

# Inter-Specific and Inter-Individual Trait Variability Matter in Surface Sediment Reworking Rates of Intertidal Benthic Foraminifera

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## Research Article

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1 **Inter-specific and inter-individual trait variability matter in surface**  
2 **sediment reworking rates of intertidal benthic foraminifera**

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26 **Abstract**

27 Although benthic foraminifera are an important component of meiofauna and contribute to  
28 carbonate production and carbon/nitrogen cycles, their role in bioturbation processes remains  
29 poorly known. Five dominant intertidal benthic foraminifera were recently classified into  
30 functional bioturbator groups according to their sediment reworking mode and intensity. Our  
31 study aimed at identifying potential drivers (i.e. size and/or travelled distance) of species-  
32 specific surface sediment reworking rate. The travelled distance and surface sediment  
33 reworking rate of *Haynesina germanica*, *Criboelphidium williamsoni*, *Ammonia tepida*,  
34 *Quinqueloculina seminulum* and *Miliammina fusca* were assessed through image analysis. Our  
35 results show that the surface sediment reworking performed by these species is not size-  
36 dependent, but dependent on their motility traits through interspecific differences in the  
37 travelled distance. Smaller species (i.e. *Quinqueloculina seminulum* and *Haynesina germanica*)  
38 contribute more to surface sediment reworking than larger ones (i.e. *Ammonia tepida*,  
39 *Criboelphidium williamsoni* and *Miliammina fusca*). These observations stress the critical role  
40 of motion behaviour in surface sediment reworking processes by intertidal foraminifera.  
41 Finally, we stress that the high inter-individual variability observed in conspecific motion  
42 behaviour may be important to decipher the role of foraminifera in sediment bioturbation.  
43 Noticeably, the species characterized by a strong inter-individual variability are also the species  
44 that have the highest surface sediment reworking rates. This last observation may inform on the  
45 species-specific phenotypic plasticity and therefore the potential for the functional role of these  
46 species to be maintained in their natural environment. This is particularly relevant in an era of  
47 global change where ecosystem balance is increasingly threatened by various stressors such as  
48 heat-waves, ocean acidification and plastic pollution.

49

50

## 51 **Keywords**

52 Benthic foraminifera – surface sediment reworking rate – intertidal mudflats – motion  
53 behaviour – interspecific variability – inter-individual variability

54

## 55 **1. Introduction**

56 Bioturbation activities of benthic fauna contribute to the structure and functioning of most  
57 marine soft-sediment ecosystems; see Kristensen et al. (2012) for a review. Sediment particle  
58 reworking typically drives (i) substrate physical properties such as granulometry and erodibility  
59 and (ii) bacterial communities (Orvain et al. 2003, 2004). This process affects chemical  
60 gradients and increases dissolved fluxes at the sediment-water interface (Orvain et al. 2004;  
61 Kristensen et al. 2012; Schratzberger and Ingels 2018; Bonaglia et al. 2020). Overall,  
62 bioturbation contributes to the mineralisation of organic matter; thereby enhancing carbon and  
63 nutrient cycling (Aller 1994; Mermillod-Blondin and Rosenberg 2006; Meysman et al. 2006;  
64 Kristensen et al. 2012).

65 Meiobenthos refers to organisms with a size ranging from 63  $\mu\text{m}$  to 1 mm that occur in a  
66 large range of both marine and freshwater environments (Mare 1942; Hulings and Gray 1971;  
67 Higgins and Thiel 1988). Their role in bioturbation processes has received an increasing amount  
68 of attention over the last decade. Beyond the fact that they may be more abundant, diverse and  
69 resilient than macro-invertebrates (Gerlach 1978; Bouchet et al. 2018, 2020), their contribution  
70 to sediment reworking and bio-irrigation is non-negligible compared to the one of macro-  
71 invertebrates (Rysgaard et al. 2000; Gross 2002; Näslund et al. 2010; Bonaglia et al. 2014;  
72 Bouchet and Seuront 2020). Through their movement and feeding activity, meiofaunal  
73 organisms further structure and constrain microbial communities that are crucial for organic  
74 matter mineralization (De Mesel et al. 2004; Moens et al. 2005; Nascimento et al. 2012). They  
75 also affect the oxygen penetration depth, increasing solute transport (e.g. sulphides) into the

76 sediment (Aller and Aller 1992; Rysgaard et al. 2000; Bonaglia et al. 2020). For instance, in an  
77 intertidal mudflat, nematode displacements have been shown to stimulate microphytobenthos  
78 accumulation in the surface biofilm leading to a shift in diatom community (D'Hondt et al.  
79 2018). Taken together, these observations strongly suggest that the role of meiofauna in  
80 bioturbation processes needs to be urgently considered in studies dealing with benthic  
81 ecosystem functioning as they play an important role in soft sediment ecosystems (Näslund et  
82 al. 2010; Nascimento et al. 2012; Bonaglia et al. 2014, 2020).

83 Traditionally, foraminifera have been overlooked in studies assessing total meiofaunal  
84 bioturbation probably, mostly because these works only considered metazoan meiofauna  
85 (Schratzberger and Ingels 2018). These abundant and diverse organisms in intertidal mudflats  
86 are able to significantly alter sediment structure through the creation of burrows and cyst  
87 building both at the interface and deeper into the sediment (Severin and Erskian 1981; Kitazato  
88 1988, 1994; Chandler 1989; Green and Chandler 1994; Gross 2000, 2002; Bouchet and Seuront  
89 2020; Deldicq et al. 2020), leading to sediment mixing (Gross 2002). Surface sediment  
90 reworking rates of the intertidal foraminiferal species *Ammonia tepida* and *Quinqueloculina*  
91 *seminulum* were recently shown as comparable to those of macrofaunal species (Bouchet and  
92 Seuront 2020). These observations highlighted the non-negligible importance of benthic  
93 foraminifera to contribute to sediment reworking processes. Furthermore, meiofauna (including  
94 foraminifera) can increase rate of solute transport and stimulate aerobic decomposition and  
95 nitrification processes in the oxic zone (Aller and Aller 1992; Aller 1994; Bonaglia et al. 2020).  
96 Recently, five dominant intertidal foraminifera have been classified in distinct functional  
97 groups (e.g. surficial-, epifaunal- and gallery-biodiffusors; see Deldicq et al. 2020) that  
98 underpinned their differences in the type and intensity of sediment reworking. Distinct species-  
99 specific behavioural patterns related to their displacement both within the sediment and at the

100 sediment-water interface were therefore hypothesized to differently affect sediment reworking  
101 rate (Deldicq et al. 2020).

102 These preliminary results on the potential of benthic foraminifera to contribute to  
103 bioturbation processes emphasize the need to further estimate surface sediment reworking rates  
104 of foraminiferal species to better understand their role in benthic ecosystem functioning. In this  
105 context, the specific objectives of the study were (i) to estimate individual surface sediment  
106 reworking rate (hereafter referred as  $SSRR_i$ ) of five dominant intertidal foraminifera species in  
107 temperate intertidal mudflats, (ii) to understand how morphological traits or those related to  
108 their displacements would influence  $SSRR_i$  and (iii) to further link these traits and  $SSRR_i$   
109 intensity to the functional groups recently introduced for benthic foraminifera (Deldicq et al.  
110 2020).

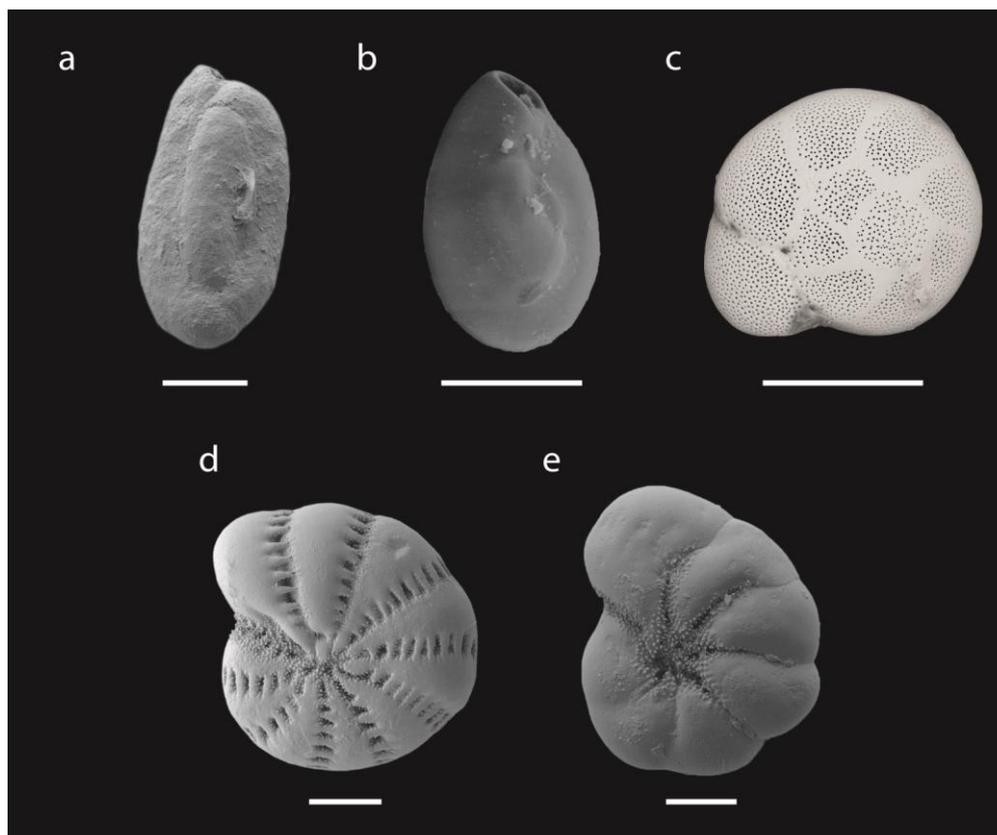
111

## 112 **2. Materials and Methods**

### 113 *2.1. Studied species*

114 Five intertidal species were selected considering their high abundance in the foraminiferal  
115 assemblage at the study site: (i) the prolate ellipsoid-shaped *Quinqueloculina seminulum* and  
116 *Miliammina fusca* (Fig. 1a,b), (ii) the trochospiral *Ammonia tepida* (Fig. 1c) and (iii) the  
117 planispiral *Haynesina germanica* and *Criboelphidium williamsoni* (Fig. 1 d,e). In contrast to  
118 the other species that have a calcareous shell, *Miliammina fusca* is an agglutinated species.

119



120

121 **Fig. 1.** SEM images of the dorsal side of the five studied foraminifera (a) *Miliammina fusca*, (b) *Quinqueloculina*  
 122 *seminulum*, (c) *Ammonia tepida*, (d) *Cribroelphidium williamsoni* and (e) *Haynesina germanica*. Scale bar = 100  
 123  $\mu\text{m}$ .

124

125 Note that *C. williamsoni*, *H. germanica* and *A. tepida* may co-occur with species that are  
 126 morphologically identical though they are genetically distinct (Pawlowski et al. 1995; Hayward  
 127 et al. 2004; Saad and Wade 2016). Despite they are morphologically similar, those species may  
 128 have different ecological requirements (Richirt et al. 2020), hence different behavioural traits.  
 129 Molecular identification is therefore needed to discriminate morphospecies before the  
 130 assessment of their behavioural traits. In our sampling site, we find *H. germanica* S16, *C.*  
 131 *williamsoni* S1 and *A. tepida* T6 (Schweizer M., personal communication). Depending at the  
 132 abundance at the time of sampling, between 8 and 33 individuals per species with similar sizes  
 133 were used for the experiment (Table 1).

134

135

136 2.2. *Sediment sampling and experimental set-up*

137 Sampling was performed in the Authie Bay (50°22'20"N, 1°35'45"E) which is an intertidal  
138 mudflat located on the French coast of the English Channel. This estuary is a well-preserved  
139 area (e.g. Henry et al. 2004) characterized by a semidiurnal macrotidal regime where tidal range  
140 can exceed 10 m during highest astronomical tides (McLusky and Elliott 2004). Among the  
141 intertidal zones located along the northern part of the French coast, the Authie Bay is the one  
142 displaying the highest diversity in foraminiferal species (Francescangeli et al. 2020).

143 Surface-sediment (0-1 cm) was collected from February to June 2018 at low tide and stored  
144 in plastic containers (100-ml). Samples were then transported to the laboratory, where it was  
145 washed through a 125- $\mu$ m mesh-size sieve. During the sampling period, temperature has  
146 increased from  $\sim 7^{\circ}\text{C}$  (February) to  $\sim 18^{\circ}\text{C}$  (June), which may have induced a seasonal effect on  
147 the organism' activity as evidenced for macrofaunal species (Pascal et al. 2019). A recent study  
148 on *Haynesina germanica* showed however, that foraminiferal *SSRRi* has a low thermal  
149 dependence in the range 6-24°C (Deldicq et al. 2021). In this study, we assume that the potential  
150 seasonal effect could be negligible through the use of an acclimation period carried out before  
151 running the experiment. Hence, living benthic foraminifera were subsequently individually  
152 sorted with a brush, identified and their pseudopodial activities checked under an inverted  
153 phase-contrast microscope (Olympus IX71, Japan). Only active individuals were subsequently  
154 imaged to measure the shell size parameter i.e. maximum length and width of each individual  
155 (Olympus SZX16, Japan, TC capture software).

156 Prior to behavioural observations, individuals were kept for 24-h at the experimental  
157 temperature (18°C) in a temperature-controlled room (MIR-154, Panasonic, Japan; temperature  
158 fluctuation  $\pm 0.3^{\circ}\text{C}$ , light intensity 170  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Behavioural observations were performed  
159 in 300-ml aquaria filled with 25–30-ml of thawed Authie Bay sediment (i.e.  $\sim 1\text{cm}$  thick) (Fig.  
160 2). We used previously frozen sediment to ensure that the sediment was free of moving macro-

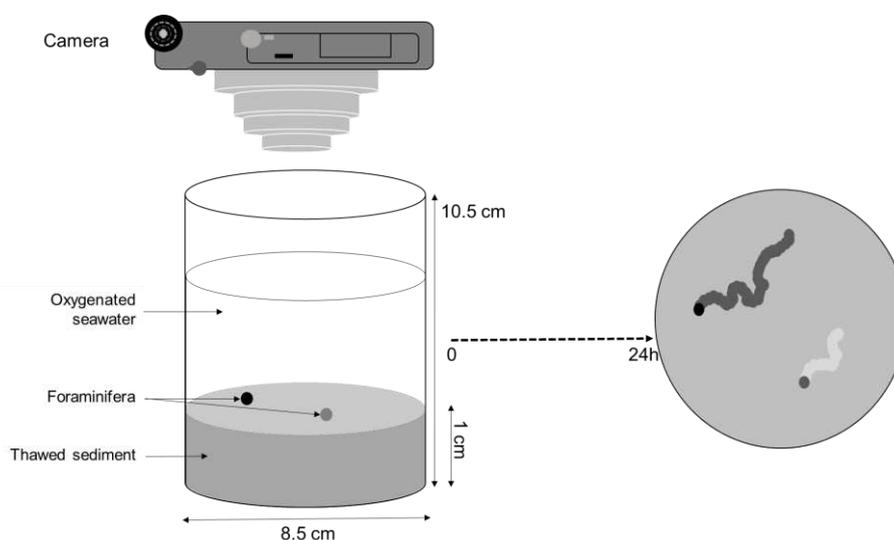
161 and meio-organisms so that the only tracks observed on the sediment surface would be those  
 162 from foraminifera.

163

### 164 2.3. Quantification of behavioural traits

165 After the acclimation period, foraminifera were randomly placed on the sediment surface  
 166 (Fig. 2), under 250-ml of natural unfiltered and air saturated seawater (salinity = 33) following  
 167 10 min of vigorous air bubbling immediately before spreading foraminifera on the sediment  
 168 surface. In total 15 experiments were performed.

169



170

171 **Fig. 2.** Experimental set-up for time-lapse assessment of foraminiferal motion-trait (left-hand side) and examples  
 172 of the movement paths of 2 foraminifera over a 24-h period (right-hand side)

173

174 Individual displacements in and on the sediment were recorded by time-lapse photography  
 175 (Fig. 2; 1 image every 10 min for 24-hours) using a digital camera (Nikon V1 with a Nikkor  
 176 10–30mm lens). For each foraminifera, 144 images were combined in the image-analysis  
 177 software Fiji to extract  $(x,y)$  coordinates using the Manual tracking plugin (Schindelin et al.  
 178 2012). A total of 230 active (i.e. moving) individuals was initially selected for the experiment.  
 179 During the experiment, it was not possible to track all individuals (i) because some burrowed

180 into the sediment up to a depth where their paths were not visible and/or (ii) because some paths  
 181 crossed and consequently individual trajectories were lost. We therefore only kept individuals  
 182 that exhibited visible tracks throughout the whole 24-h experiment so that the information  
 183 related to their behavioural traits had the same statistical weight. In total we followed the  
 184 trajectories of 103 individuals. Note that at the end of each 24-h experiment, dissolved oxygen  
 185 saturation was consistently ca. 56% in the overlying seawater directly above the sediment-water  
 186 interface (HI9829 MULTIPARAMETER METER, HANNAH INSTRUMENTS).

187 The distance travelled by each individual between two images (i.e. 10 min) was calculated  
 188 as:

$$189 \quad D_t = \sqrt{(x_t - x_{t+10})^2 + (y_t - y_{t+10})^2}$$

190 where  $(x_t, y_t)$  and  $(x_{t+10}, y_{t+10})$  are the coordinates between two successive images taken at times  
 191  $t$  and  $t + 10$  min respectively. The total distance travelled within 24 hours,  $D_{24}$ , was subsequently  
 192 calculated by summing individual  $D_t$ .

193

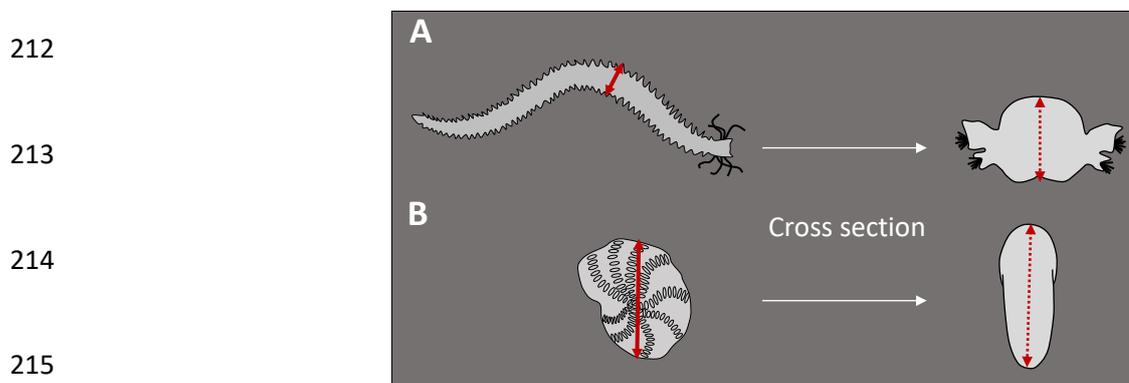
#### 194 2.4. Quantification of surface sediment reworking rates

195 To estimate the surface sediment reworking rate of intertidal foraminifera we used the  
 196 calculation method previously used for macrofaunal species such as sea urchin (Hollertz and  
 197 Duchêne 2001; Lohrer et al. 2005; Maire et al. 2008):

$$198 \quad SR = \frac{(DT \times CS)}{\Delta t}$$

199 where  $DT$  is the distance travelled during a time interval  $\Delta t$  and  $CS$  the cross section, i.e. surface  
 200 reworked along the motion plane (Maire et al. 2008, see figure 3A for an example). This  
 201 calculation method was recently applied on two intertidal foraminiferal species i.e. *Ammonia*  
 202 *tepida* and *Quinqueloculina seminulum* (Bouchet and Seuront 2020). Nevertheless, in their

203 calculations, the authors used the maximum test length rather than the cross section as the  
 204 morphological component. However, test length may not be optimal as some foraminifera such  
 205 as *Q. seminulum* and *M. fusca*, have asymmetrical shapes with test length greater than test width  
 206 (Fig. 1a,b). Noticeably, the length/width ratio is close to 1 for *A. tepida*, 1.2 for *H. germanica*  
 207 and *C. williamsoni* and to 2 for *Q. seminulum* and *M. fusca*. The use of the surface area therefore  
 208 appears to be more accurate for the calculation. However, measurement of the cross section  
 209 involves the characterisation of the organism' height (Fig. 3). Due to their small size,  
 210 foraminifera are manipulated under binocular microscope that makes very difficult to measure  
 211 their cross section as it involves a vertically-positioning of the individual (Fig. 3B).



216 **Fig. 3.** Illustration of the cross section of (A) polychaete and (B) benthic foraminifera that may be used for sediment  
 217 reworking calculation.

218

219 We therefore assume that the surface area corresponding to the larger part of the test i.e.  
 220 dorsal or umbilical sides may be used for the estimation of the surface sediment reworking  
 221 performed by foraminifera. Hence, using the measurements of maximum length and width (see  
 222 section 2.2), the surface area ( $\text{mm}^2$ ) of each individual ( $S_i$ ) was estimated under the assumption  
 223 of an ellipse-shaped shell:

224

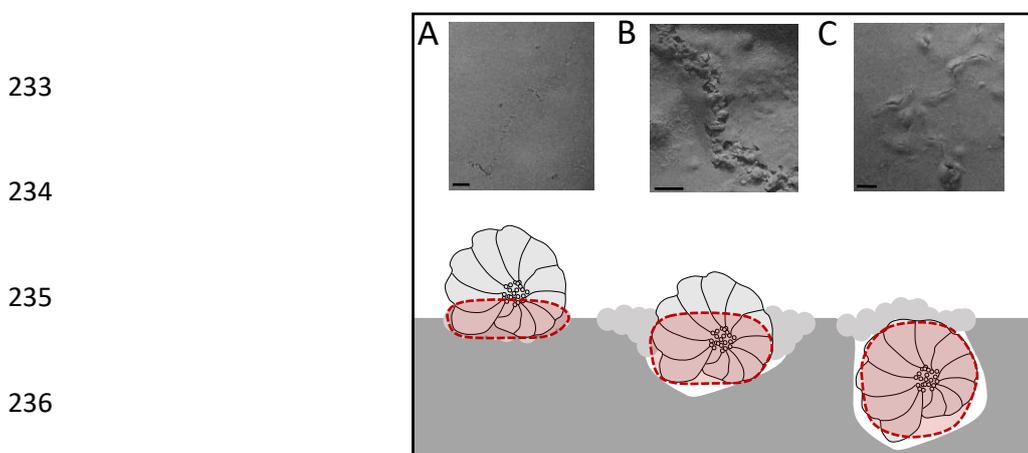
$$S_i = \pi \times \frac{\text{Length}}{2} \times \frac{\text{Width}}{2}$$

225 Since we used conspecifics of similar size, the mean surface area  $S$  for each species was then  
 226 calculated and subsequently used for the calculation of the individual surface sediment  
 227 reworking rate ( $SSRR_{it}$ ,  $\text{mm}^3 \text{ind}^{-1} 10\text{min}^{-1}$ ) as follow:

$$228 \quad SSRR_{it} = S \times D_t$$

229 where  $D_t$  is the distance travelled ( $\text{mm ind}^{-1} \text{d}^{-1}$ ) by each individual between two images (i.e.  
 230 10min).

231 In our experiments, individuals of both species can moved on the surface (Fig 4A), at the  
 232 interface (Fig 4B) or in the sediment (Fig 4C).



237 **Fig. 4.** Discrimination between the vertical positions taken by benthic foraminifera in the sediment to estimate  
 238  $SSRR_{it}$ . Images were taken from experiments containing living individuals of *H. germanica*.

239

240 When the individual was observed crawling at the sediment surface or at the interface only  
 241  $\frac{1}{3}$  and  $\frac{1}{2}$  of the mean surface area  $S$  was considered in the  $SSRR_i$  calculation respectively (Fig.  
 242 4A,B). Conversely, when the individual was observed burrowed in the sediment, the total of  
 243 the mean surface area  $S$  was used (Fig. 4C).

244 Finally, the individual surface sediment reworking rate ( $SSRR_i$ ,  $\text{mm}^3 \text{ind}^{-1} \text{day}^{-1}$ ) were  
 245 estimated as follow:

$$246 \quad SSRR_i = \sum SSRR_{i(t)}$$

247 where  $SSRR_{i(t)}$  is the individual surface sediment reworking rate between two images (i.e.  
248 within 10min).

249

## 250 2.5. Data analysis

251 Because the surface area of individual foraminifera, their travelled distances and  $SSRR_i$  were  
252 non-normally distributed (Shapiro-Wilk test,  $p < 0.05$ ), a Kruskal-Wallis test was applied to  
253 infer the presence of significant differences between species, and eventually followed by a  
254 Dunn test to identify distinct groups of measurements. All statistical analyses were performed  
255 using R.3.5.2. software (R Core Team 2019).

256

## 257 3. Results

### 258 3.1. Species-specific size

259 In our experiment, the mean surface area of *A. tepida* is almost twice as large as those of *H.*  
260 *germanica* and *Q. seminulum* (Table 1). Indeed, there were significant differences in the surface  
261 area  $S_i$  between species (KW test,  $p < 0.05$ ), and three distinct groups were identified as  $S_H$ .  
262  $germanica = S_Q.seminulum < S_M.fusca < S_C.williamsoni = S_A.tepida$  (Dunn test,  $p < 0.01$ ; Table 1).

263 **Table 1.** Number ( $n$ ) of individuals and surface area ( $\text{mm}^2$ ) measured for each species with minimal, mean  $\pm$  SD  
264 and maximal values.

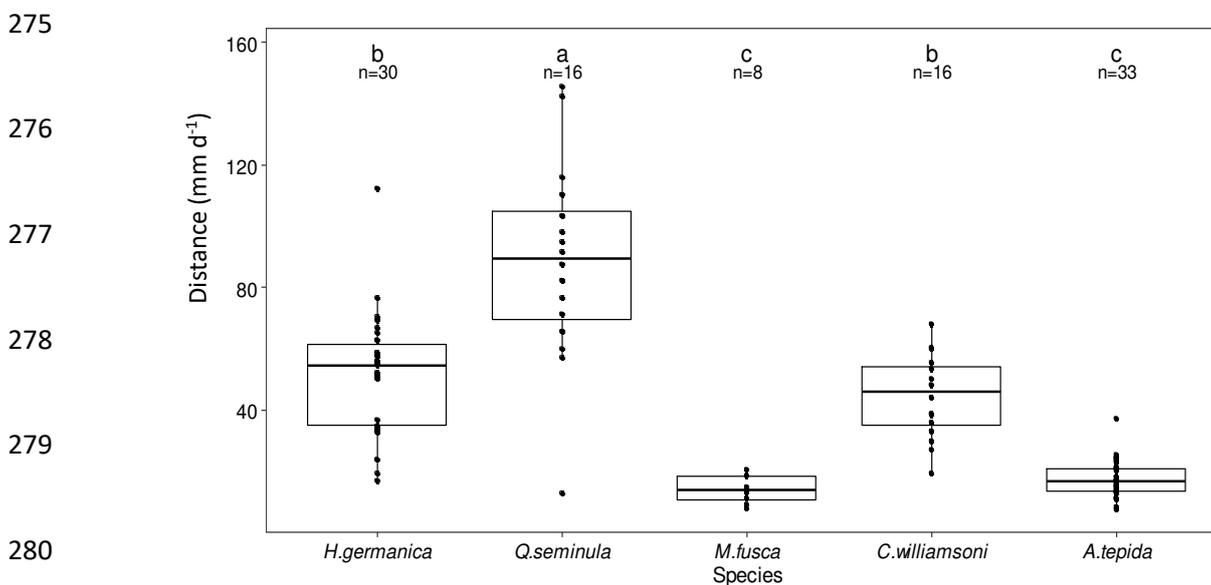
Species	n	Surface ( $\text{mm}^2$ )		
		Min	Mean $\pm$ SD	Max
<i>Haynesina germanica</i>	30	0.06	$0.12 \pm 0.02$	0.17
<i>Quinqueloculina seminulum</i>	16	0.08	$0.13 \pm 0.04$	0.22
<i>Miliammina fusca</i>	8	0.11	$0.14 \pm 0.03$	0.20
<i>Criboelphidium williamsoni</i>	16	0.13	$0.18 \pm 0.03$	0.24
<i>Ammonia tepida</i>	33	0.13	$0.21 \pm 0.03$	0.3

265

266

## 267 3.2. Travelled distance

268 Among the five studied species, *Q. seminulum* display the highest mean travelled distance,  
 269 i.e. 130 mm d<sup>-1</sup>. In contrast, *M. fusca* and *A. tepida* are the species that travelled the lowest  
 270 distances i.e. between 12 and 32 mm d<sup>-1</sup> and 17 and 37 mm d<sup>-1</sup> respectively (Fig. 5). With  
 271 intermediate value, the mean travelled distance of *H. germanica* and *C. williamsoni* ranged  
 272 between 16 and 112 mm d<sup>-1</sup> and 19 and 67 mm d<sup>-1</sup> (Fig. 5). Hence, three groups of homogeneous  
 273 travelled distance were identified:  $D_{M.fusca} = D_{A.tepida} < D_{C.williamsoni} = D_{H.germanica} < D_{Q.seminulum}$   
 274 (Fig. 5; Dunn test,  $p < 0.01$ ).



281 **Fig. 5.** Value of the travelled distance (mm) for each experiment performed on the five tested species.  
 282 The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the  
 283 interquartile range; Individual values are represented by black dots. n denotes the number of individuals  
 284 used in the experiments. Letters on top ('a', 'b' and 'c') identify significantly different groups (Dunn  
 285 test,  $p < 0.05$ ) between species.

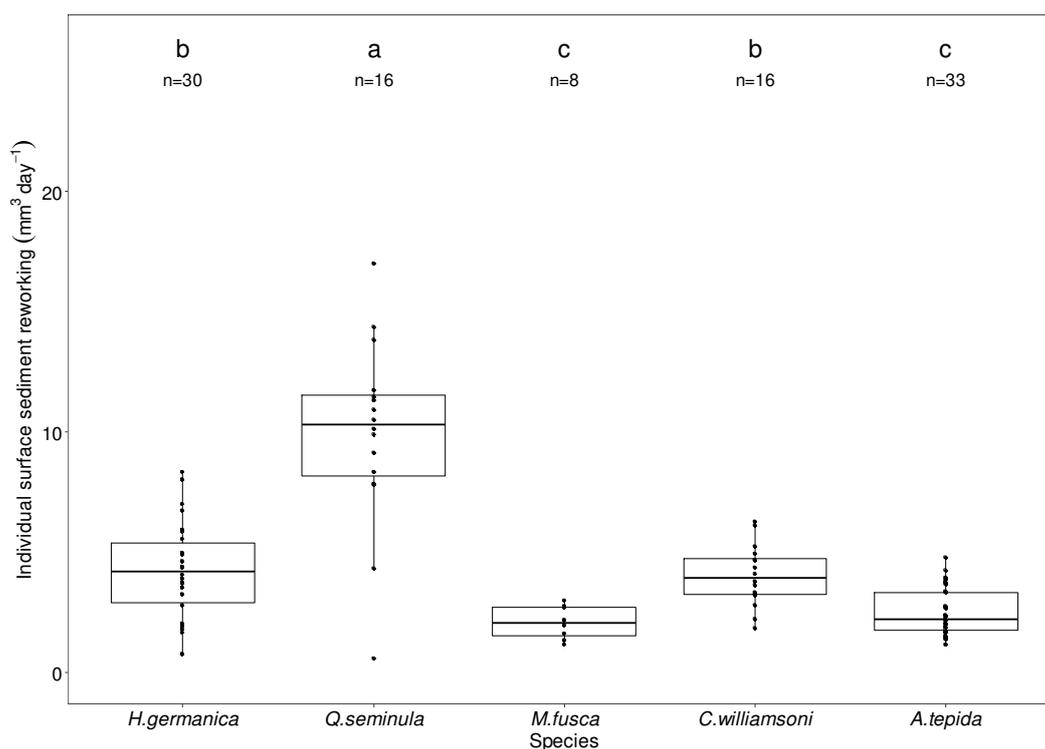
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287 Our results showed a strong intra specific variability in the distance travelled by individuals  
 288 of *H. germanica*, *C. williamsoni* and *Q. seminulum*. For instance, the travelled distance between  
 289 individuals of *Q. seminulum* may range from 12 to 142 mm d<sup>-1</sup> (Fig. 5).

290

## 291 3.3. Surface sediment reworking rate

292 Individual surface sediment reworking rates ranged from  $1.15 \text{ mm}^3 \text{ day}^{-1}$  for *M. fusca* up to  
 293  $21.6 \text{ mm}^3 \text{ day}^{-1}$  for *Q. seminulum*, and significantly differed between species (KW test,  $p < 0.05$ ;  
 294 Fig. 6). *Quinqueloculina seminulum* showed higher  $SSRR_i$  than the other species (Dunn test,  $p$   
 295  $< 0.01$ ).



296 **Fig. 6.** Value of the  $SSRR_i$  for each experiment performed on the five tested species. The box represents  
 297 the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range;  
 298 Individual values are represented by black dots. n denotes the number of individuals used in the  
 299 experiments. Letters on top ('a', 'b' and 'c') identify significantly different groups (Dunn test,  $p < 0.05$ )  
 300 between species.  
 301

302  
 303 Three groups of  $SSRR_i$  were subsequently identified as  $SSRR_{i-A. tepida} = SSRR_{i-M. fusca} < SSRR_{i-}$   
 304  $C. williamsoni} = SSRR_{i-H. germanica} < SSRR_{i-Q. seminulum}$  (Fig. 6; Dunn test,  $p < 0.01$ ). As a consequence,  
 305 the most and the least efficient surface sediment reworkers are *Q. seminulum* and *M. fusca*  
 306 respectively. As previously evidenced for the travelled distance,  $SSRR_i$  values showed a strong  
 307 intraspecific variability in *H. germanica*, *Q. seminulum* and *C. williamsoni* species. Noticeably,

308 the difference in the  $SSRR_i$  between individual of the aforementioned species may be one order  
309 of magnitude while it is restricted between 1 and 3 mm<sup>3</sup> day<sup>-1</sup> for *M. fusca* (Fig. 6)

310

#### 311 4. Discussion

##### 312 4.1. A methodological note on individual surface sediment reworking calculation

313 In the present work,  $SSRR_i$  was estimated using the surface area of the test, whereas Bouchet  
314 and Seuront (2020) considered the test length in their calculation. Hence, these authors showed  
315  $SSRR_i$  values expressed as a surface unit i.e. in cm<sup>2</sup> ind<sup>-1</sup> d<sup>-1</sup>. However, the studied foraminifera  
316 (*A. tepida* and *Q. seminulum*) moved in and on the sediment, hence were *ipso facto* displacing  
317 a volume of particles rather than a surface. The use of the surface area of the test instead of the  
318 maximum test length therefore appears as more ecologically relevant allowing to express  $SSRR_i$   
319 as volume of sediment particle displaced. Furthermore, the prolate ellipsoid-shaped test of *Q.*  
320 *seminulum* and *M. fusca* is asymmetrical with the length being much larger than the width.  
321 Similarly, within rotaliid species i.e. *A. tepida*, *H. germanica* and *C. williamsoni* test length  
322 typically is about 1.2 times larger than test width. As a consequence, the approach followed by  
323 Bouchet and Seuront (2020) most likely leads to a biased estimation of the  $SSRR_i$  values by  
324 considering only the length as representative of the test size. In addition, in the present study  
325 we consider the temporal evolution in the vertical position of each individual in our  $SSRR_i$   
326 calculation. This method allows a more rigorous estimation of the surface sediment reworking  
327 intensity of each species as it consider the real portion of the surface area of the test that is  
328 actually involve in the reworking of surface particles during individual displacement (Fig. 4).

329 Taken together, these suggest that considering both the surface area of the test as a proxy  
330 of foraminiferal test size and the position of each individual in the sediment may allow a reliable  
331 assessment of species-specific surface sediment reworking rate.

332

333 4.2.  $SSRR_i$  is not size-dependent but trait-dependent through interspecific differences in  
334 motion behaviour

335 Our results showed that the largest foraminiferal species (*A. tepida*) did not rework the  
336 sediment more than the smallest species such as *H. germanica* and *Q. seminulum*. In contrast,  
337 *Q. seminulum* can even rework up to 3 times more sediment than *A. tepida* (Fig. 6) despite a  
338 test surface area nearly twice smaller (Table 1). This result indicates that the species-specific  
339  $SSRR_i$  could be inversely size-dependent as evidenced in the five species. Specifically, the  
340 higher the surface area of the test, the lower the species-specific  $SSRR_i$ . Here, the travelled  
341 distance is likely the parameter that drives the intensity in the surface sediment reworking  
342 performed by the five foraminiferal species. These results are consistent with previous works  
343 on macro-invertebrate species, where large bivalves may have lowest sediment reworking rates  
344 than small polychaetes since the latter have more intensive displacements, i.e. different motion-  
345 behaviour traits (Mermillod-Blondin et al. 2004; Michaud et al. 2005; Gilbert et al. 2007).

346 Furthermore, differences in  $SSRR_i$  between foraminiferal species have been previously  
347 hypothesised following the assumption that species with distinct bioturbating modes would  
348 exhibit different  $SSRR_i$ ; see Deldicq et al. (2020) for further details. Noticeably, the five species  
349 considered in the present study were recently classified in the following bioturbating groups:  
350 *Q. seminulum* and *M. fusca* as gallery-biodiffusors, *H. germanica* and *A. tepida* as surficial-  
351 biodiffusors and *C. williamsoni* as an epifaunal-biodiffusor (Deldicq et al. 2020). This  
352 classification implies that they would contribute differently to benthic-ecosystem functioning  
353 (Deldicq et al. 2020). For instance, *C. williamsoni* that prefers surface sediment was classified  
354 as epifaunal-biodiffusor meaning that the species would rework particles at the surface. In  
355 contrast, *H. germanica* and *A. tepida* move in and on the sediment hence they may rework  
356 particles more deeply than *C. williamsoni* (Deldicq et al. 2020). Finally, *Q. seminulum* and *M.*

357 *fusca* prefer to be burrowed in the sediment that may likely induce the reworking of sediment  
358 particles below the interface. As these species do not occupy the same microhabitat, they may  
359 consequently exhibit difference in their  $SSRR_i$ . Therefore, to consider the functional  
360 classification of the five studied species in the estimation of their  $SSRR_i$ , we include the position  
361 of their test in the sediment.

362 Based on this study findings, it occurs that, although *C. williamsoni* is larger than *H.*  
363 *germanica* and that both species displayed similar travelled distance, the latest rework the  
364 surface-sediment more efficiently. This is consistent with previous studies which showed that  
365 gallery-biodiffusor (i.e. burrow-dwelling organism) macro-invertebrates are more efficient  
366 bioturbators than epifaunal-biodiffusors as they displaced a larger amount of sediment particles  
367 through their burrowing activity (Mermillod-Blondin et al. 2004; Michaud et al. 2005).  
368 However, in the present study, the most and the least efficient species in reworking surface  
369 sediment (i.e. *Q. seminulum* and *M. fusca*) both belong to the gallery-biodiffusor group. As a  
370 consequence, the potential link between the intensity of surface sediment reworking and the  
371 functional group of a species is not straightforward. We may suggest that the motion behaviour  
372 of foraminifera i.e. travelled distance and vertical position (e.g. Deldicq et al. 2020) both matter  
373 in their ability to rework surface-sediment. Noticeably, the  $SSRR_i$  intensity and sediment  
374 particles spatial displacement may be a function of these two behavioural traits.

375

#### 376 4.3. Inter-individual variability matters in the contribution of benthic foraminifera to $SSRR_i$

377 Beyond the interspecific variability discussed above (Section 4.2),  $SSRR_i$  of the five studied  
378 species were consistently characterised by a high inter-individual variability (i.e. up to one order  
379 of magnitude for *Q. seminulum*; see Fig. 5,6). Note that the differences identified here cannot  
380 be related to environmental factors or size, since our experiments were performed on similar-  
381 sized individuals under controlled conditions in the absence of any cues. The above mentioned

382 inter-individual variability is then more likely to be an intrinsic property of the species  
383 considered here.

384 Behavioural plasticity has previously been reported in foraminifera (Hallock and Hansen  
385 1979; Seuront and Bouchet 2015; Prazeres et al. 2017), but also in pelagic copepods (e.g.  
386 Seuront et al. 2004b) and intertidal gastropods (e.g. Chapperon and Seuront 2011a) with  
387 individuals from the same species showing both a large repertoire of behavioural traits (e.g.  
388 feeding activity, trajectory complexity, intensity of displacement) and a large variability in the  
389 values of each trait. Noticeably, in our experiments, conspecific individuals of *Q. seminulum*,  
390 *C. williamsoni* and *H. germanica* displayed a high variability in their travelled distance but also  
391 in their motion behaviour, e.g. tortuosity, vertical position (see Deldicq et al. 2020 for further  
392 details). Having a wide diversity in the behavioural repertoire between conspecific individuals  
393 may be a selective advantage for species to face long-term environmental fluctuations as  
394 previously suggested for intertidal gastropods (Chapperon and Seuront 2011a). Such  
395 evolutionary adaptation to increase survival in a changing environment can, in turn, also affect  
396 individual contribution to ecosystem processes (Maltagliati et al. 2006; Bolnick et al. 2011).  
397 Noticeably, the species characterized by the highest inter-individual variability (i.e. *Q.*  
398 *seminulum*, *C. williamsoni* and *H. germanica*) are also the species that contribute most to  $SSRR_i$   
399 (see Fig. 6). This last observation is particularly relevant as it may inform on the species-  
400 specific phenotypic plasticity and therefore the sustainability of the functional role of these  
401 species that live in a highly variable environment such as intertidal sedimentary ecosystems.

402 Taken together our observations may suggest that individual trait variations matter in the  
403  $SSRR_i$  of the five studied foraminiferal species. This is consistent with previous studies showing  
404 that inter-individual variations can have large ecological consequences on ecosystem processes  
405 such as primary production, nutrient cycling than interspecific variability (Crutsinger 2006;  
406 Lecerf and Chauvet 2008; Bolnick et al. 2011).

## 407 **Conclusion**

408 Our study revealed that bioturbation by benthic foraminifera is the result of the complex  
409 interplay between species-specific features such as motion-behaviour, phenotypic plasticity and  
410 functional classification i.e. bioturbation mode. Despite their relatively small size, these five  
411 benthic foraminiferal species showed a non-negligible sediment mixing rates at the sediment  
412 water-interface through their active displacements. Additional studies are nevertheless needed  
413 to further estimate the role of intertidal foraminifera to bioturbation processes because the  
414 species-specific traits which control their activity in and on the sediment may depend on both  
415 allogenic (e.g. temperature, food availability) and autogenic (e.g. size, age) factors. Noticeably,  
416 our experimental set-up do not provide all the food sources such as live prey that some species  
417 such as *A. tepida* may feed (e.g. Dupuy et al. 2010; Jauffrais et al. 2016b) as we used thawed  
418 sediment to eliminate macro- and meiobenthic bioturbation effects. Foraging activity is  
419 however intrinsically linked to organism displacement (e.g. Pyke 1984; Bell 1991; Seuront  
420 2010b, 2015a). It therefore stresses the need to further investigate the effect of food  
421 concentration and diversity on the  $SSRR_i$  of intertidal foraminifera. In addition, the effect of  
422 progressive oxygen depletion on foraminiferal activity hence sediment reworking intensity  
423 should be further investigated although we did not observed temporal changes in the activity of  
424 our five species during our experiments.

425

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436

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## 445 **Competing Interests**

446 The authors declare that no competing interests exist.

## 447 **Data availability statement**

448 All data generated or analysed during this study are included in this published article.

## 449 **Authors' contribution**

450 N.D. and V.M.P.B. conceived the idea of this study and V.M.P.B. obtained financial support.  
451 N.D. and V.M.P.B. provided significant input on experimental design. N.D. performed the  
452 behavioural experiments and analysed the images. N.D. analysed the data and performed the  
453 statistical analyses. N.D., L.S. and V.M.P.B. contributed to the interpretation of the data and

454 the discussion of the results presented in the manuscript. N.D. wrote the draft manuscript. N.D.,  
455 L.S. and V.M.P.B. revised the article critically for intellectual content and gave final approval  
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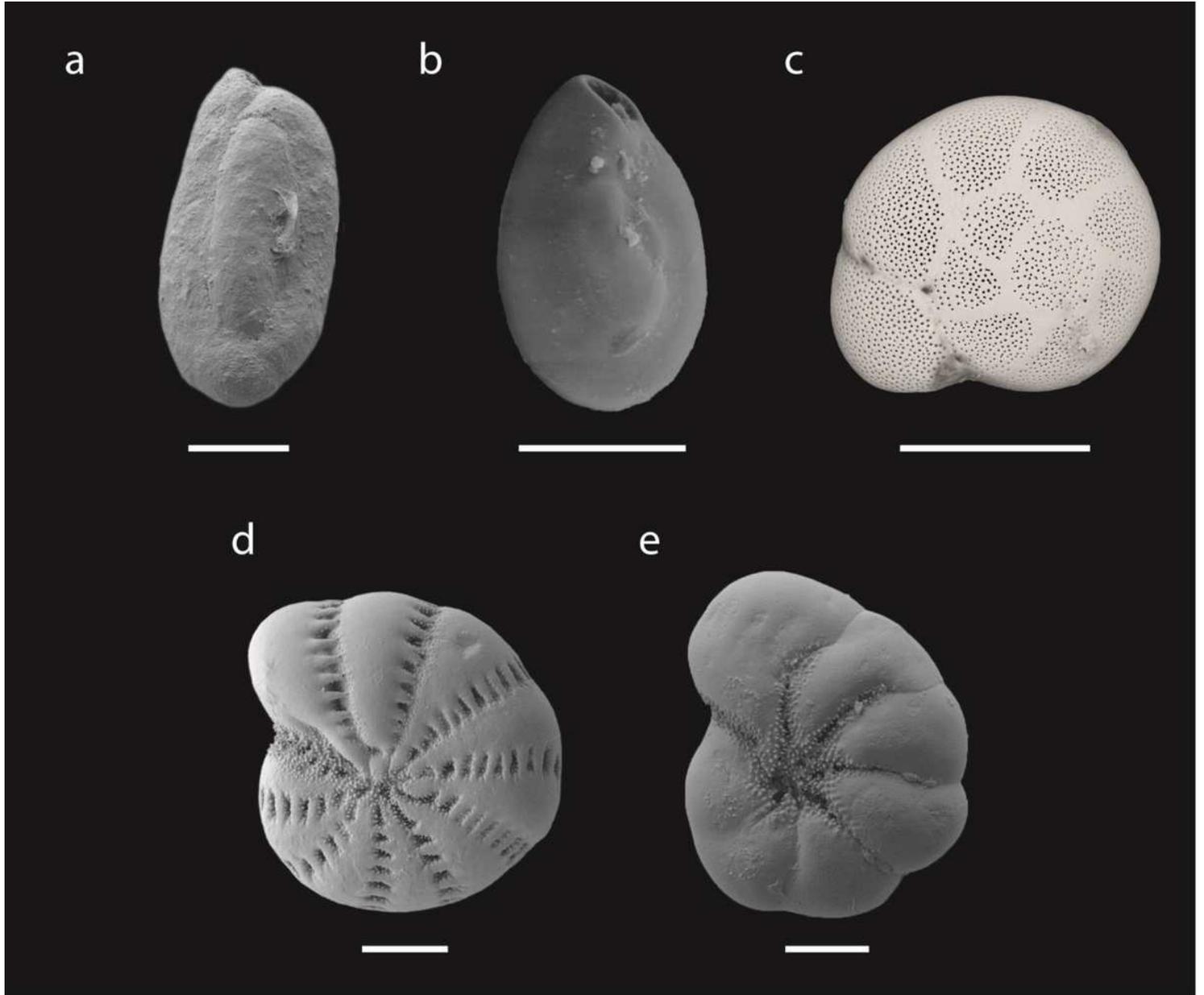
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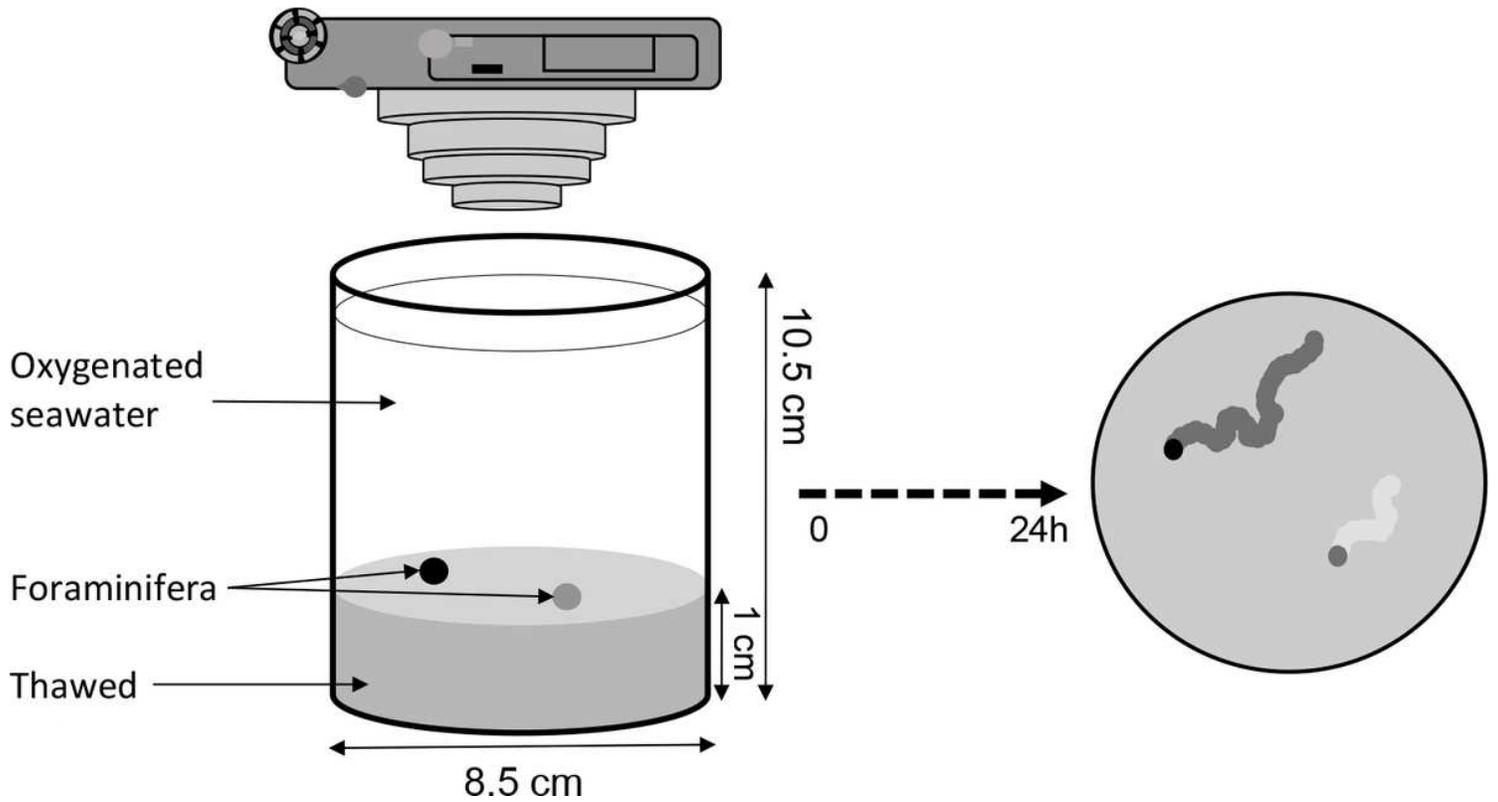
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- 644

## Figures



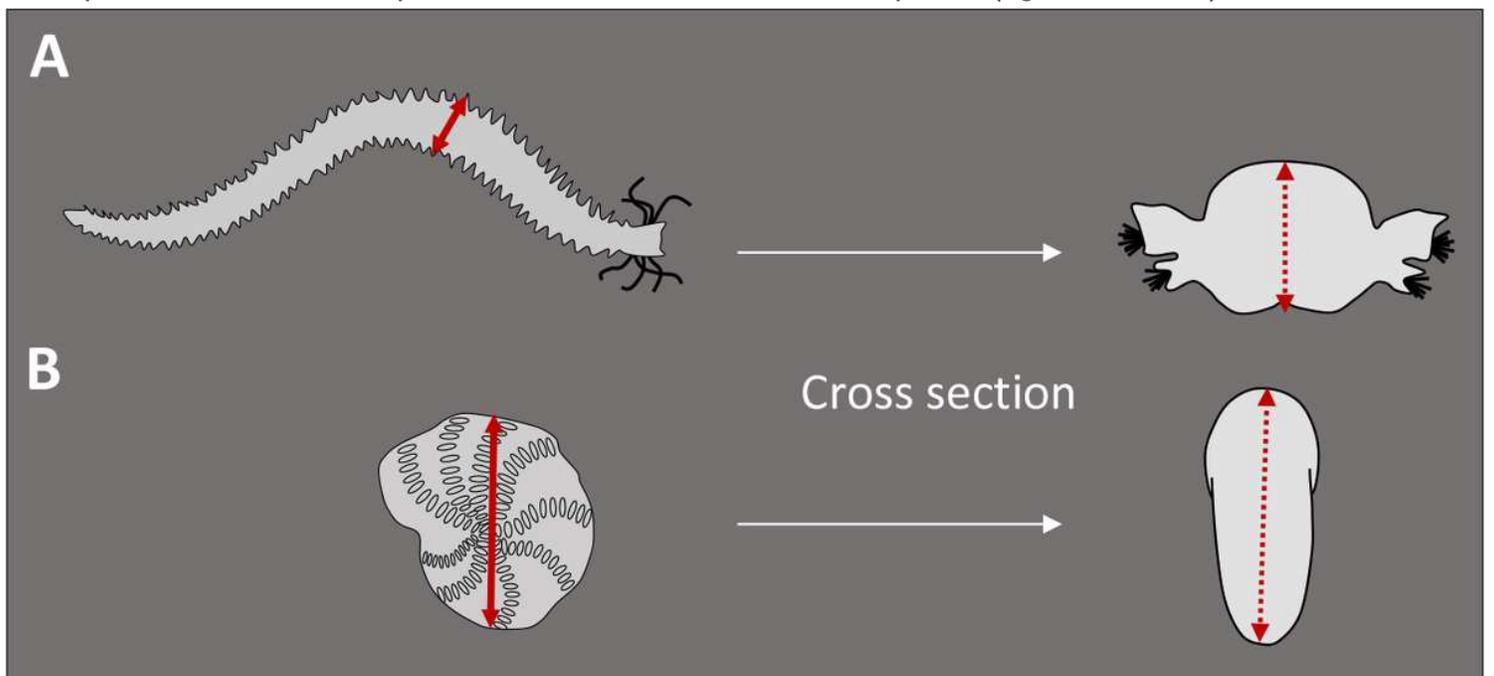
**Figure 1**

SEM images of the dorsal side of the five studied foraminifera (a) *Miliammina fusca*, (b) *Quinqueloculina seminulum*, (c) *Ammonia tepida*, (d) *Criboelphidium williamsoni* and (e) *Haynesina germanica*. Scale bar = 100 μm.



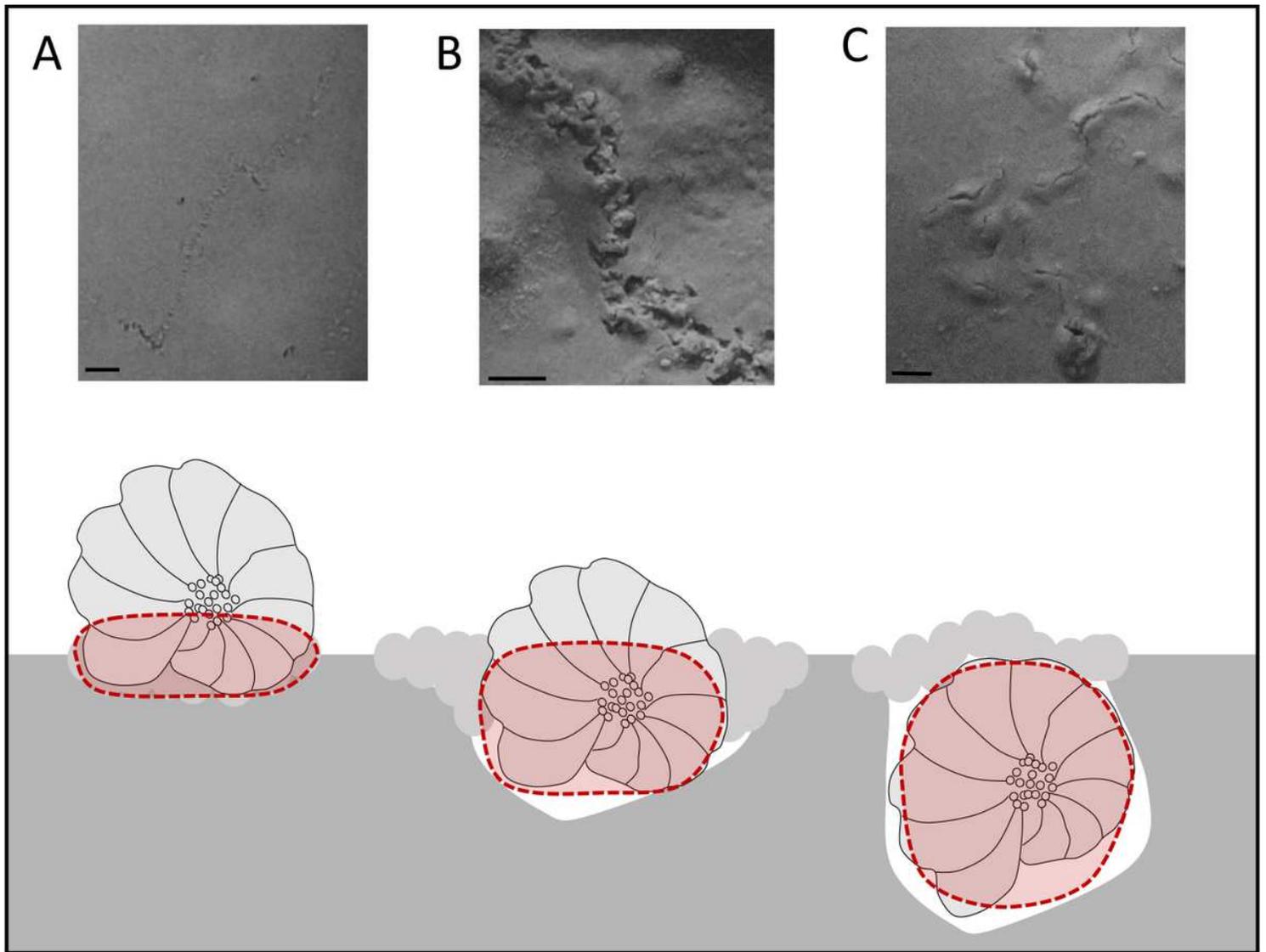
**Figure 2**

Experimental set-up for time-lapse assessment of foraminiferal motion-traits (left-hand side) and examples of the movement paths of 2 foraminifera over a 24-h period (right-hand side)



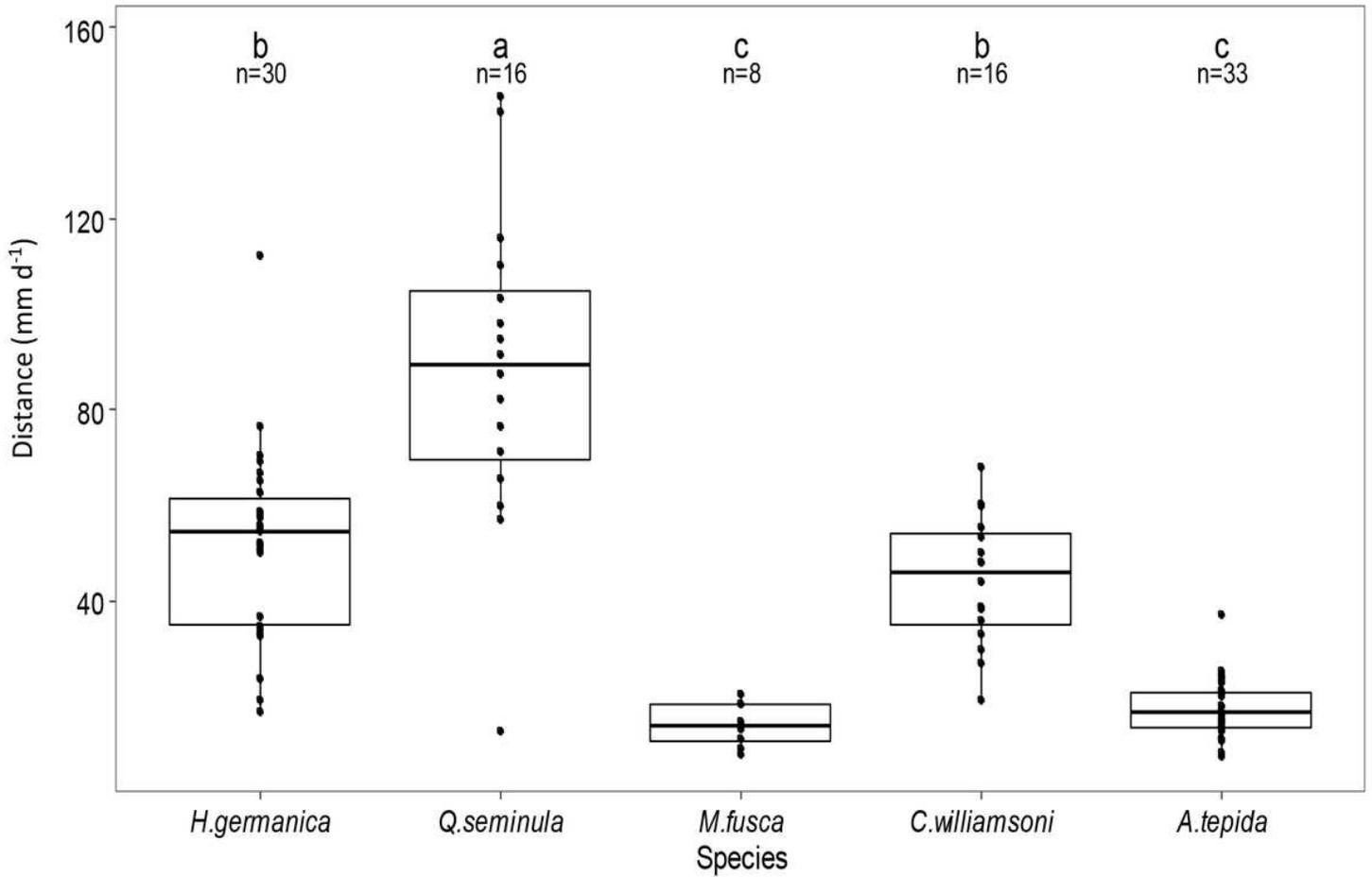
**Figure 3**

Illustration of the cross section of (A) polychaete and (B) benthic foraminifera that may be used for sediment reworking calculation.



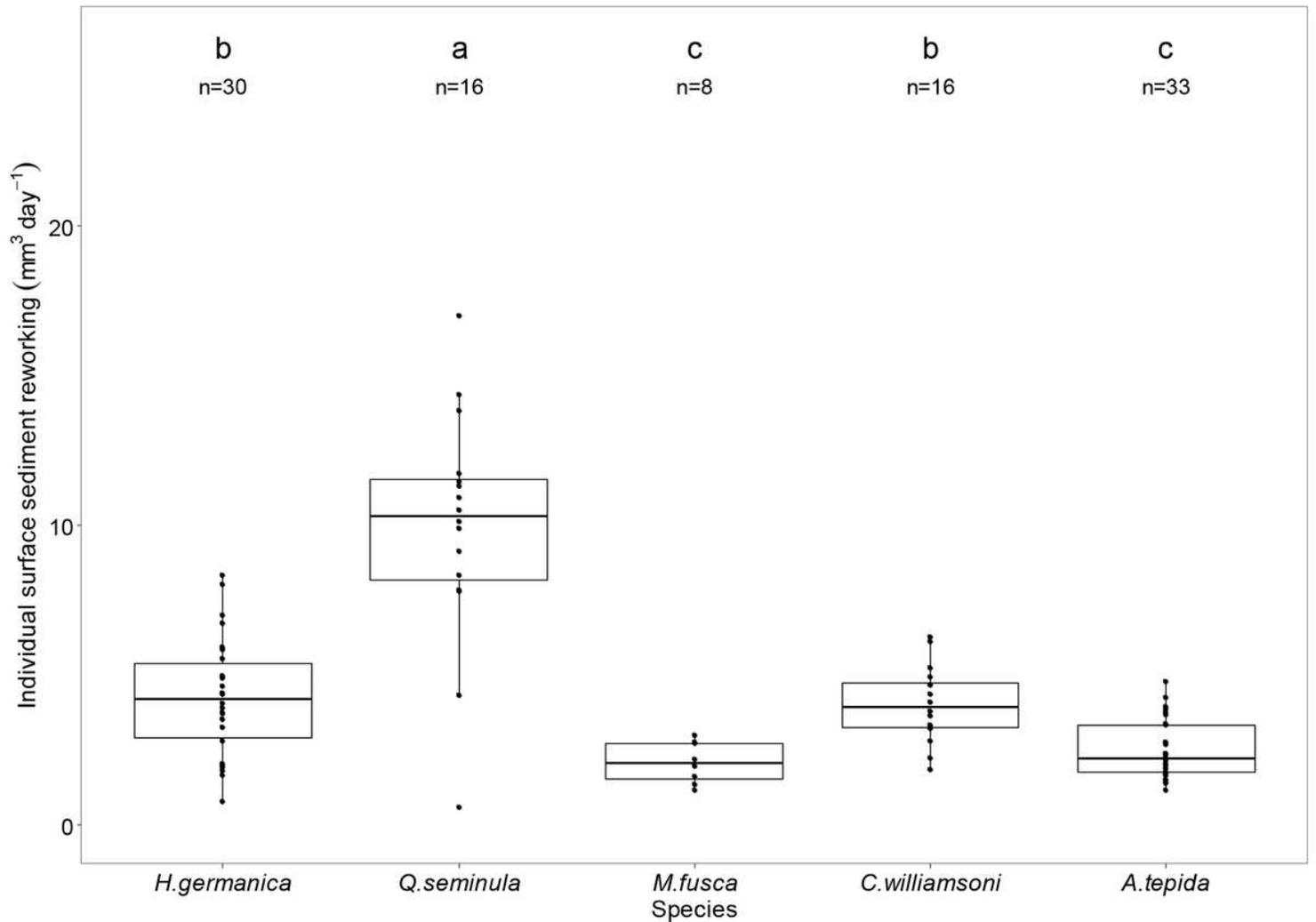
**Figure 4**

Discrimination between the vertical positions taken by benthic foraminifera in the sediment to estimate SSRRit. Images were taken from experiments containing living individuals of *H. germanica*.



**Figure 5**

Value of the travelled distance (mm) for each experiment performed on the five tested species. The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range; Individual values are represented by black dots. n denotes the number of individuals used in the experiments. Letters on top ('a', 'b' and 'c') identify significantly different groups (Dunn test,  $p < 0.05$ ) between species.



**Figure 6**

Value of the SSRRi for each experiment performed on the five tested species. The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range; Individual values are represented by black dots. n denotes the number of individuals used in the experiments. Letters on top ('a', 'b' and 'c') identify significantly different groups (Dunn test, p < 0.05) between species.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Table1.pdf](#)