H. *Uvigerina mediterranea*; I
1266 *Rectuvigerina siphogenerinoides*; J. *Trifarina angulosa*; K. *Reussella spinulosa*; L.
1267 *Fursenkoina subacuta*; M. *Sigmavirgulina tortuosa*; N. *Valvulineria bradyana*, spiral side;
1268 O. *Valvulineria bradyana*, umbilical side; P. *Eponides repandus*, spiral side; Q. *Eponides*

1269 *repandus*, umbilical side; R. *Gavelinopsis praegeri*, spiral side; S. *Gavelinopsis praegeri*,
1270 umbilical side; T. *Neoconorbina terquemi*, spiral side; U. *Neoconorbina terquemi*,
1271 umbilical side; V. *Rosalina bradyi*, spiral side; W. *Rosalina bradyi*, umbilical side; X.
1272 *Rosalina globularis*, spiral side; Y. *Rosalina globularis*, umbilical side; Z. *Rosalina*
1273 *williamsoni*, spiral side; AA. *Rosalina williamsoni*, umbilical side; AB. *Neoconorbina* sp.,
1274 spiral side; AC. *Neoconorbina* sp., umbilical side; AD. *Siphonina reticulata*. The white
1275 bars correspond to 100 µm.

1276

1277 **Figure 7.** LM images of selected foraminifera species. A. *Discorbis vilardeboanus*, spiral
1278 side; B. *Discorbis vilardeboanus*, umbilical side; C. *Cibicidoides pseudoungerianus*, spiral
1279 side; D. *Cibicidoides pseudoungerianus*, umbilical side; E. *Cibicidoides pachyderma*,
1280 spiral side; F. *Cibicidoides pachyderma*, umbilical side; G. *Lobatula lobatula*, spiral side;
1281 H. *Lobatula lobatula*, umbilical side; I. *Cibicides refulgens*, spiral side; J. *Cibicides*
1282 *refulgens*, umbilical side; K. *Planorbulina mediterranensis*, spiral side; L. *Planorbulina*
1283 *mediterranensis*, umbilical side; M. *Hanzawaia boueana*, spiral side; N. *Hanzawaia*
1284 *boueana*, umbilical side; O. *Planulina ariminensis*; P. *Planulina* sp., spiral side; Q.
1285 *Planulina* sp., umbilical side; R. *Asterigerinata mamilla*, spiral side; S. *Asterigerinata*
1286 *mamilla*, umbilical side; T. *Haynesina depressula*; U. *Haynesina germanica*; V. *Nonion*
1287 *boueanum*; W. *Nonion commune*; X. *Nonionella turgida*; Y. *Astrononion stelligerum*; Z.
1288 *Melonis affinis*; AA. *Gyroidina soldanii*, spiral side; AB. *Gyroidina soldanii*, umbilical
1289 side; AC. *Discorbinella bertheloti*, spiral side; AD. *Discorbinella bertheloti*, umbilical
1290 side. The white bars correspond to 100 µm.

1291

1292 **Figure 8.** LM images of selected foraminifera species. A. *Cancris auricola*, spiral side; B.
1293 *Cancris auricola*, umbilical side; C. *Oridorsalis umbonatus*; D. *Pullenia bulloides*; E.
1294 *Pullenia quadriloba*; F. *Aubignyna perlucida*, spiral side; G. *Aubignyna perlucida*,
1295 umbilical side; H. *Buccella* aff. *B. frigida*, spiral side; I. *Buccella* aff. *B. frigida*, umbilical
1296 side; J. *Ammonia beccarii*, spiral side; K. *Ammonia beccarii*, umbilical side; L. *Ammonia*
1297 *parkinsoniana*, spiral side; M. *Ammonia parkinsoniana*, umbilical side; N. *Ammonia*
1298 *tepida*, spiral side; O. *Ammonia tepida*, umbilical side; P. *Elphidium aculeatum*; Q.
1299 *Elphidium advenum*; R. *Elphidium complanatum*; S. *Elphidium crispum*; T. *Elphidium*
1300 *fichtelianum*; U. *Elphidium* sp.; V. *Elphidium incertum*; W. *Elphidium macellum*; X.
1301 *Elphidium* sp.1; Y. *Elphidium* aff. *E. aculeatum*; Z. *Elphidium* sp.5 Cimerman & Langer,
1302 1991; AA. *Criboelphidium* cf. *magellanicum*; AB. *Elphidium translucens*; AC.

1303 *Elphidium translucens*, lateral; AD. *Porosononion granosum*. The white bars correspond to
1304 100 µm.

1305

1306 **Figure 9.** SEM images of selected foraminifera species. A. *Nubecularia lucifuga*; B.
1307 *Elphidium advenum*; C. *Elphidium complanatum*; D. *Elphidium fichtelianum*; E. *Elphidium*
1308 *crispum*; F. *Elphidium aculeatum*; G. *Elphidium* sp.; H. *Elphidium translucens*; I.
1309 *Porosononion granosum*; J. *Lobatula lobatula*, spiral side; K. *Lobatula lobatula*, umbilical
1310 side; L. *Cibicidoides pseudoungerianus*, spiral side; M. *Cibicidoides pseudoungerianus*,
1311 umbilical side; N. *Cibicides refulgens*, spiral side; O. *Cibicides refulgens*, umbilical side;
1312 P. *Planorbulina mediterraneensis*, spiral side; Q. *Planorbulina mediterraneensis*, umbilical
1313 side; R. *Ammonia beccarii*, umbilical side; S. *Ammonia parkinsoniana*, umbilical side; T.
1314 *Ammonia tepida*, umbilical side. The white bars correspond to 100 µm.

1315

1316 **Figure 10.** SEM images of selected foraminifera species and fossil *Posidonia*. A.
1317 *Asterigerinata mamilla*, spiral side; B. *Asterigerinata mamilla*, umbilical side; C. *Rosalina*
1318 *bradyi*, spiral side; D. *Rosalina bradyi*, umbilical side; E. *Neoconorbina terquemi*, spiral
1319 side; F. *Neoconorbina terquemi*, umbilical side; G. *Reussella spinulosa*; H. *Fursenkoina*
1320 *subacuta*; I. Fossil *Posidonia* rhizome fragment; J. Fossil *Posidonia* leave fragment. The
1321 white bars correspond to 100 µm.

1322

1323 **Figure 11.** Pie-plots representing morphotypes frequencies in the collected samples. A.
1324 Mode-1 analysis, with miliolids. B. Mode-2 analysis, without miliolids.

1325

1326 **Figure 12.** Q-mode cluster analysis.

1327

1328 **Figure 13.** Benthic foraminifera specimens with curved attaching surface, typical of
1329 epiphytic forms. A. *Lobatula lobatula*; B, C. *Cibicides refulgens*. D. *Planorbulina*
1330 *mediterraneensis*.

1331

1332 **Table 1.** Grain-size analysis of the collected sample. The analysis and the results were
1333 obtained with software GRADISTAT version 4.0 (Blott and Pye, 2001).

1334

1335 **Table 2.** Foraminifera data and parameters calculated from all the samples. Fraction: grain-
1336 size fraction considered within the analysis; Total weight: total amount of dry sediment

1337 before sieving; Tot. BF: number of benthic foraminifera within each sample; BF/100g:
1338 number of benthic foraminifera normalized within 100g of sediment; SR: Species
1339 Richness; Index_{BR}: proportion of broken tests (BR) within a sample, BR/(Tot.BF+BR); H':
1340 Shannon-Weaver index; Index_{EP}: number of epiphytic specimens/total foraminifera
1341 (Mateu-Vicens et al., 2014); Index_{EP-M}: number of epiphytic specimens/total foraminifera
1342 without miliolids; FI': modified FORAM Index (Mateu-Vicens et al., 2014); I_{LS}: long vs.
1343 short life-span index (Mateu-Vicens et al., 2014); FI'_{-M}: FORAM Index modified without
1344 miliolids; I_{LS-M}: long vs. short life-span index without miliolids; K/R: ratio between keeled
1345 *Elphidium* and the sum of rounded elphidiids (e.g., *Elphidium translucens*,
1346 *Criboelphidium*, *Porosonion*) and *Haynesina*; K/R_{EXT}: ratio between keeled *Elphidium*
1347 and the sum of rounded elphidiids (e.g., *Elphidium translucens*, *Criboelphidium*,
1348 *Porosonion*) and associated taxa that display a rounded periphery (i.e., *Astrononion*,
1349 *Haynesina*, *Melonis*, *Nonion*, *Nonionella*, *Valvulineria*).

1350

1351 **Table 3.** Relative frequency (%) of the most common species within all the samples. Raw
1352 data of all species are in Appendix 1.

1353

1354 **Table 4.** Morphotype classification used in this study. Species were assigned to a specific
1355 morphotype as in literature (Langer, 1993; Mateu-Vicens et al., 2010; Mateu-Vicens et al.,
1356 2014).

1357

1358 **Table 5.** Morphotypes abundances within the different samples. Mode-1 indicates the
1359 study considering miliolids. Mode-2 indicates the study without considering miliolids. For
1360 graphical representation see Fig. 11.