

Marine Biodiversity

Basal monothalamous and pseudochambered benthic foraminifera associated with planktonic foraminiferal shells and mineral grains from the Porcupine Abyssal Plain, NE Atlantic

--Manuscript Draft--

Manuscript Number:	MARB-D-14-00083R1
Full Title:	Basal monothalamous and pseudochambered benthic foraminifera associated with planktonic foraminiferal shells and mineral grains from the Porcupine Abyssal Plain, NE Atlantic
Article Type:	S.I.: Meioscool
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Abstract:	<p>We present a survey of 'live' (stained) and dead monothalamous (single-chambered, mainly spherical) and pseudochambered (chain-like) foraminifera associated with planktonic foraminiferal shells and mineral grains, based on two samples from one abyssal plain site (F2, 4,880 m water depth) and one abyssal hill site (H4, 4,330 m water depth) on the Porcupine Abyssal Plain (PAP), northeast Atlantic. Our study is the first to focus on this poorly known component of abyssal foraminiferal faunas and highlight their abundances and diversity at the PAP. In both samples these monothalamids and pseudochambered forms represented 27-35 % and 18-23 %, respectively, of the entire 'live' and dead foraminiferal assemblage (>150 µm, 0-1 cm sediment layer). Among 1078 stained and dead specimens we recognize a total of 18 distinct morphotypes on the basis of test characteristics. Another 144 specimens could not be assigned to any morphotype and are regarded as indeterminate. Most of the monothalamids are small (<150 µm), although some incorporate planktonic foraminiferal shells to create larger structures. In absolute terms, stained and dead individuals of these morphotypes were more abundant at the abyssal hill site although data from additional samples are needed to confirm if this is representative of differences between abyssal hills and the surrounding abyssal plain at the PAP. Agglutinated spheres and domes similar to some of our abyssal forms have been reported from shelf and slope settings, but they are generally much larger. Small agglutinated spheres are very common in the abyssal Pacific, at depths close to or below the carbonate compensation depth (CCD). However, they are composed largely of siliceous particles, including mineral grains, radiolarians and diatom fragments. In contrast, carbonate oozes at the PAP, situated above the CCD, are rich in coccoliths and planktonic foraminiferal shells, which are used in the construction of agglutinated spheres and domes. Our results underline the important contribution made by largely underestimated foraminiferal taxa to abyssal communities.</p>
Response to Reviewers:	'see attachment'

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1 **Basal monothalamous and pseudochambered benthic**
2 **foraminifera associated with planktonic foraminiferal shells**
3 **and mineral grains from the Porcupine Abyssal Plain, NE**
4 **Atlantic**

6 **Paris V. Stefanoudis · Andrew J. Gooday**

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1 32 **Abstract** We present a survey of ‘live’ (stained) and dead monothalamous (single-
2 33 chambered, mainly spherical) and pseudochambered (chain-like) foraminifera
3 34 associated with planktonic foraminiferal shells and mineral grains, based on two
4 35 samples from one abyssal plain site (F2, 4,880 m water depth) and one abyssal hill site
5 36 (H4, 4,330 m water depth) on the Porcupine Abyssal Plain (PAP), northeast Atlantic.
6 37 Our study is the first to focus on this poorly known component of abyssal foraminiferal
7 38 faunas and highlight their abundances and diversity at the PAP. In both samples these
8 39 monothalamids and pseudochambered forms represented 27–35 % and 18–23 %,
9 40 respectively, of the entire ‘live’ and dead foraminiferal assemblage (>150 µm, 0–1 cm
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11 42 distinct morphotypes on the basis of test characteristics. Another 144 specimens could
12 43 not be assigned to any morphotype and are regarded as indeterminate. Most of the
13 44 monothalamids are small (<150 µm), although some incorporate planktonic
14 45 foraminiferal shells to create larger structures. In absolute terms, stained and dead
15 46 individuals of these morphotypes were more abundant at the abyssal hill site although
16 47 data from additional samples are needed to confirm if this is representative of
17 48 differences between abyssal hills and the surrounding abyssal plain at the PAP.
18 49 Agglutinated spheres and domes similar to some of our abyssal forms have been
19 50 reported from shelf and slope settings, but they are generally much larger. Small
20 51 agglutinated spheres are very common in the abyssal Pacific, at depths close to or below
21 52 the carbonate compensation depth (CCD). However, they are composed largely of
22 53 siliceous particles, including mineral grains, radiolarians and diatom fragments. In
23 54 contrast, carbonate oozes at the PAP, situated above the CCD, are rich in coccoliths and
24 55 planktonic foraminiferal shells, which are used in the construction of agglutinated
25 56 spheres and domes. Our results underline the important contribution made by largely
26 57 underestimated foraminiferal taxa to abyssal communities.

27 58

28 59 **Keywords** Single-chambered monothalamids · Pseudochambered foraminifera ·
29 60 Diversity · Deep-sea benthos · Abyssal faunas

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1 **64 Introduction**

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3 **65**

4 **66** Benthic foraminifera are one the of most abundant and species-rich groups in the deep
5 **67** sea, often accounting >50 % of the meiofauna (Snider et al. 1984; Gooday 2014) and in
6 **68** some areas a large proportion of the macrofauna (Tendal and Hessler 1977). Diversity
7 **69** and distributional patterns of hard-shelled calcareous and robustly agglutinated forms
8 **70** (mainly multichambered) have been widely documented (Murray 1991; Gooday and
9 **71** Jorissen 2012; Murray 2013), but relatively little is known about organic-walled and
10 **72** delicately agglutinated, predominantly monothalamous (single-chambered) species,
11 **73** hereafter termed monothalamids (Pawłowski et al. 2013). Due to their fragile nature
12 **74** these taxa have a poor fossil record (Tappan and Loeblich 1988; Mackensen et al. 1990)
13 **75** resulting in an incomplete picture of past foraminiferal communities. In modern oceans
14 **76** these delicate species can constitute a dominant element of deep-sea foraminiferal
15 **77** assemblages (Tendal and Hessler 1977; Bernstein et al. 1978; Snider et al. 1984;
16 **78** Nozawa et al. 2006), particularly at abyssal plains below the carbonate compensation
17 **79** depth (CCD) (Schröder et al. 1988).

18 **80** Monothalamids encompass a wide variety of organic-walled and agglutinated
19 **81** taxa with spherical, flask-shaped, tubular or more complex test morphologies and in
20 **82** some cases a soft, flexible test wall. Their internal structure is relatively simple and
21 **83** deep-sea species often contain masses of waste pellets, termed stercomata. They
22 **84** represent the basal radiation of foraminifera that gave rise to morphologically diverse
23 **85** groups of multichambered calcareous and agglutinated forms (Pawłowski et al. 2003;
24 **86** Pawłowski et al. 2013). Monothalamids are generally poorly known and usually
25 **87** overlooked in faunal studies of the deep-sea benthos. Many species are undescribed and
26 **88** their often simple morphologies, which lack prominent features, make their
27 **89** identification problematic. Nevertheless, monothalamids are a highly diverse group,
28 **90** often constituting >30 % of the total foraminiferal species pool and are thought to
29 **91** represent a significant undocumented source of biodiversity on the ocean floor (Gooday
30 **92** et al. 2004; Enge et al. 2012). Recently developed molecular techniques, including
31 **93** ultra-deep sequencing of foraminiferal microbarcodes in environmental DNA samples,
32 **94** have emphasized their dominance (>80 %) in deep-sea foraminiferal assemblages
33 **95** (Lecroq et al. 2011).

1 96 During the analysis of foraminiferal samples from the Porcupine Abyssal Plain
2 97 (PAP) in the northeast Atlantic (>4,300 m water depth) we encountered monothalamids
3 98 and chain-like agglutinated forms (considered pseudochambered sensu Mikhalevich,
4 99 2005) that were associated with planktonic foraminiferal shells and mineral grains. The
5 100 vast majority comprised tiny agglutinated spheres and domes (50–150 μm) that formed
6 101 larger structures (often >300 μm) by incorporating planktonic shells and mineral grains
7 102 as part of their test or by using these as a substrate. Small trochamminaceans (<100 μm)
8 103 from the same area are also commonly found on the shells of planktonic foraminifera
9 104 (Gooday et al. 2010).

10 105 Benthic foraminifera attached to hard substrates have been known to science for
11 106 well over a century (Loeblich and Tappan 1987). Scientific expeditions in the Southern
12 107 Ocean and the North Atlantic Ocean reported organic-walled and agglutinated
13 108 foraminiferal species, some of them monothalamous, that are sessile on a variety of
14 109 substrates such as stones, molluscan shells, sponge spicules and benthic foraminiferal
15 110 shells (Heron-Allen and Earland 1913; Heron-Allen and Earland 1932; Earland 1933;
16 111 Earland 1934; Earland 1936). However, most of these studies described attached forms
17 112 from shelf and the slope settings (sublittoral to upper bathyal) and none of them concern
18 113 tiny agglutinated foraminifera from the abyssal deep sea.

19 114 The purpose of this paper is to: (1) briefly characterize these primitive
20 115 monothalamids and chain-like taxa from the PAP that live attached to, or are lodged
21 116 between, planktonic shells or mineral grains; (2) compare them with similar forms
22 117 found in other ocean basins such as the Pacific; (3) assess their contribution to the
23 118 abundance and diversity of the entire foraminiferal assemblages at the PAP.

24 119

25 120 **Materials and Methods**

26 121

27 122 Sample collection and laboratory processing

28 123

29 124 Two core samples (25.5 cm^2 surface area) were collected during R.S.S. *James Cook*
30 125 Cruise 062 (JC062) (July-August 2011) at an abyssal plain site (F2; station JC062-77,
31 126 4,818 m water depth) and a somewhat shallower, abyssal hill site (H4; station JC062-
32 127 126, 4,330 m water depth) within the area of the PAP (Fig. 1; Table 1). Onboard the

1 128 ship, the cores were sliced into layers down to 10-cm depth and each slice fixed in 10 %
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3 129 buffered formalin. The present work, which is part of a larger study of foraminifera
4
5 130 from the PAP, is based on the 0–1 cm sediment layer.

6 131 In the laboratory, the 0–0.5 cm and 0.5–1.0 cm slices of cores from the F2 and
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8 132 H4 sites, were gently washed through two sieves (mesh sizes: 300 μm and 150 μm)
9
10 133 using filtered tap water. Residues $>300 \mu\text{m}$ and 150–300 μm were stained with Rose
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12 134 Bengal (1 g dissolved in 1 L of tap water) overnight and sorted for all ‘live’ (stained)
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14 135 and dead foraminifera in water in a Petrie dish under a binocular microscope. In order to
15
16 136 ensure that the stained material was foraminiferal protoplasm, specimens were
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18 137 transferred to glass slides with glycerine and examined under a high power compound
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20 138 microscope. Delicate taxa were either stored on glass cavity slides in glycerol or in 2-ml
21
22 139 Nalgene cryovials in 10 % buffered formalin.

23 140 The specimens considered in the present paper were informally assigned to
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25 141 morphotypes (morphologically similar specimens) on the basis of test morphology and
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27 142 wall structure.

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30 144 Light and scanning electron microscopy

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34 146 Specimens placed in water in a glass cavity slide were photographed using a NIKON
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36 147 Coolpix 4500 camera mounted on an Olympus SZX10 compound microscope. Selected
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38 148 specimens were dried onto aluminium scanning electron microscopy (SEM) stubs, gold
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40 149 sputter coated and subsequently examined by SEM using a LEO 1450VP (variable
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42 150 pressure) scanning electron microscope.

43 151

44 152 **Results**

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48 154 Entire benthic foraminiferal assemblages

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52 156 Densities for the entire ‘live’ assemblage (i.e. all foraminiferal taxa, multichambered as
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54 157 well as monothalamids, in the 150–300 and $>300 \mu\text{m}$ combined) were 49 individuals.10
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56 158 cm^{-2} at the abyssal plain site (F2) and 84 indiv.10 cm^{-2} at the abyssal hill site (H4). The
57
58 159 corresponding values for the entire dead assemblages were 611 indiv.10 cm^{-2} (F2) and

1 160 1206 indiv.10 cm⁻² (H4). For the monothalamids and pseudochambered forms
2
3 161 considered here, 42 ‘live’ individuals (16.5 indiv.10 cm⁻²) were counted at the abyssal
4
5 162 plain site (F2) and 59 ‘live’ individuals (23.1 indiv.10 cm⁻²) at the abyssal hill site (H4).
6
7 163 The corresponding values for the dead assemblages were 356 individuals (139.3
8
9 164 indiv.10 cm⁻²) (F2) and 567 individuals (222.2 indiv.10 cm⁻²) (H4). The majority of the
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11 165 specimens (‘live’ and dead) in both sites were concentrated in the 0–0.5 cm (Table 2).
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13 166 In both samples these two groups represented 27–35 % and 18–23 % of the ‘live’ and
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15 167 dead fauna respectively (Table 2). In the case of an additional 42 (F2) and 156 (H4)
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17 168 individuals it was impossible to determine using Rose Bengal staining if they were
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19 169 ‘live’ or dead. These ‘live’ specimens represented 10 % and 20 % of the total number of
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21 170 monothalamids and pseudochambered forms found at the abyssal plain and abyssal hill
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23 171 site respectively (Table 2).

24 172

25 173 Diversity of monothalamous and pseudochambered foraminifera

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28 175 Overall, we recognized a total of 18 distinct forms among 1078 monothalamous and
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30 176 pseudochambered foraminifera picked from the samples at the two sites (Table 3). None
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32 177 can be placed in a described species. We regard them as morphotypes although those
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34 178 with consistent, well-defined morphologies are probably distinct species. A further 144
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36 179 monothalamous specimens could not be assigned to any morphotype and were regarded
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38 180 indeterminate. They will not be considered further.

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41 182 *Monothalamids attached to or lodged between planktonic foraminiferal shells*

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45 184 The majority (11) of the 18 forms are soft spheres that are sessile on a planktonic
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47 185 foraminiferal shell or are lodged between two or more planktonic shells. These
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49 186 monothalamous foraminifera exhibit a wide morphological diversity and contain some
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51 187 of the most abundant forms (Table 3). They include the following types.

52 188 1. *Thin-walled sphere* (Figs. 2a–b; Type 1 in Table 3). A thin-walled
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54 189 agglutinated sphere (<150 µm in maximum dimension) containing stercomata usually
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56 190 confined between several (>2) planktonic shells.

1 191 2. *Sphere with long flimsy tubes* (Figs. 2c–e; Type 2 in Table 3). Easily
2 192 recognizable and abundant form with one or more long flimsy tubes extending out of
3 193 the main, approximately spherical, test. In some cases the tubes are 2 to 3 times the
4 194 length of the main test, which is between 100–150 μm in maximum dimension. The
5 195 specimens are attached to one or more planktonic shells and occasionally incorporate
6 196 small quartz grains, in which case the specimens are somewhat larger (approx. 200 μm)
7 197 (Fig. 2c).

8 198 3. *Dome with cap attached to large planktonic foraminiferal shell* (Figs. 2f–h;
9 199 Type 3 in Table 3). A small dome (approx. 100 μm) attached to a large planktonic shell
10 200 on one side and capped by a much smaller shell on the other side. This simple type is
11 201 very common in both sites (Table 3). The wall is mainly composed of coccoliths (Fig.
12 202 2h).

13 203 4. *Delicate thick-walled sphere with red-stained interior* (Figs. 3a–e; Type 4 in
14 204 Table 3). Agglutinated spherical test with red-stained protoplasm, containing sparse
15 205 stercomata. It usually forms a large structure $>300 \mu\text{m}$ due to the incorporation of
16 206 several large planktonic shells, although the sphere itself is never more than 100 μm in
17 207 diameter. The test has a thick wall and is commonly exposed on one end (i.e. not
18 208 covered by planktonic shells). A typical feature is the presence of one or more round
19 209 openings on the exposed surface through which the red-stained test interior is visible.
20 210 These openings are encircled by a slightly raised rim (Figs. 3a–c) and appear to be a
21 211 natural feature rather than the result of damage to the test wall. When dried on a SEM
22 212 stub, the sphere shrinks and the openings deform, indicating that the wall is flexible to
23 213 some degree (Figs. 3d–e).

24 214 5. *Round, slightly opaque sphere with red-stained interior* (Figs. 3f–h; Type 5 in
25 215 Table 3). Round agglutinated sphere (approx. 200 μm diameter) with a few attached
26 216 planktonic shells. The agglutinated material of the test comprises a mixture of
27 217 coccoliths and small mineral grains, in many cases plate-like, giving the sphere a
28 218 slightly reflective and opaque appearance. The interior contains stercomata but these
29 219 cannot be seen clearly through the wall.

30 220 6. *Crithionina-like sphere* (Figs. 3i–k; Type 6 in Table 3). A distinctive form
31 221 with a thick white test made of finely agglutinated particles (mainly coccoliths). These

1 222 specimens resemble the well-known agglutinated genus *Crithionina*, although they are
2 223 much smaller (<150 µm) than any described species of the genus.

3 224 7. '*Classic dome*' (Figs. 4a–d; Type 7 in Table 3). Small (approx. 100 µm
4 225 diameter), more or less spherical agglutinated sphere on top of a large planktonic shell,
5 226 with many smaller shells incorporated into the test, occasionally also mineral grains. It
6 227 contains numerous stercomata, which makes it difficult to distinguish 'live' from dead
7 228 individuals. This monothalamid is termed 'classic dome', and is by far the most
8 229 abundant morphotype at both sites.

9 230 8. *Sphere with short tube* (Figs. 4e–f; Type 8 in Table 3). Monothalamous
10 231 morphotype incorporating planktonic shells and similar in appearance to the 'classic
11 232 dome'. It differs in that the test gives rise to a short tube, rarely longer than the main test
12 233 (100–150 µm diameter). SEM images reveal coccoliths as the main agglutinated
13 234 constituent for both the test and the tube.

14 235 9. *Red sphere with stercomata, between planktonic shells* (Figs. 5a–e; Type 9 in
15 236 Table 3). An agglutinated, more or less spherical test (approx. 100 µm diameter)
16 237 attached to planktonic shells to form a much larger, irregular-shaped structure. In most
17 238 specimens some shells have to be removed in order to reveal the sphere (Figs. 5b–c). As
18 239 the sphere contains numerous large stercomata, stained individuals have a dark red color.
19 240 When dried on the SEM stub the sphere shrinks, but stercomata are still clearly visible
20 241 (Fig. 5e).

21 242 10. *Thin-walled red sphere attached to large planktonic shell* (Figs 5f–g; Type
22 243 10 in Table 3). Agglutinated sphere (100–150 µm diameter) attached to a large
23 244 planktonic shell and incorporating smaller shells in its test. This form resembles 'classic
24 245 dome', but has a thinner wall and specimens are always brightly stained, suggesting that
25 246 stercomata are absent or sparse.

26 247 11. *Soft sphere lodged between two planktonic shells* (Fig. 5h; Type 11 in Table
27 248 3). Finely agglutinated sphere with flexible wall and smooth surface, lodged between
28 249 two large planktonic shells. The test (approx. 100 µm in maximum dimension) of the
29 250 single specimen incorporates tiny planktonic shells, imparting a whitish/grey color
30 251 when viewed under the stereomicroscope. The faded grey color suggests that the
31 252 protoplasm contains stercomata.

32 253

1 254 *Monothalamids associated with mineral grains*
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5 256 12. *Monothalamids associated with mineral grains* (Figs. 6a–c; Type 12 in Table 3).
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7 257 The foraminiferans in this category are small, spherical or domed monothalamids that
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9 258 use mineral grains to construct their test. The grains comprise a variety of whitish,
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11 259 yellow and orange particles, some of them plate-like, thus often resembling the
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13 260 agglutinated genus *Psammospaera*. They are found either free-living, with maximum
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15 261 dimension up to 150 μm , or attached to planktonic foraminiferal shells and/or quartz
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17 262 grains, to form much larger structures. The spheres and domes included in this category
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19 263 are difficult to separate into distinct morphotypes.
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21 264
22 265 *Tubular monothalamids*
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25 267 The following tubular morphotypes are associated with planktonic shells.
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27 268 13. *Spherical chamber with tubes* (Figs. 6d–f; Type 13 in Table 3). This form
28
29 269 comprises a small (approx. 50 μm diameter), spherical, agglutinated chamber that gives
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31 270 rise to two narrow rigid tubes (each approximately 100 μm long and 15 μm diameter)
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33 271 from opposite ends of its test, although only the base of one tube is present in the
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35 272 figured specimen. Large coccoliths are the main agglutinated particle.
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37 273 14. *Short, soft-walled tube* (Figs. 6g–i; Type 14 in Table 14). A short (<150 μm)
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39 274 curved, soft-walled tube, open at both ends and apparently complete, sitting on top of a
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41 275 planktonic foraminiferal shell.
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44 277 *Pseudochambered (chain-like) forms*
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47 279 A number of forms have tests comprising a series of swellings or chamber-like
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49 280 segments (regarded as pseudochambers), which are sessile on, or surrounded by,
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51 281 planktonic foraminiferal shells. We recognize four forms based on the number of
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53 282 pseudochambers and planktonic shells involved, and the presence/absence of stercomata.
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55 283 15. *Double dome* (Figs. 7a–c; Type 15 in Table 3). Two more or less spherical
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57 284 domes attached to a planktonic shell, each approximately 100 μm long, linked by a
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1 285 short “bridge” and containing dark stercomata. Both domes are composed of small
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3 286 planktonic shells set in a matrix of coccoliths.

4 287 16. *Pseudochambers linked with stolons* (Figs. 7d–f; Type 16 in Table 3).

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6 288 Domed pseudochambers (approx. 100 µm diameter) associated with planktonic shells
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8 289 containing dark stercomata and linked by narrow stolons made of coccoliths. In some
9
10 290 cases the stolons are open at one end (Fig. 7f). This morphotype resembles “double
11 291 dome” but the pseudochambers are flatter and shrink when dried on a SEM stub.

12 292 17. *Chain with thick tube* (Figs. 7g–i; Type 17 in Table 3) Two pseudochambers
13 293 (approx. 50 and 100 µm long) connected by a relatively thick tube and attached to two
14 294 large planktonic shells. The entire structure (pseudochambers and tube) is about 300 µm
15 295 long. The wall is composed of coccoliths and mineral grains imparting a shiny
16 296 appearance under the stereomicroscope.

17 297 18. *Indeterminate chain of chambers* (Figs. 7j–l; Type 18 in Table 3). Complex
18 298 chains comprising several pseudochambers of variable size that incorporate small
19 299 planktonic foraminiferal shells, extending across one or more large planktonic shells
20 300 and connected with narrow stolons. The incorporation of planktonic shells makes the
21 301 arrangement of the pseudochambers and the relationship between them very difficult to
22 302 decipher.

23 303

24 304 Occurrence at abyssal hill and abyssal plain sites

25 305

26 306 Our examination of the two samples suggests some differences in the contribution of
27 307 morphotypes between the abyssal hill and abyssal plain sites. However, analyses of
28 308 additional replicates will be necessary to confirm these patterns. In absolute terms,
29 309 monothalamid and pseudochambered foraminifera were more abundant at the abyssal
30 310 hill site (H4) compared to the abyssal plain site (F2), for both the ‘live’ (23 vs. 17
31 311 indiv.10 cm⁻²) and the dead fauna (222 vs. 140 indiv.10 cm⁻²) (see Table 2). Most
32 312 morphotypes, including the three most abundant ones (Types 2–3, 7 in Table 3), had
33 313 comparable relative abundances (i.e. percentage of the total number of monothalamids)
34 314 at both sites, but there were some exceptions. Monothalamids with test composed of
35 315 mineral grains (Type 12 in Table 3) were found almost exclusively at the abyssal hill
36 316 site while delicate thick-walled spheres with red stained interior (Type 4 in Table 3)

1 317 were only encountered on the abyssal plain site. Moreover, spheres with short tube
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3 318 (Type 8 in Table 3) were more abundant at the abyssal hill site while pseudo-chambered
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5 319 forms (Types 15–18, Table 3) were more abundant at the abyssal plain site. Some
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7 320 monothalamids (Types 13–14 in Table 3) and pseudo-chambered forms (Types 15, 17 in
8
9 321 Table 3) were confined either to the abyssal hill or abyssal plain site, but as they were
10
11 322 all uncommon, and in some cases were singletons, little can be concluded regarding
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13 323 their distribution.

14 324

15 325 **Discussion**

17 326

19 327 Limitations of dataset

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23 329 Because of their delicate nature, the foraminifera described here might be vulnerable to
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25 330 mechanical damage, particularly during the sieving of sediment samples. Those
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27 331 particularly prone to breakage would include chain-like forms in which the segments
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29 332 are joined by fragile stolons that often span more than one planktonic shell (Fig. 7). The
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31 333 sieving process was carried out as gently as possible and most of the specimens that we
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33 334 examined appeared to be intact. It is possible that the 'spheres with long flimsy tubes'
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35 335 (Figs. 2c–e) represent fragments of chain-like formations in which the tubes link
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37 336 together several chambers, although we have no direct evidence for this interpretation.

38 337 The recognition of 'live' individuals was sometimes problematic, particularly in
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40 338 the case of forms in which the test contents were dominated by stercomata, for example
41
42 339 the 'classic dome' (Fig. 4a; Type 7 in Table 3). Another problem in some forms was
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44 340 that the central chamber was obscured by planktonic shells, which had to be removed in
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46 341 order to reveal whether or not the contents were stained (e.g. Figs. 5a–c; Type 9 in
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48 342 Table 3). This procedure both damages the specimen and is time-consuming. Because
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50 343 of these problems, the numbers of 'live' specimens may have been underestimated.
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52 344 Because the present analysis was confined to the 0–1 cm sediment layer, further
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54 345 staining of deeper layers is necessary to examine if these foraminifera live at greater
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56 346 depths within the sediment. Moreover, as this study was based on only two samples,
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58 347 replicates are needed in order to confirm the differences between the abyssal hill and
59
60 348 abyssal plain sites.

1 349
2
3 350 Comparison with other studies
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5 351
6 352 *Continental margin monothalamids*
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8 353
9
10 354 There are certain similarities between the abyssal morphotypes considered here and
11 355 monothalamous foraminifera illustrated in earlier publications. In particular
12 356 monothalamids associated with mineral grains resemble some illustrations of
13 357 *Psammosphaera fusca* from the North Sea (Heron-Allen and Earland 1913; e.g. Plate II
14 358 figs. 3.10–3.12). Here, specimens of *P. fusca* used a variety of particles to construct
15 359 their tests, mainly mineral grains but also dead foraminiferal shells. Heron-Allen and
16 360 Earland (1913) reported both free-living and sessile forms of this species, the latter
17 361 attached to sponge spicules, larger foraminiferal tests and molluscan shells. These
18 362 authors also recorded *Crithionina mamilla*, which was found on similar substrates.
19 363 This species resembles our *Crithionia*-like sphere in having a white thick-walled test.
20 364 However, *P. fusca* and *C. mamilla* were reported from shelf and slope settings (16–
21 365 1,600 m) rather than abyssal depths and were much larger (approx. 550–1,150 µm) than
22 366 our morphotypes, which in most cases did not exceed 150 µm. Differences in food
23 367 supply linked to differences in depth probably explain their larger size.
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25 368
26
27 369 *Abyssal environments: differences between Pacific and Atlantic monothalamids*
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29 370
30
31 371 Snider et al. (1984) analysed box-core samples taken at 5,800 m depth in the North
32 372 Pacific in order to assess the composition and distribution of the meio- and nanofauna.
33 373 They found that an important part of the abundance and biomass of benthic foraminifera
34 374 comprised small (<100 µm diameter) ‘sac-shaped’ individuals, which they called
35 375 *Crithionina*. These were presumably some sorts of agglutinated spheres. In the Kaplan
36 376 East area of the abyssal eastern Equatorial Pacific, Nozawa et al. (2006) reported tiny
37 377 free-living agglutinated spheres termed ‘indeterminate psammosphaerids’ that were
38 378 consistently more abundant (usually 60–80 % of the total ‘live’ assemblage) than other
39 379 foraminifera. A small (<100 µm diameter) agglutinated spherical form was described
40 380 from the Kaplan Central site by Ohkawara et al. (2009) as *Saccamina minimus*. This

1 381 species incorporated radiolarian tests and shard-like diatom fragments in its test and
2
3 382 contained stercomata.

4 383 The abundance of small agglutinated spheres at abyssal sites in both the Pacific
5
6 384 and Atlantic Ocean (Gooday et al., 1995; our samples) is striking. However, they differ
7
8 385 in the nature of particles used to construct the test - mainly siliceous in the Pacific and
9
10 386 mainly calcareous in the Atlantic. Much of the abyssal Pacific lies close to or below the
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12 387 CCD (Berger 1978) and thus few planktonic foraminiferal shells are available in
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14 388 seafloor sediments. As a result, most agglutinated spheres are made of fine mineral
15
16 389 particles and siliceous biogenic material, mainly radiolarians and diatom fragments
17
18 390 (Nozawa et al. 2006; Ohkawara et al. 2009). They are also predominantly free-living
19
20 391 and not attached to substrates. At the PAP, on the other hand, the CCD is much deeper
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22 392 (Biscaye et al. 1976) and the sediment is mainly a carbonate ooze with abundant
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24 393 planktonic foraminiferal shells and coccoliths, which monothalamous spheres and
25
26 394 domes use to construct their tests. In particular, they typically incorporate planktonic
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28 395 shells into their test or attach themselves to the surfaces of large planktonic shells. As a
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30 396 result, they often form large and complex structures (>300 μm), which appear
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32 397 superficially quite different from the tiny monothalamids found in the Pacific Ocean.

33 398

34 399 Distribution across the abyssal hill and abyssal plain sites

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37 401 Topographic high points can generate distinctive environmental conditions. Thistle et
38
39 402 al. (1999) reported faunal and ecological differences between high points (seamounts)
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41 403 and flat areas. High points tend to have stronger currents (Roden 1987) and coarser
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43 404 sediment (Levin and Thomas 1989). Our abyssal hill site resembles a small seamount
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45 405 (see Fig. 1; Table 1). Thus, we would expect stronger currents and coarser sediment
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47 406 compared to the abyssal plain site, which might affect the abundance and species
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49 407 composition of sediment-dwelling fauna (Kaufmann et al. 1989; Levin et al. 1994)
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51 408 including the foraminifera (Kaminski 1985). Our observations suggest that this is true
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53 409 for monothalamous and pseudochambered foraminifera, as their densities are greater at
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55 410 the abyssal hill site. Furthermore, monothalamids that incorporate mineral grains as part
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57 411 of their test are almost exclusively restricted to this elevated setting where larger quartz
58
59 412 grains are available. Taking into account the patchy distribution of benthic foraminifera

1 413 in abyssal environments (Bernstein and Meador 1979), replicate samples will clearly be
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3 414 necessary to confirm this pattern. However, if confirmed, this would have implications
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5 415 for the role of abyssal hills in generating faunal heterogeneity.
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7 416

8 417 **Concluding remarks**

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11 419 Our preliminary study provides evidence for the prevalence of certain types of basal
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13 420 ('primitive') foraminifera at the PAP area of the northeast Atlantic. They represent a
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15 421 subset of the diverse and largely undescribed monothalamids that flourish in the deep
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17 422 sea and represent an important component of abyssal benthic communities. The forms
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19 423 that we describe are all associated with planktonic foraminiferal shells, an important
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21 424 component of the sand fraction of sediments at the PAP, which is situated above the
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23 425 CCD. In the abyssal Pacific, where the CCD is shallower, radiolarian tests take the
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25 426 place of planktonic foraminifera as sand-sized components of the sediment. Currently,
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27 427 there are many problems associated with the study of these abyssal monothalamids,
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29 428 among them, distinguishing 'live' from dead individuals and obtaining molecular
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31 429 genetic data in order to address their phylogenetic relationships. These remain important
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33 430 challenges for the future.

34 431 The fossil record of monothalamous foraminifera is generally poor (Tappan and
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36 432 Loeblich, 1988). Some apparently delicate agglutinated species have been found in
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38 433 ancient marine sediments (e.g., Nestell and Tolmacheva 2004; Nestell et al., 2009) and
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40 434 agglutinated tests that resemble testate amoebae are known from Neoproterozoic
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42 435 sediments (Porter and Knoll, 2000). We are not aware of any forms in the fossil record
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44 436 similar to those described here, although it is possible that they may be discovered
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46 437 eventually in Late Cretaceous sediments deposited in the North Atlantic and Western
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48 438 Tethys (now Western Mediterranean) Oceans, in some cases above the CCD. These
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50 439 sediments have yielded diverse deep-water agglutinated foraminiferal assemblages (e.g.,
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52 440 Kuhnt et al., 1989; Kuhnt and Kaminski, 1989), some resembling komokiaceans. The
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54 441 planktonic shells from which many of the PAP forms are constructed could easily
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56 442 become detached, causing the test structure to disintegrate, but the organic components
57
58 443 might survive fossilization.

59 444

1 445 **Acknowledgements** We thank the captain and the crew of the R.S.S. *James Cook* and the scientists
2 446 participating in *James Cook* cruise 062 for their assistance with the field operations. We are very grateful
3
4 447 to the Meioscool organizers Daniela Zeppilli and Aurelie Francois and all the other anonymous helpers
5 448 for the very successful workshop in Brest, France (26th–29th November) and to Dr Zeppilli for her
6 449 invitation to contribute to the Meioscool special issue of *Marine Biodiversity*. We also thank Dr Kirsty
7 450 Morris for kindly helping us with preparing Fig. 1, and two anonymous reviewers for their comments,
8 451 which helped to improve the manuscript. One of us (PVS) is jointly funded by NERC and the School of
9 452 Ocean and Earth Sciences, University of Southampton. This research contributes to the NERC-funded
10 453 efforts of the Autonomous Ecological Survey of the Abyss project (AESAs, Henry Ruhl, Principal
11 454 Investigator) and the Porcupine Abyssal Plain - Sustained Observatory.
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59 478
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69 483
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- 1 484 **References**
2
3 485
4 486 Berger WH (1978) Sedimentation of deep-sea carbonate; maps and models of variations and fluctuations.
5
6 487 J Foramin Res 8:286–302
7 488 Bernstein BB, Hessler RR, Smith R, Jumars PA (1978) Spatial dispersion of benthic Foraminifera in
8
9 489 abyssal central North Pacific. Limnol Oceanogr 23:401–416
10 490 Bernstein BB, Meador JP (1979) Temporal persistence of biological patch structure in an abyssal benthic
11
12 491 community. Mar Biol 51:179–183 doi:Doi 10.1007/Bf00555197
13 492 Biscaye PE, Kolla V, Turekian KK (1976) Distribution of calcium carbonate in surface sediments of the
14
15 493 Atlantic Ocean. J Geophys Res 81:2595–2603 doi:Doi 10.1029/Jc081i015p02595
16 494 Earland A (1933) Foraminifera. Part II. South Georgia. Discovery Rep 7:27–138
17 495 Earland A (1934) Foraminifera. Part III. The Falklands sector of the Antarctic (excluding South Georgia).
18
19 496 Discovery Rep 10:1–208, pls.201–210
20 497 Earland A (1936) Foraminifera. Part IV. Additional records from the Weddel Sea sector from material
21
22 498 obtained by the S.Y. 'Scotia'. Discovery Rep 10:1–76
23 499 Enge AJ, Kucera M, Heinz P (2012) Diversity and microhabitats of living benthic foraminifera in the
24
25 500 abyssal Northeast Pacific. Mar Micropaleontol 96–97:84–104 doi:Doi
26
27 501 10.1016/J.Marmicro.2012.08.004
28 502 Gooday AJ, Carstens M, Thiel H (1995) Microforaminifera and nanoforaminifera from abyssal northeast
29
30 503 Atlantic sediments: a preliminary report. Int Rev Ges Hydrobio 80:361–383 doi:Doi
31
32 504 10.1002/Iroh.19950800223
33 505 Gooday AJ, Hori S, Todo Y, Okamoto T, Kitazato H, Sabbatini A (2004) Soft-walled, monothalamous
34
35 506 benthic foraminiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and
36
37 507 biogeography. Deep-Sea Res Pt I 51:33–53 doi:Doi 10.1016/J.Dsr.2003.07.002
38 508 Gooday AJ, Malzone MG, Bett BJ, Lamont PA (2010) Decadal-scale changes in shallow-infaunal
39
40 509 foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. Deep-Sea Res Pt II
41
42 510 57:1362–1382
43 511 Gooday AJ, Jorissen FJ (2012) Benthic foraminiferal biogeography: controls on global distribution
44
45 512 patterns in deep-water settings. Annu Rev Mar Sci 4:237–262 doi:Doi 10.1146/Annurev-Marine-
46
47 513 120709-142737
48 514 Gooday AJ (2014) Deep-sea benthic foraminifera. Earth Systems and Environmental Sciences:1–20.
49
50 515 <http://dx.doi.org/10.1016/B978-0-12-409548-9.09071-0>. Accessed 29 May 2014
51 516 Heron-Allen E, Earland A (1913) On some foraminifera from the North Sea, etc, dredged by the Fisheries
52
53 517 cruiser 'Goldseeker' (International North Sea Investigations - Scotland). II. On the distribution of
54
55 518 *Saccamina sphaerica* (M. Sars) and *Psammosphaera fusca* (Schulze) in the North Sea:
56
57 519 particularly with reference to the suggested identity of the two species. J R Microsc Soc:1–26
58 520 Heron-Allen E, Earland A (1932) The ice-free area of the Falkland Islands and adjacent seas. Discovery
59
60 521 Rep 4:291–460
61
62
63
64
65

- 1 522 Kaminski MA (1985) Evidence for control of abyssal agglutinated foraminiferal community structure by
2 523 substrate disturbance - results from the Hebble Area. *Mar Geol* 66:113-131 doi:Doi
3 524 10.1016/0025-3227(85)90025-8
4
5 525 Kaufmann RS, Wakefield WW, Genin A (1989) Distribution of epibenthic megafauna and lebensspuren
6 526 on two central North Pacific seamounts. *Deep-Sea Res Pt I* 36:1863–1896 doi:Doi
7 527 10.1016/0198-0149(89)90116-7
8
9 528 Kuhnt W, Kaminski M (1989) Upper Cretaceous deep-water agglutinated benthic foraminiferal
10 529 assemblages from the Western Mediterranean and adjacent areas. In: Wiedmann J (ed)
11 530 Cretaceous of the Western Tethys. Proceedings of the Third International Cretaceous
12 531 Symposium, Tübingen, Scheizerbart'sche Verlagsbuchhandlung, Stuttgart, pp 91–120
13
14 532 Kuhnt W, Kaminski MA, Moullade M (1989) Late Cretaceous deep-water agglutinated foraminiferal
15 533 assemblages from the North Atlantic and its marginal seas. *Geol Rundsch* 78:1121–1140
16
17 534 Lecroq B et al. (2011) Ultra-deep sequencing of foraminiferal microbarcodes unveils hidden richness of
18 535 early monothalamous lineages in deep-sea sediments. *P Natl Acad Sci USA* 108:13177–13182
19 536 doi:Doi 10.1073/Pnas.1018426108
20
21 537 Levin LA, Thomas CL (1989) The influence of hydrodynamic regime on infaunal assemblages inhabiting
22 538 carbonate sediments on central Pacific seamounts. *Deep-Sea Res Pt I* 36:1897–1915 doi:Doi
23 539 10.1016/0198-0149(89)90117-9
24
25 540 Levin LA, Leithold EL, Gross TF, Huggett CL, Dibacco C (1994) Contrasting effects of substrate
26 541 mobility on infaunal assemblages inhabiting two high-energy settings on Fieberling Guyot. *J*
27 542 *Mar Res* 52:489–522 doi:Doi 10.1357/0022240943077028
28
29 543 Loeblich AR, Tappan H (1987) Foraminiferal genera and their classification. Van Nostrand Reinhold,
30 544 New York
31
32 545 Mackensen A, Grobe H, Kuhn G (1990) Benthic foraminiferal assemblages from the eastern Weddell Sea
33 546 between 68 and 73 S: distribution, ecology and fossilization potential. *Mar Micropaleontol*
34 547 16:241–283
35
36 548 Mikhalevich VI (2005) Polymerization and oligomerization in foraminiferal evolution. *Stud Geol Polon*
37 549 124:117–141
38
39 550 Murray JW (1991) Ecology and palaeoecology of benthic foraminifera. Longman Scientific & Technical,
40 551 New York
41
42 552 Murray JW (2013) Living benthic foraminifera: biogeographical distributions and the significance of rare
43 553 morphospecies. *J Micropaleontol* 32:1–58
44
45 554 Nestell GP, Tolmacheva TY (2004) Early Ordovician foraminifers from the Lava Section, northwestern
46 555 Russia. *Micropaleontol* 50:253–280
47
48 556 Nestell GP, Mestre A, Heredia S (2009) First Ordovician foraminifera from South America: a Darriwilian
49 557 (Middle Ordovician) fauna from the San Juan Formation, Argentina. *Micropaleontol* 55:329–344
50
51 558 Nozawa F, Kitazato H, Tsuchiya M, Gooday AJ (2006) 'Live' benthic foraminifera at an abyssal site in
52 559 the equatorial Pacific nodule province: Abundance, diversity and taxonomic composition. *Deep-*
53 560 *Sea Res Pt I* 53:1406–1422 doi:Doi 10.1016/J.Dsr.2006.06.001
54
55
56
57
58
59
60
61
62
63
64
65

1 561 Ohkawara N, Kitazato H, Uematsu K, Gooday AJ (2009) A minute new species of *Saccamina*
2 562 (monothalamous Foraminifera; Protista) from the abyssal Pacific. *J Micropalaeontol* 28:143–151
3 563 doi:Doi 10.1144/Jm.28.2.143
4 564 Pawlowski J et al. (2003) The evolution of early Foraminifera. *P Natl Acad Sci* 30:11494–11498
5 565 Pawlowski J, Holzmann M, Tyszka J (2013) New supraordinal classification of Foraminifera: molecules
6 566 meet morphology. *Mar Micropaleontol* 100:1–10 doi:Doi 10.1016/J.Marmicro.2013.04.002
7 567 Porter SM, Knoll AH (2000) Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped
8 568 microfossils in the Chuar Group, Grand Canyon. *Paleobiol* 26: 360–385
9 569 Roden GI (1987) Effects of seamounts and seamount chains on ocean circulation and thermohaline
10 570 structure. In: Keating BH, Fryer P, Batiza R, Boehlert GW (eds) *Seamounts, Islands and Atolls*.
11 571 American Geophysical Union, Washington, D. C, pp 335–354
12 572 Schröder CJ, Scott DB, Medioli FS, Bernstein BB, Hessler RR (1988) Larger agglutinated Foraminifera:
13 573 comparison of assemblages from central North Pacific and Western North Atlantic (Nares
14 574 Abyssal Plain). *J Foramin Res* 18:25–41
15 575 Snider LJ, Burnett BR, Hessler RR (1984) The composition and distribution of meiofauna and nanobiota
16 576 in a central North Pacific deep-sea area. *Deep-Sea Res Pt I* 31:1225–1249 doi:Doi
17 577 10.1016/0198-0149(84)90059-1
18 578 Tappan H, Loeblich AR (1988) Foraminiferal evolution, diversification, and extinction. *J Paleontol*
19 579 62:695–714
20 580 Tendal OS, Hessler RR (1977) An introduction to the biology and systematics of Komokiacea
21 581 (*Textulariina*, Foraminiferida). *Galathea Rep* 14:165–194
22 582 Thistle D, Levin LA, Gooday AJ, Pfannkuche O, Lambshead PJD (1999) Physical reworking by near-
23 583 bottom flow alters the metazoan meiofauna of Fieberling Guyot (northeast Pacific). *Deep-Sea*
24 584 *Res Pt I* 46:2041–2052 doi:Doi 10.1016/S0967-0637(99)00040-0
25 585
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1 597 **Tables**

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4 **Table 1** Locality data

Station	Date	°N	°W	Depth (m)	Topography
JC062-77	August 2011	48° 52.530'	16° 17.570'	4,818	Abyssal Plain (F2)
JC062-126	August 2011	49° 04.443'	16° 15.831'	4,330	Abyssal Hill (H4)

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2 **Table 2** Counts (N) of monothalamid and pseudochambered morphotypes, including fragments and
 3 indeterminate specimens, from the 0–0.5 cm and 0.5–1 cm sediment layers. Densities (individuals per 10
 4 cm²) are shown in brackets after the counts per sample. Also shown are their relative abundance (%)
 5 amongst the entire ‘live’ (stained) and dead assemblage (multichambered and monothalamid taxa) from
 6 the two samples (>150-μm fraction) for the two layers combined (i.e. 0–1 cm). The percentages for the
 7 ‘live’ category represent their proportion among the total number of monothalamids and
 8 pseudochambered morphotypes present in the 0–1 cm. SL = sediment layer, F2 = abyssal plain, H4 =
 9 abyssal hill

	‘Live’ (stained)			Dead			‘Live		
	N		%	N		%	N		%
	0–0.5	0.5–1	0–1	0–0.5	0.5–1	0–1	0–0.5	0.5–1	0–1
SL (cm)									
F2	29 (11.4)	13 (5.1)	34.7	340 (133)	16 (6.3)	22.9	22 (8.6)	20 (7.8)	9.6
H4	46 (18)	13 (5.1)	27.4	434 (170)	133 (52.2)	18.4	17 (6.7)	139 (54.5)	19.9

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Table 3 Occurrence of monothalamid and pseudochambered morphotypes associated with planktonic foraminiferal shells and mineral grains in PAP samples (>150- μm fraction). L = 'live' (stained), D = dead. The numbers in the left-hand column correspond to those in the text

Morphotypes	Figure	F2 (abyssal plain)			H4 (abyssal hill)		
		L	D	?live	L	D	?live
<i>Monothalamids attached to or lodged between planktonic foraminiferal shells</i>							
1) Thin-walled sphere	2a,b	0	0	3	2	0	0
2) Sphere with long flimsy tubes	2c,d,e	3	78	8	7	113	1
3) Dome with cap attached to large planktonic foraminiferal shell	2f,g,h	1	34	0	7	55	0
4) Delicate thick-walled sphere with red-stained interior	3a,b,c,d,e	9	0	0	0	0	0
5) Round, slightly opaque sphere with red-stained interior	3f,g,h	1	0	0	1	0	0
6) <i>Crithionina</i> -like sphere	3i,j,k	0	5	0	1	7	1
7) 'Classic dome'	4a,b,c,d	19	155	12	30	271	25
8) Sphere with short tube	4e,f	1	2	0	3	29	0
9) Red sphere with stercomata, between planktonic shells	5a,b,c,d,e	5	9	0	5	2	3
10) Thin-walled red sphere attached to large planktonic shell	5f,g	1	0	0	3	0	1
11) Soft sphere lodged between two planktonic shells	5h	2	0	0	0	4	0
<i>Monothalamids associated with mineral grains</i>							
12) Monothalamids associated with mineral grains	6a,b,c	0	4	0	0	60	0
<i>Monothalamids associated with tubes</i>							
13) Spherical chamber with tubes	6d,e,f	0	0	0	0	8	0
14) Short, soft-walled tube	6g,h,i	0	0	0	0	1	0
<i>Pseudochambered (chain-like) forms</i>							
15) Double dome	7a,b,c	0	0	0	0	4	0
16) Pseudochambers linked with stolons	7d,e,f	0	15	0	0	9	0
17) Chain with thick tube	7g,h,i	0	1	0	0	0	0
18) Indeterminate chain of chambers	7j,k,l	0	53	0	0	4	0
Total		42	356	23	59	567	31

1 645

2 646 **Figures**

3 647

4 648 **Fig. 1** Bathymetry map of the PAP area showing the positions of our two study sites, F2 (abyssal plain
5 649 site) and H4 (abyssal hill site), in relation to the PAP central site, which is the focus of long-term time-
6 650 series sampling at the Porcupine Abyssal Plain Sustained Observatory (e.g. Gooday et al., 2010)

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8 652 **Fig. 2** Monothalamids attached to, or lodged between, planktonic foraminiferal shells. Reflected light
9 653 images (**a, c, d, f**); SEM images (**b, e, g, h**). Thin-walled sphere (**a, b**). Sphere with long flimsy tubes (**c-**
10 654 **e**). Dome with cap attached to large planktonic foraminiferal shell (**f-h**)

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12 656 **Fig. 3** Monothalamids attached to, or lodged between, planktonic foraminiferal shells. Reflected light
13 657 images (**a-c, f, i**); SEM images (**d, e, g, h, j, k**). Delicate thick-walled spheres with red stained interior
14 658 (**a-c**); SEM images of the third (**c**) specimen (**d, e**). Round, slightly opaque sphere with red stained
15 659 interior (**f-h**). *Crithionina*-like sphere (**i-k**)

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17 661 **Fig. 4** Monothalamids attached to, or lodged between, planktonic foraminiferal shells. Reflected light
18 662 images (**a, b, e**); SEM images (**c, d, f**). ‘Classic dome’ (**a-d**). Sphere with short tube (**e, f**)

19 663

20 664 **Fig. 5** Monothalamids attached to, or lodged between, planktonic foraminiferal shells. Reflected light
21 665 images (**a-c, f-h**); SEM images (**d, e**). Red sphere with stercomata, between planktonic shells (**a-e**).
22 666 Thin-walled red sphere attached to large planktonic shell (**f, g**). Soft sphere lodged between two
23 667 planktonic shells (**h**)

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25 669 **Fig. 6** Monothalamid associated with mineral grains and tubes. Reflected light images (**a, d, g**); SEM
26 670 images (**b, c, e, f, h, i**). Monothalamids utilizing yellow, orange and transparent mineral grains for
27 671 constructing their test (**a**); SEM images of a specimen attached to a planktonic shell (**b**) and a free-living
28 672 form (**c**). Spherical chamber with tubes (**d-f**). Short, soft-walled tube (**g-i**)

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30 674 **Fig. 7** Pseudochambered (chain-like) morphotypes. Reflected light images (**a, b, d, e, g, j-l**); SEM
31 675 images (**c, f, h, i**). Double dome (**a-c**). Pseudochambers linked with stolons (**d-f**). Chain with thick tube
32 676 (**g-i**). Indeterminate chain of chambers (**j-l**)

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Figure1
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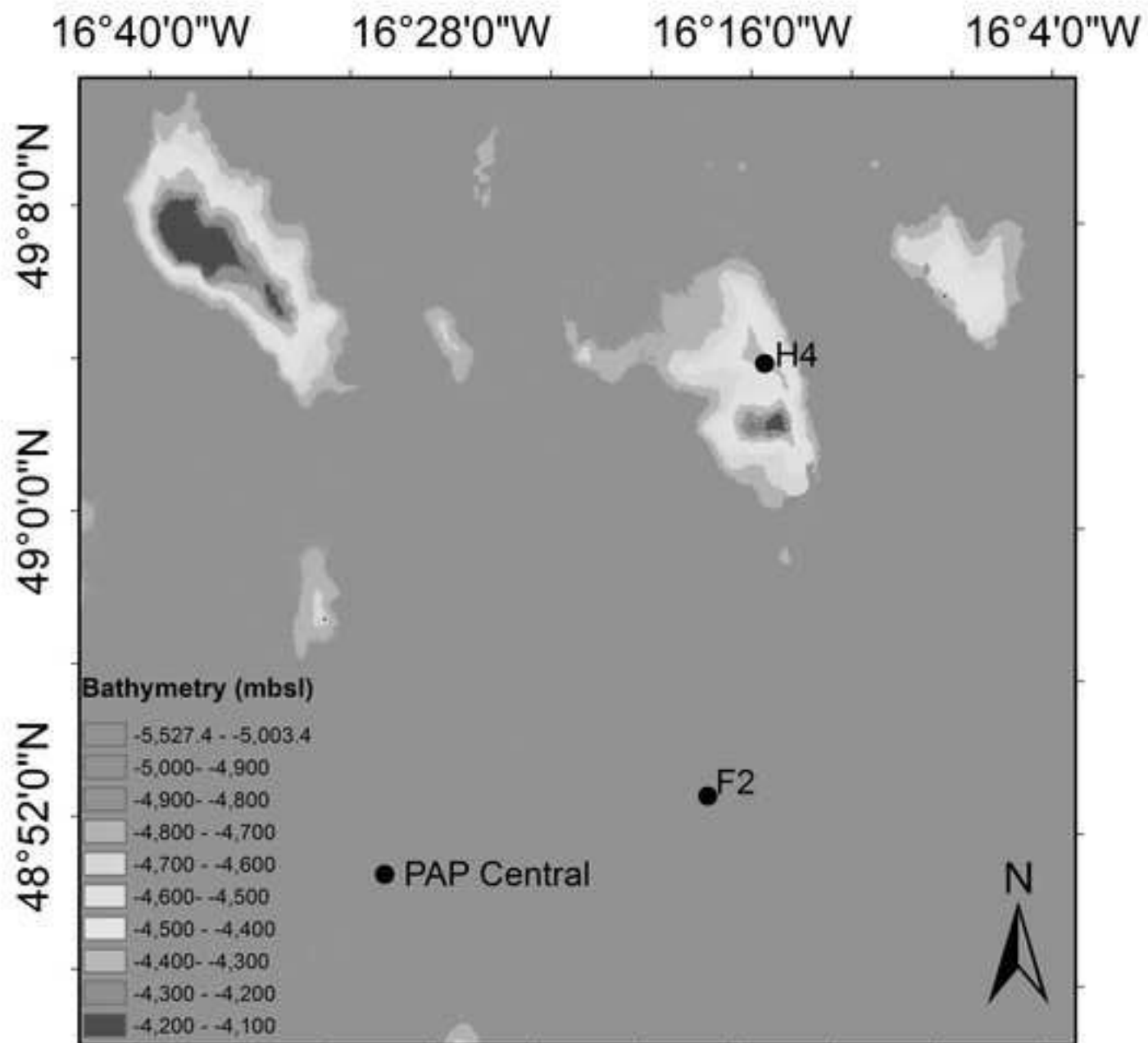


Figure 2
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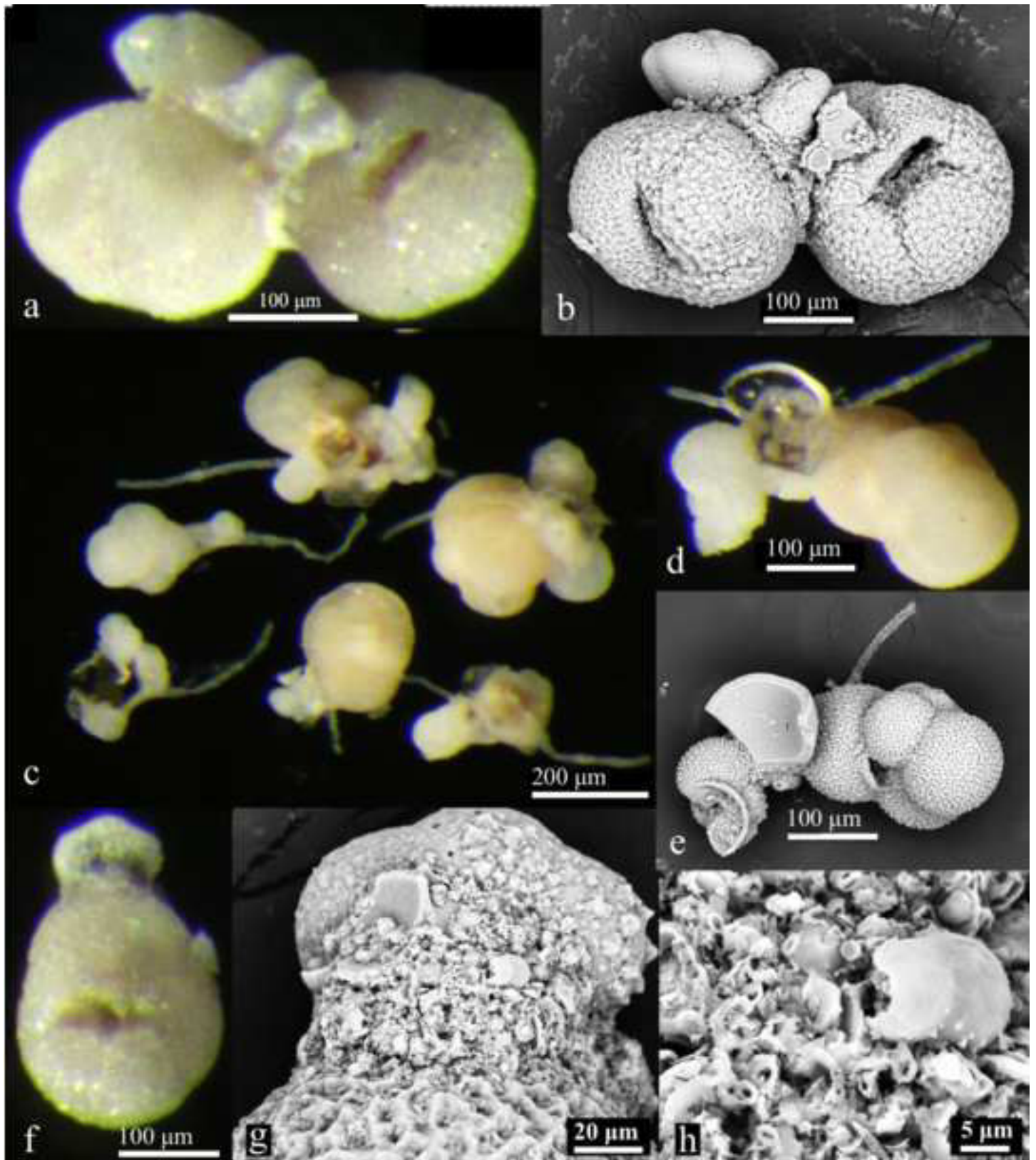


Figure3
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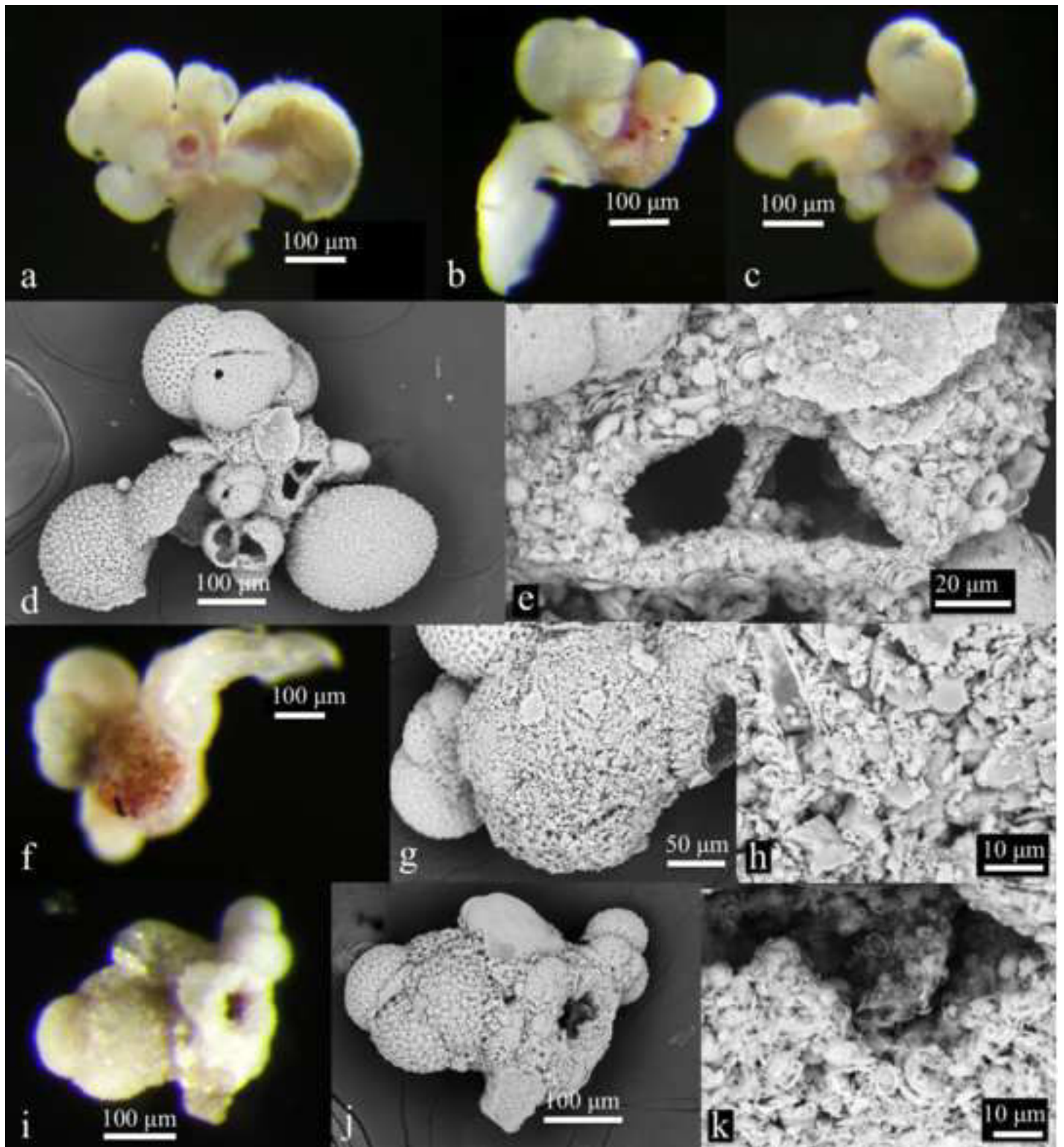


Figure4
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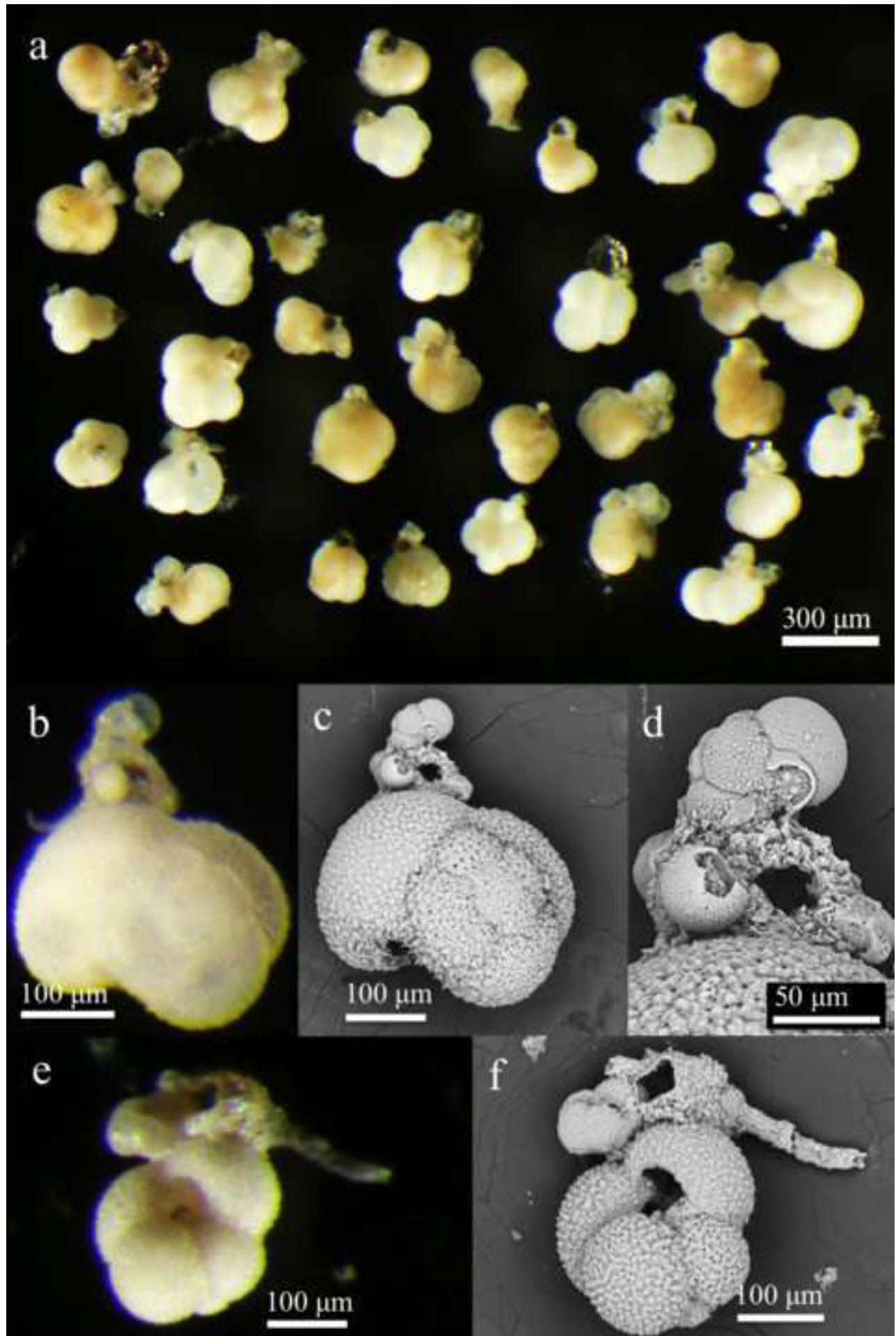


Figure 5
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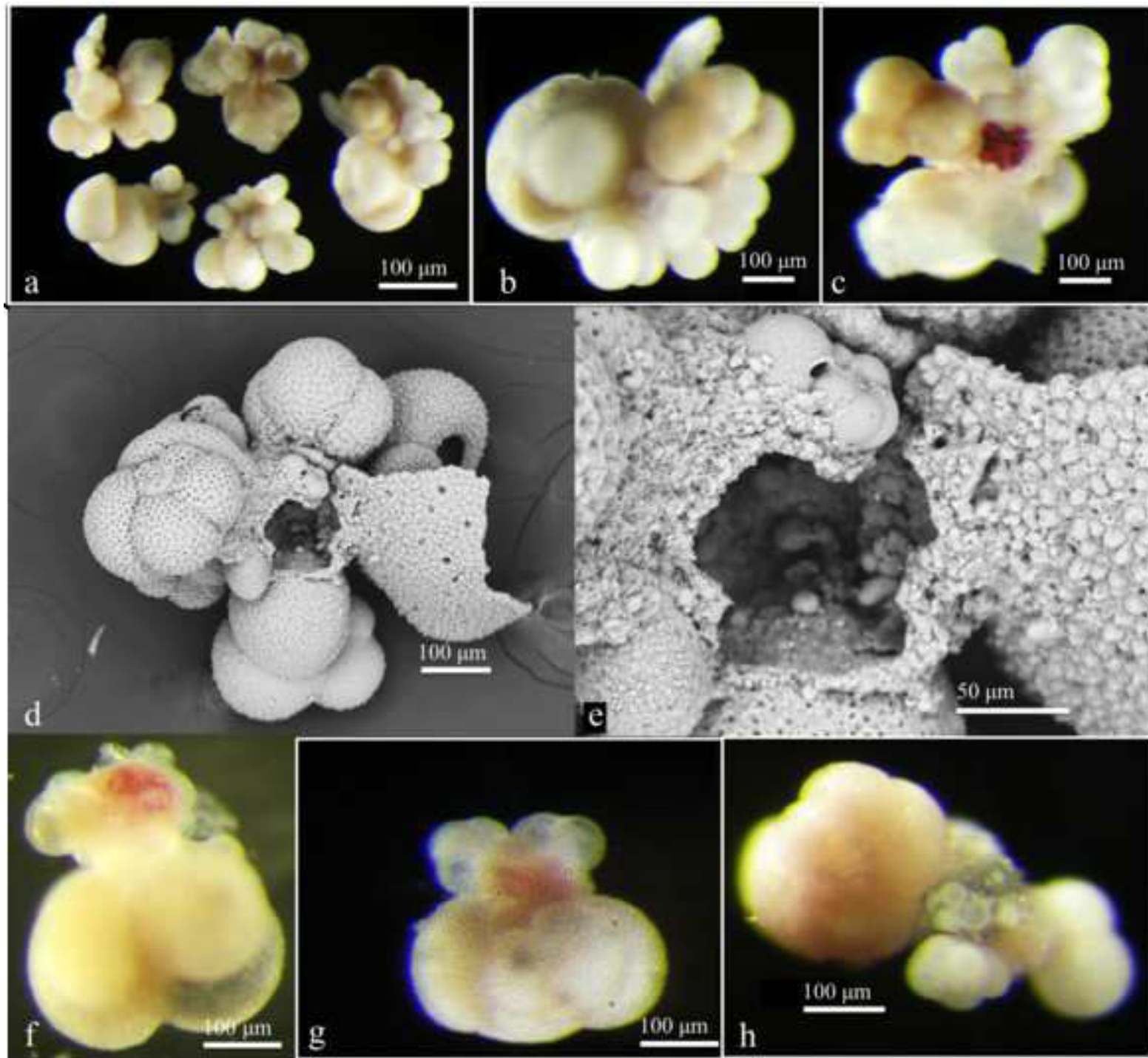


Figure6
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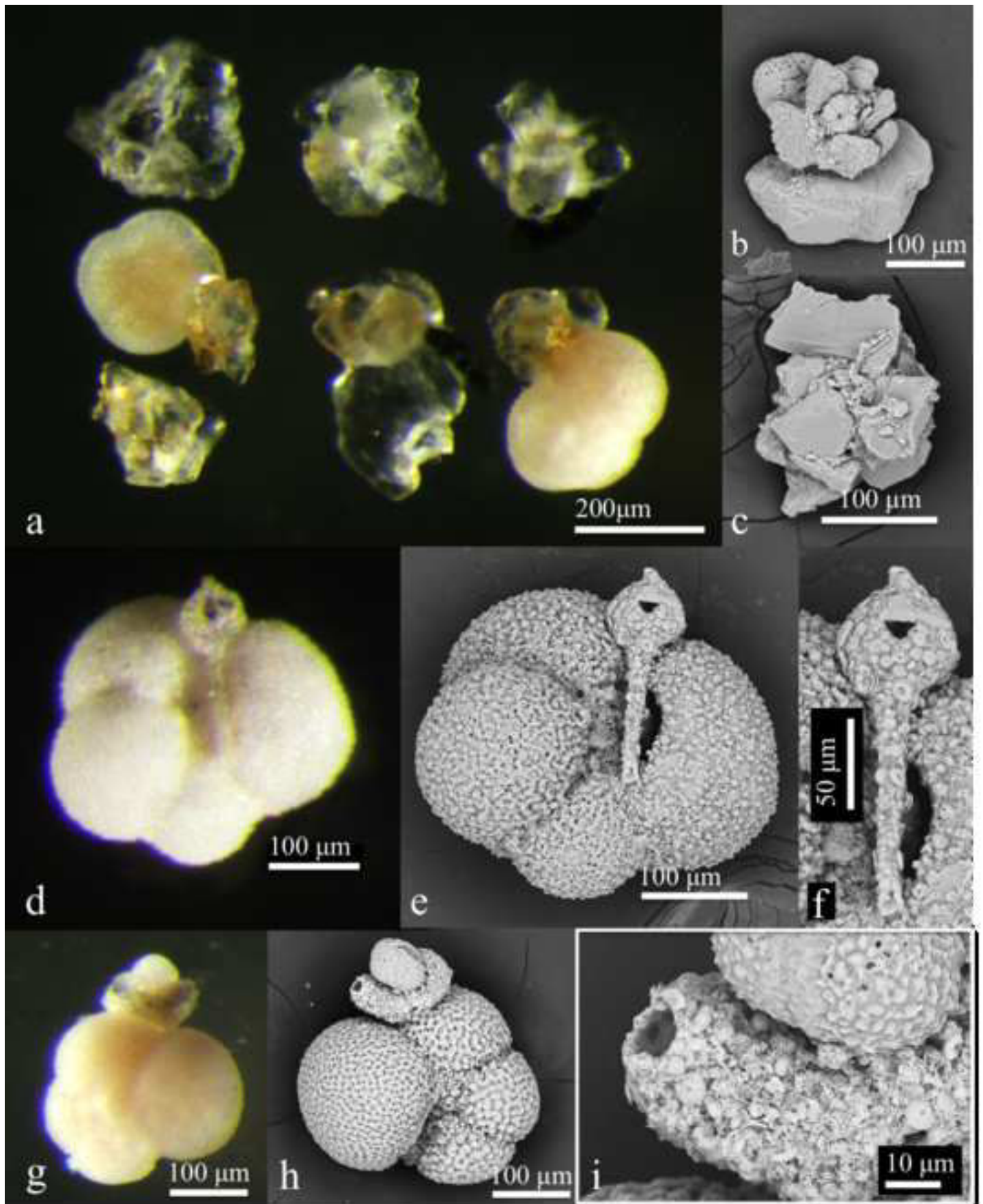


Figure 7

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