

1           **Benthic foraminifera as proxy for fossil seagrass from the Lower Pleistocene deposits**  
2                               **of the Stirone River (Emilia-Romagna, Italy)**

3           Luca Mariani<sup>a,\*</sup>, Giovanni Coletti<sup>a</sup>, Giulia Bosio<sup>a</sup>, Claudia Tentorio<sup>a</sup>, Guillem Mateu  
4           Vicens<sup>b</sup>, Valentina Alice Bracchi<sup>a</sup>, Daniela Basso<sup>a</sup>, Elisa Malinverno<sup>a</sup>

5           <sup>a</sup> Dipartimento di Scienze dell’Ambiente e della Terra, Università degli Studi di Milano-Bicocca,  
6           20126 Milano, Italy

7           <sup>b</sup> Interdisciplinary Ecology Group - Marine Ecology and Systematics Group, Universitat de les Illes  
8           Balears, Cra. de Valldemossa, Km. 7.5, 07122 Palma de Mallorca, Spain

9           \* Corresponding author.

10          E-mail address: l.mariani35@campus.unimib.it (L. Mariani).

11  
12          **Abstract**

13          This paper analyses and describes the benthic foraminiferal associations within the Pleistocene  
14          deposits of the Stirone River (Emilia-Romagna, Italy), with the purpose of testing foraminifera as  
15          Indirect Palaeo-Seagrass Indicators (IPSIs). Our analyses focused on two different biofacies: a  
16          *Thalassinoides* biofacies, characterised by an oligotypic biotic assemblage and a *Pinna* biofacies  
17          representing an infralittoral soft bottom colonised by marine phanerogams and characterized by  
18          high biodiversity. To strengthen the analyses, we have compared the Stirone foraminiferal  
19          association with the one of Fauglia (Tuscany, Italy), in which a well-preserved, early Pleistocene,  
20          fossil *Posidonia* meadow, is present. The aim of this work is to provide qualitative and quantitative  
21          parameters that can be used to recognize past vegetated environments, where fossil seagrass are no  
22          longer present. Considering the influence of ecological constraints and diagenetic processes on the  
23          foraminiferal assemblages, several indexes such as the Index<sub>EP</sub>, the modified FORAM index (FI’),  
24          the “long vs. short life-span index” (I<sub>LS</sub>), and the K/R<sub>EXT</sub> (keeled/rounded morphotypes) have been  
25          calculated and a morphotype-based analysis has been provided. Among the tested indexes, the latter

26 proved to be the most reliable IPSI, in association with the presence of morphotype A\*,  
27 permanently attached, encrusting foraminifera and the abundance of Rosalinidae.

28

29 **Keywords:** Paleoenvironmental reconstructions; IPSI; Seagrass meadows; Epiphytic foraminifera;  
30 Quaternary

31

## 32 **1. Introduction**

33 The ecological significance and environmental importance of seagrass-related habitats is widely  
34 known. Seagrass meadows generally present a higher biodiversity than the surrounding unvegetated  
35 marine areas (e.g., Brasier, 1975; Hirst & Attrill, 2008; Barnes & Barnes, 2012). They provide  
36 indisputable ecosystem benefits and services (Sanchez-Vidal et al., 2021), including water quality  
37 improvement (de los Santos et al., 2020), carbon dioxide sequestration (Deyanova et al., 2017),  
38 stabilization of the seafloor, coastal protection and sediment production (Gacia et al., 2003;  
39 Ondiviela et al., 2014), and climate change mitigation (Duarte et al., 2013). With the term “seagrass  
40 meadows”, we identify large stretches of shelf environment (up to 100s m<sup>2</sup>) dominated by marine  
41 angiosperms (e.g., *Posidonia* spp., *Cymodocea* spp.) (Reich et al., 2015b). Patchy seagrass  
42 meadows are also common. They are widespread worldwide in shallow coastal waters, at all  
43 latitudes, from Greenland to New Zealand (Cullen-Unsworth et al., 2013; Reich et al., 2015b).

44 Nowadays the effects of climate change highlighted the importance of the relationship  
45 between environmental dynamics, such as sea-level fluctuations and temperature variations, and  
46 marine biodiversity. This is especially relevant in sensitive environments such as seagrass meadows  
47 (Alvarez Zarikian et al., 2000; Mateu-Vicens et al., 2014; Unsworth et al., 2014; Arias-Ortiz et al.,  
48 2018). In this respect, the recognition of seagrass-related palaeoenvironments in the fossil record

49 could help us in investigating habitat dynamics in response to environmental changes (Reich et al.,  
50 2015b).

51 Although several studies of modern seagrass habitats and associated communities have been  
52 carried out (e.g., Heck et al., 1989; Langer, 1993; Boström & Bonsdorff, 1997; Barnes & Barnes,  
53 2012; Mateu-Vicens et al., 2014; Benedetti & Frezza, 2016; Sanchez-Vidal et al., 2021), only few  
54 detailed studies on fossil seagrass meadows and related palaeocommunities exist (e.g., Brasier,  
55 1975; Eva, 1980; Dominici, 2001; Domning, 2001; Vélez-Juarbe, 2014; Baceta & Mateu-Vicens,  
56 2021; Bosio et al., 2021; Pavia et al., 2022).

57 The most significant reason for this numerical disparity is that seagrass roots, leaves and  
58 pollens decompose easily. Thus, even if finding well-preserved fossil seagrasses is not impossible,  
59 these occurrences are rare (e.g., Brasier, 1975; Ivany et al., 1990; Hesse et al., 1999; Moissette et  
60 al., 2007; Bosio et al., 2021). Furthermore, the recognition of patchy seagrass meadow  
61 environments in the fossil record is even more limited (Zuschin and Hohenegger, 1998; Kusworo et  
62 al., 2015). The most ancient examples of well-preserved fossil marine plants are reported from the  
63 Upper Cretaceous of the Netherlands (Debey, 1848, 1851; Pomel, 1849; Voigt & Domke, 1955;  
64 Voigt, 1981), Japan (Koriba & Miki, 1931; Oishi, 1931), Germany (Hosius & Von der Marck,  
65 1880), and USA (Dilcher, 2016). Few other examples are reported from the Cenozoic (e.g., Ivany et  
66 al., 1990, Van der Ham et al., 2007; Van der Ham et al., 2017). The most recent fossil seagrasses  
67 are reported from the Pleistocene of 1) the Kritika Member of the Rhodes Formation in Greece  
68 (Moissette et al., 2007), 2) the Arda River outcrops of Emilia-Romagna (Italy; Brunetti & Vecchi,  
69 2005, 2012), 3) the Fauglia sand quarry of Tuscany (Italy; Bosio et al., 2021) and 4) the Stirone  
70 River outcrops near Parma and Piacenza (Italy; Raffi & Serpagli, 2003), which is the study site  
71 described in this paper.

72 Due to their scarce preservation potential, the recognition of paleo-seagrass meadows  
73 commonly relies on indirect evidence (Brasier, 1975; Eva, 1980; Langer, 1993; Domning, 2001;  
74 Beavington-Penney et al., 2004; Leonard-Pingel, 2005; Reuter et al., 2010; Vélez-Juarbe, 2014;

75 Reich, 2014; Reich et al., 2015b; Forsey, 2016; Mariani et al., 2022). Generally, these proxies are  
76 either based on the presence and morphology of fossil organisms that are usually associated with  
77 seagrasses (Brasier, 1975; Eva, 1980; Reuter et al., 2010) or on taphonomic and sedimentological  
78 indicators considered as typical of seagrass-dominated environments. Reich et al. (2015b) defined  
79 all these indicators as IPSIs (Indirect Palaeo-Seagrass Indicators) and critically reviewed them,  
80 exploring their usefulness in detecting fossil seagrass-related environments, where plant remains are  
81 no longer present. These IPSIs have been summarized in different categories, based on the different  
82 criteria used to infer the presence of a palaeo-seagrass meadow: i) taxonomic groups, including  
83 benthic foraminiferal assemblages (e.g., Betzler et al., 2000; Puga-Bernabéu et al., 2007; Mariani et  
84 al., 2022), coralline red algae (e.g., Beavigton-Penney et al., 2004), hydroids (e.g., Hughes et al.,  
85 1991), corals (e.g., Budd et al., 1996), bryozoans (e.g., Di Martino & Taylor, 2014), molluscs  
86 (bivalve taxa such as Pinnidae and chemosymbiotic species, gastropods; e.g., Pérès & Picard, 1964;  
87 Reich, 2014; Basso et al., 2015; Koskeridou et al., 2019; Bracchi et al., 2014, 2016, 2020; Pavia et  
88 al., 2022), ostracods (e.g., Forsey, 2016), echinoderms (Ivany et al., 1990), fish otoliths (Green,  
89 2002), dugongid remains (e.g., Vélez-Juarbe, 2014); ii) sedimentological features, such as grain size  
90 and sorting, since in modern seagrass meadows sediments are poorly sorted and display an  
91 abundant fine fraction (Fornos & Ahr, 1997), the presence of fining-upward sequences (Wanless,  
92 1981), and the abundance of “constructive” micrite envelopes (Perry, 1999); iii) taphonomic  
93 features, including the taphonomic signature of skeletal remains (Leonard-Pingel, 2005; Reich et  
94 al., 2014), the presence of root casts (Cramer & Hawkins, 2009) and root etchings on shells  
95 (Parsons & Brett, 1991); iv) geochemical features, such as the carbon isotopic signal of mollusc  
96 shells (Reich et al., 2015a), and molecular seagrass biomarkers (e.g., De Leeuw et al., 1995).

97         Regarding the IPSIs based on taxonomic groups, many of them are related to epiphytic  
98 carbonate producers, i.e., those organisms that present a mineralized skeleton and grow on a phytal  
99 substrate (Mazzella et al., 1989; Langer, 1993; De Falco et al., 2008; Mateu-Vicens et al., 2014;  
100 Brandano et al., 2016). The main carbonate-producing biota associated with seagrass meadows are

101 foraminifera and calcareous algae, thus allowing to name “GA-Foralgal” or “RA-Foralgal”  
102 (depending on the abundance of green or red calcareous algae) the typical seagrass-related  
103 carbonate factories, also including other skeletal components such as molluscs and bryozoans  
104 (Brandano et al., 2019).

105 Foraminiferal abundance within seagrass meadows has been widely studied by different  
106 authors (e.g., Den Hartog, 1979; Langer, 1993; Mateu-Vicens et al., 2014). Foraminifera have the  
107 advantage of being globally distributed and are usually abundant also in small samples (e.g.,  
108 Murray, 2006). Furthermore, foraminifera have short reproductive cycles (Murray, 1991) making  
109 them useful to track environmental changes over short periods of time (Hallock et al., 2003;  
110 Pergent-Martini et al., 2005). Although foraminifera represent only a part of the trophic niches and  
111 guilds of an environment (Barras et al., 2013), their ecological diversification is large enough to  
112 obtain reliable reconstructions (e.g., Murray, 2006; Jorissen et al., 2007). Thus, benthic foraminifera  
113 present an extraordinary potential as (palaeo)ecological proxies (e.g., Murray, 2006; Benedetti &  
114 Frezza, 2016).

115 According to Langer (1993) and Mateu-Vicens et al. (2014), the analysis of epiphytic  
116 benthic foraminifera for palaeoecological purposes can be based on ecomorphological  
117 characteristics, overcoming problems related to the taxonomic identification at species level.  
118 Epiphytic foraminifera have been divided into five different groups based on: i) type of motility; ii)  
119 life span; iii) feeding mode; and iv) test morphology and structure. More recently, following the  
120 classification provided by Langer (1993), Mateu-Vicens et al. (2014) established five  
121 ecomorphological groups (morphotypes) to analyse epiphytic benthic foraminifera (Fig. 1): A\*)  
122 long-lived (> 10 months) sessile species, permanently attached to the substrate (e.g., *Planorbulina*  
123 *mediterraneensis*, *Nubecularia lucifuga*); SB) symbiont-bearing long-lived (> 10 months) taxa (e.g.,  
124 *Amphistegina*, *Peneroplis*, *Sorites*); B) short-lived (3-5 months), generally motile, taxa that  
125 temporarily attach their tests to the substrate using organic materials (e.g., *Ammonia*, Cibicididae,  
126 Rosalinidae); C) motile, short-lived, suspension-feeding foraminifera (e.g., keeled elphidiids,

127 *Astrononion*, *Criboelphidium*); D\*) short-lived (< 4 months), permanently motile, grazing  
128 foraminifera, such as opportunistic species with porcelaneous or agglutinated test that live within  
129 rhizomes and sediment particles (e.g., small miliolids, textulariids). Based on this, several authors  
130 used foraminiferal associations as indirect indicators of palaeo-seagrass meadows in the geological  
131 record (e.g., Colom, 1942; Blanc-Vernet, 1969; Mateu, 1970; Brasier, 1975; Blanc-Vernet et al.,  
132 1979; Langer, 1993; Ribes et al., 2000; Beavington-Penney et al., 2004; Mateu-Vicens et al., 2010,  
133 2012, 2014; Frezza et al., 2011; Tommasetti et al., 2016; Coletti et al., 2021; Baceta et al., 2021;  
134 Mariani et al., 2022).

135 This paper analyses the benthic foraminiferal associations of a Pleistocene succession  
136 exposed along the Stirone River, in the province of Parma (Northern Italy). As reported in literature,  
137 these deposits host rare but well-preserved seagrass rhizomes (Raffi & Serpagli, 2003) and common  
138 seagrass remains (Bracchi et al., 2020). Furthermore, the occurrence of several specimens of the  
139 bivalve *Pinna nobilis* in life position further supports the presence of a palaeo-seagrass meadow, or  
140 at least of a vegetated substrate (Bracchi et al., 2020). The aim of this paper is thus to describe  
141 quantitatively and qualitatively the foraminiferal assemblages of these deposits and to test them as  
142 valuable IPSI, with indices that can be applied in settings where seagrass remains are no longer  
143 preserved.

144

## 145 **2. Geological setting**

146 The studied outcrop is located along the Stirone River, near the village of San Nicomede, between  
147 the provinces of Piacenza and Parma (44°50'38.53"N, 9°59'2.52"E) (Fig. 2). The Stirone River  
148 carves its way through a continuous upper Miocene (Messinian) to Pleistocene succession (Papani  
149 & Pelosio, 1962; Pelosio & Raffi, 1974; Mary et al., 1993; Channell et al., 1994; Pervesler et al.,  
150 2011; Gunderson et al., 2012). In the studied locality, easily accessible and well-exposed deposits  
151 crop out for about 100 m along the riverbanks. These deposits belong to the Castell'Arquato Basin  
152 (CAB), a small wedge-top basin developed since the upper Miocene (Messinian) above the Northern

153 Appennines orogenic wedge (Roveri & Taviani, 2003; Pervesler et al., 2011; Ghielmi, 2013; Cau et  
154 al., 2015). After the Messinian salinity crisis, the newly restored marine conditions resulted in the  
155 deposition of deep marine sediments in the CAB (Ceregato et al., 2007; Calabrese & Di Dio, 2009).  
156 These deposits constitute the basal part of the succession. During the Pliocene and the Pleistocene,  
157 the depositional environment experienced a general regressive trend, from epibathyal to shelfal  
158 conditions (Gunderson et al., 2012; Coletti et al., 2018). Before the end of the early Pleistocene, this  
159 shallowing upward trend culminated in the deposition of continental deposits (Cigala Fulgosi, 1976;  
160 Pelosio & Raffi, 1977; Ciangherotti et al., 1997; Esu, 2008; Esu & Girotti, 2015). Several authors  
161 interpreted the general late Cenozoic depositional environment of the Stirone River as a  
162 fluviodeltaic system within a tectonically active basin, dominated by fluvial floods and related  
163 hyperpycnal flows (Mutti et al., 1996, 2003; Martini et al., 2002), as it is typical for structurally  
164 confined basins characterised by phases of advancement and retreats of fan-delta systems (Einsele,  
165 2000).

166 The deposits analysed in this paper belong to two of the lithozones identified by Crippa et al.  
167 (2019) along the Stirone River succession (Fig. 2, 3): i) the upper part of Lithozone 2, which  
168 consists of silty sands organized in metre-thick beds and heavily bioturbated sand-infilled and  
169 cemented *Thalassinoides* burrows, and ii) Lithozone 3, which consists of grey sandy to muddy  
170 sediments with Pinnidae specimens in life position (Dominici, 2001), corresponding to the *Pinna*  
171 biofacies described by Bracchi et al. (2020). More precisely, the section investigated in this paper  
172 corresponds to the 56-77 m interval of Crippa et al. (2019). This interval has been dated to the  
173 Calabrian (Early Pleistocene) (Crippa et al., 2019), based on nannofossils (zone CNPL7; Backman  
174 et al. 2012), foraminifera (*Globigerina cariacensis* zone; Cita et al., 2012 and references therein),  
175 and magnetostratigraphy (Gunderson et al., 2012; Monesi et al., 2016).

176

### 177 **3. Materials and methods**

### 178 **3.1 Field work**

179 The Stirone deposits were investigated by describing lithology, macrofossils distribution, and  
180 sedimentary structures. A stratigraphic section was measured at centimetre-scale with a Jacob's  
181 staff, characterizing bed thickness, dip and dip-direction (Fig. 4). A total of 12 samples were  
182 collected at different stratigraphic heights along the two Lithozones (Figs. 2, 3, 4), together with the  
183 samples collected for the analysis of molluscs carried out by Bracchi et al. (2020). Samples R1 and  
184 R2 were collected within the upper section of Lithozone 2 in the sediments surrounding  
185 *Thalassinoides* ichnofossils. Samples S1, S2, S3, S5, S6, S7, S8, S9, S10 and S12 were collected in  
186 Lithozone 3 in correspondence of Pinnidae specimens in life position (S3, S5, S6, S9, S12),  
187 alongside Pinnidae specimens not in life position (S2) and randomly within the sediments of the  
188 Pinnidae biofacies (S1, S7, S8, S10). All samples were obtained by collecting at least 20 g of  
189 sediment, after slightly digging inside the deposits to remove the weathered material on the surface.

190

### 191 **3.2 Sediments and foraminiferal analysis**

#### 192 **3.2.1 Granulometry and foraminiferal assemblages**

193 Grain-size analyses were performed on each sample with a Malvern Mastersizer 2000E™ Laser  
194 granulometer at the Università degli Studi di Milano-Bicocca. Grain-size distribution and  
195 sedimentological parameters were analysed through the software GRADISTAT Version 4.0 (Blott  
196 & Pye, 2001) (Table 1). For micropaleontological analyses, a small amount of each sample (Table  
197 2) was weighted and treated with 30 % hydrogen peroxide to remove organic matter (Dimiza et al.,  
198 2016). Each sample was then wet-sieved through a 125- $\mu\text{m}$ -sized mesh, in order to separate the  
199 fraction for the picking of benthic foraminifera. We decided to identify benthic foraminifera in the  
200  $> 125 \mu\text{m}$  fraction to avoid counting juvenile forms, which are often abundant and difficult to  
201 identify (Malek et al., 2014). Before proceeding with the picking, the sieved fractions were oven-



202 dried at 40°, weighted and divided into equal fractions using a microsplitter, to obtain sub-samples  
203 containing at least 300 specimens (Buzas, 1990; Murray, 1991; Murray, 2006; Lòpez-Belzunce,  
204 2014). Handpicking was performed under a ZEISS Olympus SZ61 stereo microscope equipped with  
205 a high-resolution camera. We relied on Foraminiferi Padani (Agip S.p.A., 1982), Loeblich and  
206 Tappan (1988), Cimerman and Langer (1991), Langer and Schmidt-Sinns (2006), Milker and  
207 Schmiedl (2012), the Foraminifera.eu-Project (Hesemann, 2020), and the World Register of Marine  
208 Species (WoRMS Editorial Board, 2021) for the taxonomic identification of foraminifera. SEM  
209 imaging of epiphytic foraminifera was performed using a FEG (SEM-FEG) Gemini 500 Zeiss  
210 scanning electron microscope at the Università degli Studi di Milano-Bicocca. For each sample, all  
211 foraminifera identified and relative counts are provided in the supplementary materials (Appendix  
212 1), and the following parameters were calculated: i) the standardized abundance of benthic  
213 foraminifera (n/100 g of sediment), ii) the relative abundance (%) of each species, and iii) the ratio  
214 between broken and total number of tests.

215 A Q-mode cluster analysis of species abundances across the samples, based on the Bray-  
216 Curtis similarity index, was performed with the software Primer v.6. No data transformation was  
217 applied.

### 218 **3.2.2 Environmental indices**

219 Epiphytic foraminiferal species were assigned to the different morphotypes (A\* to D\*) proposed by  
220 Langer (1993) and Mateu-Vicens et al. (2014). The abundance of each morphotype was calculated  
221 for each sample through the Index<sub>EP</sub> i.e., the ratio between the number of epiphytic and total benthic  
222 foraminifera (Mateu-Vicens et al., 2014).

223 Two indices, created for the analysis of modern environments, were tested on the  
224 foraminiferal fossil assemblage:

225 i) the modified FORAM Index (FI') developed by Mateu-Vicens et al. (2014) based on  
226 Hallock et al. (2003) FORAM Index. FI' is expressed as:

$$227 \quad FI' = 10 \times (P_{A^*} + P_{SB}) \times P_{D^*} + 2 \times (P_B + P_C),$$

228 where  $P_{A^*}$ ,  $P_{SB}$ ,  $P_B$ ,  $P_C$ , and  $P_{D^*}$  indicate the relative abundance of the foraminifera morphotypes.  
229 Values of  $FI' > 4$  indicate optimal environmental conditions, whereas values of  $FI' < 2$  are indicative  
230 of stressed conditions (Mateu-Vicens et al., 2014);

231 ii) the “long vs. short life-span” index ( $I_{LS}$ ) developed by Mateu-Vicens et al. (2014).  $I_{LS}$ ,  
232 which consists of the ratio between longer-living and short-living forms, was built to highlight the  
233 differences between well-preserved and stressed *Posidonia oceanica* meadows (Mateu-Vicens et  
234 al., 2014) and is expressed as:

$$235 \quad I_{LS} = (3.5 \times (P_{A^*} + P_{SB}) + 0.01) / (P_{D^*} + 0.01)$$

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

238 The  $K/R_{EXT}$  index from Mariani et al. (2022) was also calculated in each sample. It consists  
239 of the ratio between keeled *Elphidium* and the sum of rounded elphidiids (e.g., *Criboelphidium*,  
240 *Porosononion*), and other related genera that display a rounded periphery (i.e., *Astrononion*,  
241 *Haynesina*, *Melonis*, *Nonion*, *Nonionella*, *Pullenia*, *Valvulineria*). Values of  $K/R_{EXT} > 0.4$  point to  
242 the presence of vegetated substrate nearby. In this work, to facilitate the definition of this index, we  
243 introduce two new morphotypes, namely  $K$  and  $R$ , useful for the  $K/R$  analysis (Fig. 1). Morphotype  
244  $K$  is constituted by epiphytic keeled *Elphidium*, whereas morphotype  $R$  includes the group of  
245 generally infaunal foraminifera that display a rounded periphery. This classification does not  
246 overlap with the epiphytic morphotypes from Langer (1993) and Mateu-Vicens et al. (2014). Thus,  
247 specimens belonging to morphotype  $C$  can be either placed into morphotype  $K$  or  $R$ .

248 Statistical analyses were performed with the software RStudio (RStudio Team, 2020). In  
249 particular, a bivariate statistical analysis was performed considering the relationship between  
250  $K/R_{EXT}$  and morphotype  $A^*$  abundance, taking into account all the samples from Stirone and the  
251 samples from the Fauglia site, described by Mariani et al. (2022). The correlation between the two  
252 variables has been tested and a correlation coefficient was calculated. Only one sample from the  
253 latter site (P11) was excluded from the analysis, as an outlier.

254

## 255 **4. Results**

### 256 **4.1 Field observation and stratigraphic section**

257 The measured stratigraphic section consists of a 20-m-thick mixed carbonate-siliciclastic succession  
258 (Fig. 4). The base of the succession consists of 2 meters of slightly NE dipping (with an average  
259 attitude of 042/18), fine sandy to coarse silty deposits. These deposits, which belong to Lithozone 2  
260 of Crippa et al. (2019), can be divided into a 1.5-m-thick poorly consolidated layer, followed  
261 upward by a 0.5-m-thick cemented layer. The different cementation of the two layers is deeply  
262 enhanced by erosion (Fig. 4). Both layers are intensely bioturbated by *Thalassinoides*. Within this  
263 lithozone, macrofossils are scarce and consist solely of shells of the mollusc *Aequipecten*  
264 *opercularis*. In the present work, we will refer to these deposits as the *Thalassinoides* biofacies.  
265 Upwards, the stratigraphic section continues with a 19-m-thick, slightly N to NNE dipping (with an  
266 average attitude of 005/20), massive to laminated, very fine sandy to coarse silty deposits. These  
267 layers, which belong to the Lithozone 3 of Crippa et al. (2019), are mostly characterized by poorly  
268 cemented sediments, except for a 1-m-thick interval located at about 7.5 m from the base of this  
269 facies (approximately 9.5 m from the base of the entire section), which consists of two well  
270 cemented layers separated by a very thin and poorly cemented interval. The different cementation  
271 of the strata is once again enhanced by the erosion. Within Lithozone 3 macrofossils are common,  
272 easily recognizable, and mainly consist of molluscs (Dominici, 2001; Bracchi et al., 2020), solitary  
273 scleractinians, bryozoans, echinoids and fragments of red calcareous algae. *Pinna nobilis* specimens  
274 in life position were recorded (Fig. 3, 4; *Pinna* biofacies). The measured section ends with a well-  
275 cemented biocalcarenite layer.

276

### 277 **4.2 Foraminiferal analysis and skeletal assemblage**

278 The associate sediments display noticeable differences between the samples from the two facies. In  
279 the *Thalassinoides* biofacies, the bioclastic fraction is scarce, mainly constituted by planktic

280 foraminifera, while terrigenous grains (e.g., quartz) dominate the deposit. In the *Pinna* biofacies the  
281 bioclastic fraction (mainly consisting of benthic foraminifera, molluscs, ostracods and echinoderms  
282 associated with rare erect bryozoans fragments and planktic foraminifera) is more relevant. Plant  
283 remains are also common in this biofacies.

284 In the analysed samples, we identified i) 83 species of hyaline benthic foraminifera, ii) 4  
285 genera of agglutinated foraminifera and iii) 7 genera of miliolids (Figs. 5, 6). Hyaline benthic  
286 foraminifera were identified at species level and selected species were clustered in different groups  
287 to perform statistical analyses (Table 3, 4). Agglutinated foraminifera (*Bannerella gibbosa*, *Sahulia*  
288 spp., *Spiroplectinella* spp., *Textularia* spp.) were counted as a single group. Miliolids (*Adelosina*  
289 spp., *Cycloforina* spp., *Miliolinella* spp., *Quinqueloculina* spp., *Siphonaperta* spp., *Spiroloculina*  
290 spp., *Triloculina* spp.) were also clustered as a single group. All other species identified are reported  
291 in the supplementary material (Appendix 1).

292 The standardised abundance of benthic foraminifera presents the lowest values within the  
293 *Thalassinoides* biofacies (samples R1 and R2) with an average value of 16.858 specimens/100 g of  
294 sediment, whereas in the *Pinna* biofacies the values are one order of magnitude higher, with an  
295 average value of 134.466 specimens per 100 g of sediment. The abundance of broken tests shows  
296 no significant difference among the samples.

297 The average abundances of the species (Table 3) in the *Thalassinoides* and *Pinna* biofacies  
298 were used to calculate the similarity matrix and to plot the corresponding dendrogram (Fig. 7). Two  
299 main sample groups are separated at 55% similarity. The first group corresponds to  
300 the *Thalassinoides* biofacies, and includes *A. beccarii*, *A. parkinsoniana*, *B.*  
301 *spathulata*, *Buccella* aff. *frigida*, *C. carinata*, *C. refulgens*, *C. pachyderma*, *E. translucens*, *G.*  
302 *subglobosa*, *N. boueanum* and *N. terquemi* as the most common taxa.

303 The second group of samples corresponds to the *Pinna* biofacies, and is characterized by  
304 the presence of *Planorbulina mediterraneensis*, *C. carinata*, *C. refulgens*, *N. terquemi* (with a much  
305 higher abundance than in the *Thalassinoides* facies), and miliolids (except for samples S2, S3 and

306 S7). Further subdivisions (Fig. 7) are based on the abundance of certain species in particular  
307 samples. For instance, S5, S6 and S8 contain frequent *Asterigerinata mamilla*; S1 and S12 are  
308 characterized by *L. lobatula*; S2 and S3 form a group with locally frequent *A. beccarii* and *B.*  
309 *spathulata*, *B. elongata*, *C. pachyderma*, *G. subglobosa*, *N. boueanum*, and scarce small miliolids.

310 Within the *Thalassinoides* biofacies, the ammoniid group and the Bolivinidae are present  
311 with higher abundances (8.7%). Buliminidae display low values in both *Thalassinoides* and *Pinna*  
312 biofacies, whereas Cassidulinidae are abundant in both the biofacies (around 8%). Cibicididae  
313 constitute nearly 20% of the assemblage in both biofacies and are slightly more abundant within the  
314 *Thalassinoides* biofacies. Within Cibicididae, *L. lobatula* is slightly more abundant in the *Pinna*  
315 biofacies. The group of keeled *Elphidium* (morphotype K) is abundant in both facies, presenting a  
316 slightly higher value in the *Pinna* biofacies (7.4%) compared to the *Thalassinoides* biofacies  
317 (5.9%). Rosalinidae are much more abundant in the *Pinna* biofacies (18.6%). The rounded  
318 periphery group (morphotype R) is highly common within the *Thalassinoides* biofacies (22.1%).  
319 Uvigerinidae are rare in both levels. Agglutinated foraminifera are mostly not abundant but are  
320 slightly more common in the *Pinna* (3.7%) than in the *Thalassinoides* biofacies (2.5%). Miliolids  
321 are abundant in the *Pinna* biofacies (9.1%) and scarce in the *Thalassinoides* biofacies (0.8%).

322 Epiphytic foraminifera were assigned to different morphotypes of Mateu-Vicens et al.  
323 (2010, 2014) (Table 4). Morphotype A\* only contains *P. mediterraneensis* and consequently its  
324 abundance is equal to the abundance of this species, which is absent in the *Thalassinoides* biofacies  
325 and present in every sample of the *Pinna* biofacies (but its abundance is low: 1.1%). No specimens  
326 belonging to morphotype SB have been observed. Morphotype B (*Ammonia* group, *A. mamilla*,  
327 *Aubignyna perlucida*, *B. aff. frigida*, Cibicididae, *Discorbinella bertheloti*, *Eponides repandus*,  
328 *Hanzawaia boueana*, Rosalinidae) are equally common in both biofacies, with values around 44%.  
329 Morphotype C (*A. stelligerum*, *Criboelphidium* sp., keeled *Elphidium* group) is slightly more  
330 abundant in the *Pinna* biofacies (7.7%) compared to the *Thalassinoides* biofacies (5.9%).  
331 Morphotype D\* (agglutinated foraminifera and miliolids) is much more abundant in the *Pinna*

332 biofacies (12.8%), and rather scarce in the *Thalassinoides* one (3.4%). Index<sub>EP</sub> is higher for the  
333 *Pinna* biofacies, with an average value of 0.66, compared to the 0.53 of the *Thalassinoides*  
334 biofacies.

335 FI' display the lowest values in sample R1 and R2 (*Thalassinoides* biofacies), with an  
336 average of 1.02, whereas the average value for the *Pinna* biofacies is slightly higher (1.27). I<sub>LS</sub>  
337 index shows very low values in all samples, without clear trends.

338 K/R<sub>EXT</sub> presents higher values in the samples from the *Pinna* biofacies (average of 0.91),  
339 and distinctly lower values in the *Thalassinoides* biofacies (average of 0.27).

340 The bivariate statistical model, considering the relationship between K/R<sub>EXT</sub> and  
341 morphotype A\* abundance, display a mild-strength linear correlation. Pearson and Spearman  
342 correlations are 0.54 and 0.53, respectively. R<sup>2</sup> display a statistically significant value of 0.29.

343

## 344 **5. Discussion**

### 345 **5.1 Foraminiferal assemblages in a seagrass-related palaeoenvironment**

346 The preservation of seagrass remains within the fossil record is extremely rare and mainly related  
347 to processes such as silicification or rapid burial by fine-grained sediments (e.g., Ivany et al., 1990;  
348 Moissette et al., 2007; Van der Ham et al., 2007; Reich et al., 2015; Dilcher, 2016; Van der Ham et  
349 al., 2017; Bosio et al., 2021). On the other hand, seagrass related carbonate producing-organisms  
350 have a much higher fossilization potential. In the Stirone area, the presence of a palaeo-meadow is  
351 indicated by both direct (seagrass rhizomes reported by Raffi & Serpagli, 2003) and indirect  
352 observations (*Pinna nobilis* in life position reported by Bracchi et al., 2020). *P. nobilis* is a large  
353 endemic bivalve of the Mediterranean, occurring between 0 and 60 m of water depth and commonly  
354 associated with *Posidonia oceanica* and *Cymodocea nodosa* meadows (Pérès & Picard, 1964;  
355 Gómez-Alba, 1988; Lemer et al., 2014; Basso et al., 2015). Although due to its fragile shell this  
356 mollusc displays a relatively low preservation potential compared to other bivalves (Beesley et al.,  
357 1998), its occurrence in life position has been used as an IPSI (Reuter & Piller, 2011; Reuter et al.,

2012; Reich et al., 2015b; Tomassetti et al., 2022). The *Pinna* biofacies of the Stirone River displays many *P. nobilis* specimens in life position and includes large amounts of tiny plant frustules. Based on these features and the molluscan assemblage of the facies, Bracchi et al. (2020) suggest the presence of a vegetated substrate, possibly *Cymodocea* meadow (although the occurrence of a patchy meadow with both plants cannot be excluded). Overall, the palaeoenvironmental reconstruction of the *Pinna* biofacies of the Stirone River suggests a shallow (less than 15 m) infralittoral seafloor, colonised by marine phanerogams, and characterised by periods of high terrigenous influx (Bracchi et al., 2020). Sedimentological evidence, especially grain size, suggest that the *Thalassinoides* biofacies also represents an infralittoral environment, even if bioturbation has obliterated most sedimentary structures (Crippa et al., 2019). *Thalassinoides* is a system of horizontal, unlined, cylindrical burrows possibly joined by vertical or oblique shafts (Pervesler et al., 2011), generally produced by crustaceans in shallow water settings (Curran & Frey, 1977; Belt et al., 1983; Ekdale et al., 1984; Frey et al., 1984; Kamola, 1984; Miller & Knox, 1985; Myrow, 1995; Pervesler & Uchman, 2009; De Araújo et al., 2021). Although not limited to shallow water settings (e.g., Crimes, 1977; Link & Bottjer, 1982; Ekdale & Bromley, 1984), *Thalassinoides* burrows are commonly reported in intertidal-subtidal deposits characterised by fine-grained sediments like those of the Stirone River (Table 1; Fig. 3), thus supporting the shallow-water interpretation of this biofacies. The benthic foraminiferal associations of the two studied facies is consistent with the interpretation based on molluscs (Bracchi et al., 2020) and ichnofacies (Pervesler et al., 2011), thus confirming that the analysed Stirone section displays a slightly deepening-upward sequence (Crippa et al., 2019). High abundances of the foraminifera of the *Ammonia* group and associated taxa (e.g., *Buccella*) support this interpretation for the *Thalassinoides* biofacies, while the higher biodiversity associated to *Pinna* biofacies is consistent with a seagrass-related environment.

Q-mode cluster analysis (Fig. 7) allows to recognise two groups corresponding to the two biofacies (*Thalassinoides* and *Pinna*) and to the lithozones described by Crippa et al. (2019).

384 *Thalassinoides* biofacies is dominated by foraminiferal taxa grouped in low-oxygen foraminiferal  
385 assemblages (LOFA; Bernhard & Sen Gupta, 1999), which is consistent with high riverine  
386 terrigenous and nutrient input. The assemblage of the *Pinna* biofacies is instead representative of a  
387 seagrass environment, based on the presence of *P. mediterraneensis* and the abundance of small  
388 epiphytic foraminifera (*Planorbulinatum mediterraneensis* sensu Colom, 1942). Moreover, several  
389 sub-biofacies can be distinguished based on differences in the foraminiferal assemblages, mostly  
390 referring to the small miliolids and LOFA taxa. In particular, very abundant LOFA and scarce  
391 miliolids (samples S2 and S3) might indicate punctual episodes of high riverine influence or,  
392 alternatively, they may represent transitional settings between the terrigenous-dominated and the  
393 well-developed seagrass environments.

394  $Index_{EP}$  displays higher average values within the *Pinna* biofacies as compared to the  
395 *Thalassinoides* biofacies (average value of 0.66 for the former and 0.53 for the latter; Table 2). This  
396 means that almost 70% of the species within the *Pinna* biofacies might have lived on a phytal  
397 substrate, compared to the 50% of potential epiphytes of the *Thalassinoides* facies. If *Ammonia* spp.  
398 (and related genera such as *Aubignyna* and *Buccella*) are excluded from the epiphytic association,  
399 since they are not exclusive of seagrass meadows, the difference is enhanced (0.39 of the  
400 *Thalassinoides* biofacies vs. 0.62 of the *Pinna* biofacies). Although *Ammonia* is often reported to be  
401 present within vegetated seafloors, especially in those characterised by a high content of organic  
402 matter (Frezza et al., 2011; Mateu-Vicens et al., 2014), this genus can populate a wide range of  
403 coastal, shallow-water environments (Murray, 2006). Nonetheless, here we have considered  
404 *Ammonia* group as part of the epiphytic taxa, following different authors (e.g., Mateu-Vicens et al.,  
405 2014; Mariani et al., 2022), in order to facilitate comparisons with other sites.

406 In modern environments, epiphytic photosymbiotic foraminifera (morphotype SB, e.g.,  
407 *Amphistegina*, *Peneroplis*, *Sorites*) are indicative of shallow, well-illuminated environments and are  
408 usually, but not always, associated to flat, long-lasting, vegetated substrates (Langer, 1993; Murray,  
409 2006; Mateu-Vicens et al., 2014; Reich et al., 2015). *Peneroplis* can be found on seagrass rhizomes



410 and leaves (Hohenegger, 1994; Renema, 2006), but also on algal and sandy substrates (Hohenegger,  
411 1994). Similarly, *Amphistegina* can be very abundant within seagrass meadows (Riordan et al.,  
412 2012), but its distribution is not exclusively related to the presence of a vegetated substrate. Both  
413 peneroplids and soritids are limited by the 14°C (or even colder) isotherm (Langer & Hottinger,  
414 2000; Beavington-Penney & Racey, 2004; Murray, 2006), while *Amphistegina* is limited by the  
415 14°C winter isotherm (Langer et al., 2012; El Kateb et al., 2018). Therefore, although the presence  
416 of morphotype SB foraminifera in the fossil record may be indicative for vegetated habitats (e.g.,  
417 *Orbitolites* in the Eocene; Beavington-Penney et al., 2006; Tomassetti et al., 2016; Coletti et al.,  
418 2021), their absence is not necessarily evidence for the lack of phytal substrates. For the Stirone  
419 *Pinna* biofacies, the lack of this group is definitively more likely related to the cold climate of the  
420 early Pleistocene (Prista et al., 2015).

421 Morphotype A\*, represented here by *P. mediterraneis* only, is one of the most reliable  
422 IPSIs (Mariani et al., 2022) and a useful indicator to distinguish between palaeo-seagrass meadows  
423 and other phytal substrates (e.g., macroalgae; Mateu-Vicens et al., 2010). Indeed, *P.*  
424 *mediterraneis* is present in every samples from the *Pinna* biofacies, whereas in the  
425 *Thalassinoidea* biofacies it is absent (Table 3, 5; Fig. 8). Morphotype B\* dominates in both  
426 biofacies, constituting about 45% of the entire epiphytic assemblage (Fig. 8; Table 5). According to  
427 Murray (2006) and Benedetti and Frezza (2016), morphotype B\* usually constitutes 25-85% of  
428 vegetated seafloor assemblages (both seagrass and algae), suggesting its dependence on the  
429 presence of a vegetated substrate. However, its large frequency within the *Thalassinoidea* biofacies  
430 indicates that its abundance cannot be solely related to the presence of seagrasses. Some species that  
431 belong to morphotype B are not directly related to a phytal substrate but can colonize a large variety  
432 of environments (e.g., *Ammonia*, *Buccella*), whereas other species, such as *Lobatula lobatula*, are  
433 generally more linked to marine vegetation (Jorissen et al., 1995), even if nowadays it is commonly  
434 found in almost vegetation-free environments in colder climates (e.g., Hald & Korsun, 1997). Also,  
435 Rosalinidae (e.g., *Rosalina* spp., *Neoconorbina terquemi*) and Asterigerinidae (*Asterigerinata*

436 *mamilla*), are generally linked to vegetated sea-bottoms (Langer, 1988; Panieri et al., 2005; Frezza  
437 & Carboni, 2009). In our case, both Rosalinidae and *A. mamilla* are much more abundant within the  
438 *Pinna* biofacies (Table 3, 5). Morphotype C is slightly more abundant in the *Pinna* biofacies, but it  
439 also includes motile suspension feeders that are not strictly epiphytic taxa (Fig. 8; Table 4, 5).  
440 Murray (1991) suggested that elphidiids can range from epifaunal to infaunal, with elphidiids with  
441 an acute periphery, such as *Elphidium crispum* or *Elphidium aculeatum*, generally linked to phytal  
442 substrates (e.g., Langer, 1993; Mateu-Vicens et al., 2014), as this test shape seems to facilitate their  
443 motility on algae and plants. On the other hand, elphidiids with rounded periphery and other genera  
444 such as *Astrononion* or *Criboelphidium* are not solely epiphytes but can conduct an infaunal mode  
445 of life. Morphotype D\* is constituted by stress-tolerant taxa with a short life-span, such as small  
446 miliolids and agglutinated foraminifera (Langer, 1993). These species could be adapted to nutrient-  
447 rich environments, such as seagrass rhizomes (Mateu-Vicens et al., 2014). In the Stirone River,  
448 samples from the *Pinna* biofacies display a larger abundance of morphotype D\* specimens,  
449 especially miliolids (Fig. 8; Table 5). Miliolids are in general very abundant in shallow water  
450 seagrass meadows (Frezza et al., 2011), but not exclusively. Moreover, their abundance must be  
451 carefully considered because, they are strongly affected by diagenetic processes due to their high-  
452 Mg-calcite tests (Budd & Hiatt, 1993).

453         The FI' index is based on the abundance of epiphytic foraminifera and has been successfully  
454 implemented in the modern Mediterranean Sea as a proxy of water quality (e.g., El Kateb et al.,  
455 2020; Khokhlova et al., 2022). This index presents low values in both biofacies and display only a  
456 minor difference between the samples of the *Thalassinoides* and *Pinna* biofacies (Table 2). As  
457 suggested by Mariani et al. (2022), the application of FI' to fossil context might be hindered by  
458 diagenesis (e.g., the preferential dissolution of miliolids). Similarly, I<sub>LS</sub> (which is used to assess the  
459 ecological status of modern seagrass meadows) displays no significant differences between the  
460 samples of the two biofacies. Overall, the use of FI' and I<sub>LS</sub> alone is not recommended as an IPSI  
461 but can be helpful for the palaeoenvironmental reconstruction of the seagrass-related deposits.

462 Actually, their low values in the Stirone River deposits might suggest that the local palaeo-seagrass  
463 were growing under stressed conditions. The presence of mud-loving, deeper water, opportunistic  
464 foraminifera (e.g., *Bolivina*, *Bulimina*, Cassidulinidae), could be related to episodic pulses of fluvial  
465 discharge which are considered an important factor in the evolution of the Stirone environment by  
466 both Crippa et al. (2019) and Bracchi et al. (2020). Although some of these foraminiferal taxa are  
467 very common in cold climates (and thus their abundance could be related to the cold climate of the  
468 Calabrian), the overall distribution of *Ammonia* group and infaunal taxa (e.g., Bolivinidae,  
469 Buliminidae, Cassidulinidae, morphotype R foraminifera) within the Stirone River sediments could  
470 be also connected to river-related organic-matter input and not solely to seagrass distribution.

471 K/R<sub>EXT</sub> index confirms to be one of the most significant tools to perform this kind of  
472 palaeoenvironmental reconstructions, and its use as IPSI can be considered very important (Mariani  
473 et al., 2022). Indeed, in the seagrass-related palaeoenvironment (*Pinna* biofacies), K/R<sub>EXT</sub> displays  
474 remarkably higher values than in the *Thalassinoides* biofacies (Table 2).

475

## 476 **5.2 Comparison with a similar study site: the case of Fauglia**

477 To enhance the observations collected within the Stirone river deposits and strengthen the  
478 application of benthic foraminifera as IPSIs, in this section we compare the results from this case  
479 study with the fossil *P. oceanica* meadow of Fauglia (Tuscany, Italy). Both the successions belong  
480 to the Calabrian (lower Pleistocene) and are located at relatively close latitude, thus excluding large  
481 differences in climate. The Fauglia succession formed in a shallow, low- to moderate-energy,  
482 marine environment, as indicated by the presence of in situ *P. oceanica* rhizomes, a *Cladocora*  
483 *caespitosa* bank, an oyster reef and abundant foraminifera of the *Ammonia* group (Bosio et al.,  
484 2021; Mariani et al., 2022). As for the Stirone River deposits, Fauglia benthic foraminiferal  
485 associations were analysed inside different deposits: within *Posidonia*-bearing layers and in a *C.*  
486 *caespitosa* bank.

487           Based on the morphotypes analysis, morphotype B is the most abundant group in both sites.  
488 In particular, Cibicididae and Rosalinidae are the most abundant families in both the palaeo-  
489 meadows deposits. In Fauglia, Cibicididae display a higher frequency in the seagrass-related  
490 intervals, whereas in the *Cladocora* bank their abundance is much lower. On the other hand, in the  
491 Stirone outcrop, Cibicididae are similarly distributed between vegetated and non-vegetated settings.  
492 In both sites, Rosalinidae displays higher abundance in the seagrass-related deposits, indicating  
493 Rosalinidae as one of the most clearly seagrass-related family. In both successions, morphotype A\*  
494 foraminifera only occur in seagrass-related deposits, thus indicating the presence of morphotype A\*  
495 foraminifera as a highly reliable IPSI. Also, the presence of foraminifera with a curved basal  
496 surface, such as Cibicididae and *P. mediterraneensis* specimens, indicates that possibly they lived  
497 attached onto a firm substrate, which most likely consisted of seagrass leaves and rhizomes (Langer  
498 et al., 1993). Anyway, this feature is not undoubtedly diagnostic of a phytal substrate, as small  
499 benthic foraminifera could develop a curved attachment surface even in correspondence of non-  
500 phytal substrate (Mariani et al., 2022). Morphotype C abundance is similar in both the study sites.  
501 In both sites morphotype K taxa are more common in seagrass related deposits, while morphotype  
502 R foraminifera are much more common in the layers that are not associated with seagrasses. This  
503 clearly testifies in favour of the usefulness of the  $K/R_{EXT}$  index as indirect indicator of the presence  
504 of a palaeo-seagrass meadow. Although other tests based on recent foraminiferal assemblages  
505 would be necessary, considering the data collected in this paper and in the study of the  
506 exceptionally well-preserved Pleistocene seagrass meadow of Fauglia (Bosio et al., 2021; Mariani  
507 et al., 2022), values of  $K/R_{EXT}$  higher than 0.4 could be used as an indirect indicator of a seagrass-  
508 related palaeoenvironment (Table 2; Fig. 8). Indeed, in every samples collected within the seagrass-  
509 related layers the value of this index is higher than 0.4, whereas in the other samples is always  
510 lower than this threshold.

511           The preferential dissolution of miliolids observed in Fauglia (Mariani et al., 2022) further  
512 suggests evaluating Morphotype D\* with caution. Indeed, miliolids and agglutinated foraminifera

513 are more influenced by diagenesis than foraminifera with hyaline, pure calcite tests. However, this  
514 is not the case of the Stirone deposits, in which morphotype D\* are well-preserved in all the  
515 samples and evidence of dissolution processes are not shown.

516 If we do not consider miliolids, the morphotype abundances are similar in both study sites  
517 (Fig. 8), testifying that excluding the taxa that are mostly affected by diagenesis could be useful to  
518 identify fossil seagrass meadows.

519 Finally, the higher abundance of foraminifera of the *Ammonia* group suggests that the  
520 Fauglia *Posidonia* meadow probably developed closer to the coastline than the Stirone River  
521 palaeo-seagrass meadow.

522

### 523 **5.3 The usefulness of K/R<sub>EXT</sub> index: insights and perspectives**

524 Based on the evidence from known paleo-seagrass settings, such as those documented at the Fauglia  
525 and Stirone outcrops, the K/R<sub>EXT</sub> index and the abundance of Morphotype A\* foraminifera appear  
526 as the most promising indicators of such palaeo-environment. Both indices are based on  
527 morphological characters, more than species identifications. This means that they could be easily  
528 calculated even in more ancient successions than Stirone or Fauglia, where lowest-level  
529 taxonomical identification can be difficult to perform. Most likely, they could be calculated also in  
530 thin sections. This approach would also allow for the comparison of widely different sites, because  
531 even if the taxa are different, morphotypes can be recognized and the morphotype analysis could  
532 still be carried out.

533 A bivariate statistical analysis was performed considering the relationship between K/R<sub>EXT</sub>  
534 and the abundance of morphotype A\* among all of the samples from the Stirone river deposits and  
535 the Fauglia successions (Fig. 9), with the exception of sample P11 from Fauglia, which was  
536 excluded from the analysis due to the very pervasive diagenetic processes. This analysis shows that  
537 the values from the two sites are comparable and that there is a weak positive correlation between  
538 the value of K/R<sub>EXT</sub> and the abundance of permanently attached foraminifera (Fig. 9). However, the

539 occurrence of morphotype A\* taxa is always indicative of fossil seagrass meadows, independently  
540 from its abundance. This model will be integrated in future with new data that will be collected  
541 from different fossil and modern foraminiferal associations, both in seagrass-related environments  
542 and in environments with no phytal substrate.

543

## 544 **6. Conclusion**

545 Benthic foraminifera were analysed from two different shallow water paleo-settings outcropping  
546 along the Stirone River. In particular, our results on the foraminifera confirm the occurrence of a  
547 vegetated marine palaeoenvironment in correspondence of the *Pinna* biofacies accordingly to  
548 Bracchi et al. (2020). On the other hand, the *Thalassinoides* facies represents a palaeoenvironment  
549 devoid of seagrass.

550 The morphotype analysis of benthic foraminifera confirmed their effective application as  
551 Indirect Palaeo-Seagrass Indicators (IPSIs), as demonstrated from a similar vegetated palaeo-setting  
552 at Fauglia (Mariani et al., 2022). In particular:

553 i) when we exclude the taxa that are mostly affected by diagenesis (e.g., miliolids), it is  
554 possible to reproduce comparable signals in different fossil seagrass meadows.

555 ii) the lack of photosymbiotic foraminifera (e.g., *Amphistegina*, *Sorites*, *Peneroplis*), was  
556 most likely related to the low early Pleistocene temperatures in this area, which did not allow the  
557 development of these species.

558 iii) the presence of permanently attached, encrusting foraminifera, confirmed as one of the  
559 most reliable IPSI, as well as the abundance of Rosalinidae.

560 iv) among the tested indexes, the  $K/R_{EXT}$  proved to be the most reliable in this kind of  
561 analysis, displaying values higher than 0.4 when calculated within seagrass-related environments.

562 Further analyses are required in order to improve the  $K/R_{EXT}$  index, making it comparable  
563 between different successions in terms of spatial and time distribution.

564

565 **Author contributions**

566 **Luca Mariani:** Conceptualization, Methodology, Formal analysis, Investigation, Writing –  
567 Original Draft, Visualization, Supervision, Project administration. **Giovanni Coletti:**  
568 Conceptualization, Resources, Writing – Review & Editing. **Giulia Bosio:** Formal analysis,  
569 Investigation, Data Curation. **Claudia Tentorio:** Investigation. **Guillem Mateu Vicens:** Formal  
570 analysis, Supervision, Writing – Review & Editing. **Valentina Alice Bracchi:** Writing – Review &  
571 Editing. **Daniela Basso:** Writing – Review & Editing. **Elisa Malinverno:** Resources, Writing –  
572 Review & Editing, Project administration, Funding acquisition.

573

574 **Data availability**

575 Datasets related to this article can be found at <https://board.unimib.it/datasets/hrgfj7xfgs>, an open-  
576 source online data repository hosted at Mendeley Data (Mariani et al., 2022).

577

578 **Declaration of competing interest**

579 The authors declare that they have no known competing financial interests or personal relationships  
580 that could have appeared to influence the work reported in this paper.

581

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1053

## 1054 **Figures**

1055 **Fig. 1** Epiphytic benthic foraminifera morphotype categories, modified from Langer et al. (1993)  
1056 and Mateu-Vicens et al. (2014). Morphotype categories for the K/R analysis (Mariani et al., 2022)  
1057 are also present.

1058 **Fig. 2** A. Simplified geologic map of the analysed area. It is possible to appreciate the Stirone River  
1059 section. Modified from Crippa et al. (2019). B. Satellite image of the analysed Stirone River section  
1060 (Google Earth), with the location of the sampling sites.

1061 **Fig. 3** Field views and photos of the lower Pleistocene deposits cropping out at the Stirone River  
1062 section, with location of some collected samples. A. Overview of the two analysed biofacies. The  
1063 white arrow indicates a *Thalassinoides* burrow specimen. B. *Thalassinoides* biofacies. The white  
1064 arrows indicate *Thalassinoides* specimens. C. *Pinna* biofacies. The arrow indicates a *Pinna nobilis*  
1065 specimens in life position. D. *Pinna nobilis* specimens within the *Pinna* biofacies. E. *Pinna*  
1066 biofacies outcropping on the southern side of the Stirone River. F. Stratigraphic contact between the  
1067 upper level of the *Pinna* biofacies and the overlying biocalcarenes.

1068 **Fig. 4** Stratigraphic log of the analysed section of the Stirone River. Is it possible to appreciate the  
1069 contact between the *Thalassinoides* biofacies (in purple), the *Pinna* biofacies (in green) and the  
1070 upper biocalcarenes (in yellow). The curve of the K/R<sub>EXT</sub> values is also reported, showing the  
1071 differences between the two biofacies.

1072 **Fig. 5** LM images of selected foraminifera species. A. *Sahulia conica*; B. *Cycloforina* sp.; C.  
1073 *Spiroloculina* sp.; D. *Bolivina elongata*; E. *Bolivina alata*; F. *Bolivina spathulate*; G. *Cassidulina*  
1074 *carinata*; H. *Ammonia beccarii*, spiral side; I. *A. beccarii*, umbilical side; J. *Reussella spinulosa*; K.  
1075 *Planorbulina mediterranensis*, spiral side; L. *P. mediterranensis*, umbilical side; M. *Rosalina*  
1076 *bradyi*, spiral side; N. *R. bradyi*, umbilical side; O. *Neoconorbina terquemi*, spiral side; P. *Cibicides*  
1077 *refulgens*, spiral side; Q. *C. refulgens*, umbilical side; R. *Lobatula lobatula*, spiral side; S. *L.*  
1078 *lobatula*, umbilical side; T. *N. terquemi*, spiral side. Specimen with two proloculus; U. *Melonis*  
1079 *affinis*; V. *Nonion boueanum*; W. *Haynesina germanica*; X. *Valvulineria bradyana*; Y. *Hanzawaia*  
1080 *boueana*; Z. *Uvigerina mediterranea*; AA. *Elphidium translucens*; AB. *Elphidium aculeatum*; AC.  
1081 *Elphidium fichtelianum*; AD. *Elphidium crispum*. The white bars correspond to 100 µm.

1082 **Fig. 6** SEM images of selected foraminifera species and seagrass remains. A. *Planorbulina*  
1083 *mediterranensis*, umbilical side; B. *P. mediterranensis*, spiral side; C. *Asterigerinata mamilla*, spiral  
1084 side; D. *Cassidulina carinata*; E. *Neoconorbina terquemi*, spiral side; F. *N. terquemi*, umbilical  
1085 side; G. *Cibicides refulgens*, umbilical side; H. *C. refulgens*, spiral side; I. *Lobatula lobatula*, spiral  
1086 side; J. *L. lobatula*, umbilical side; K. *Nonion boueanum*; L. *Elphidium translucens*; M. *Elphidium*  
1087 *crispum*; N. *Elphidium macellum*; O. *Elphidium fichtelianum*; P. *Elphidium advenum*; Q. *Elphidium*  
1088 *aculeatum*; R. *E. aculeatum*.

1089 **Fig. 7** Q-mode cluster analysis.

1090 **Fig. 8** Pieplots resulting from the morphotype analysis for each studied sample. Average plots for  
1091 the *Pinna* biofacies (S) and *Thalassinoides* biofacies (R), are present. Average plots for the two



1092 biofacies without considering miliolids are also present. Average pieplots from the Fauglia  
1093 foraminiferal associations are also present (see Mariani et al., 2022).

1094 **Fig. 9** Bivariate analysis and linear regression model.

1095

## 1096 **Tables**

1097 **Table 1** Grain-size analysis of the collected sample. The analysis and the results were obtained with  
1098 software GRADISTAT version 4.0 (Blott and Pye, 2001).

1099 **Table 2** Foraminifera data and parameters calculated from all the samples. Total weight: total  
1100 weight of sediment before sieving; Tot. BF: Total number of benthic foraminifera counted and  
1101 considered for the analysis for each sample, after the splitting; BF/100g: standardized number of  
1102 benthic foraminifera within 100 g of sediment; Index<sub>BR</sub>: proportion of broken tests (BR) within a  
1103 sample,  $BR/(Tot. BF + BR)$ ; Index<sub>EP</sub>: number of epiphytic specimens/total foraminifera; Index<sub>EP-  
1104 *Ammonia*</sub>: Index<sub>EP</sub> without considering *Ammonia* (and related genera such as *Aubignyna* and *Buccella*)  
1105 as epiphytic specimens; FI': modified foraminifera index (Mateu-Vicens et al., 2014); I<sub>LS</sub>: long vs.  
1106 short life-span index (Mateu-Vicens et al., 2014); K/R<sub>EXT</sub>: ratio between morphotype K (keeled  
1107 *Elphidium*) and morphotype R foraminifera (e.g., rounded elphidiids, *Astrononion*, *Haynesina*,  
1108 *Nonion*, *Pullenia*, *Valvulineria*) (Mariani et al., 2022).

1109 **Table 3** Relative percentage frequency of the analysed foraminiferal groups and of the common taxa (i.e.,  
1110 those with an abundance higher than 5%).

1111 **Table 4** Morphotype classification and foraminifera groups used in this study. Species were assigned to a  
1112 specific morphotype as in literature (Langer, 1993; Mateu-Vicens et al., 2010; Mateu-Vicens et al., 2014;  
1113 Mariani et al., 2022).

1114 **Table 5** Morphotypes abundances within each sample and average abundance of each morphotype within the  
1115 two lithozones of the Stirone river deposits.