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1 First deep-sea *Hamigera* (Demospongiae: Porifera) species associated 2 with Cold-Water Corals (CWC) on antipodal latitudes of the world 3

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12 Abstract

13
14
15 Cold-water corals (CWC) are known to be deep-sea biodiversity hotspots, yet there is
16 still a huge knowledge gap regarding their associated fauna. As so, CWC ecosystems
17 pose as a perfect environment for the discovery of new species. In this context two
18 new species of *Hamigera* (Demospongiae) have been recorded associated with CWC
19 in antipodal parts of the world: *Hamigera bibiloniae* sp. nov. from the Blanes Canyon
20 (north-western Mediterranean Sea) and *Hamigera kellyae* sp. nov. from the
21 Clementsville Seamount (Macquire Ridge, New Zealand). Both species represent first
22 deep-sea records of the previously shallow-water restricted *Hamigera*, and mostly
23 differ from of the previously considered shallow water genus in their huge spicule
24 size, mostly doubling that of shallow-water congeneric species.

25 Furthermore, the current geographical distribution of *Hamigera*, being only present in
26 the Mediterranean and Pacific areas, might suggest a Tethyan affinity of *H. bibiloniae*
27 sp. nov. proposing a potential role of deep-sea habitats as climatic refugees.

28
29 **Keywords:** New species; Porifera; Sponges; *Hamigera*; Deep-Sea; Cold-Water
30 Corals; ROV; Clementsville Seamount, Macquire Ridge, New Zealand; Blanes
31 Canyon, Mediterranean Sea.

32 33 34 1. Introduction 35

36 While the current concept of Cold-Water Corals (CWC) encompasses several
37 unrelated taxa within the classes Hexacorallia and Octocorallia (*sensu* Freiwald &
38 Roberts, 2006), only scleractinians are considered as framework-forming CWC
39 (Roberts et al., 2009). Framework-forming CWC are slow growing species with a

40 cosmopolitan distribution across the globe (Etnoyer & Morgan, 2005; Schroeder et
41 al., 2005; Tracey et al., 2011), being able to build reefs of up to hundreds of meters
42 (Jensen & Frederiksen, 1992; Ríos et al., 2017) or even entire coral mounds (Corbera
43 et al., 2019). While the current concept of CWC encompasses several unrelated taxa
44 within the classes Hexacorallia and Octocorallia (*sensu* Freiwald & Roberts, 2006),
45 only scleractinians are considered as framework-forming CWC (Roberts et al., 2009),
46 with six species being considered to be the main reef builders of the deep: *Lophelia*
47 *pertusa* (Linnaeus, 1758), *Madrepora oculata* (Linnaeus, 1758) *Goniocorella dumosa*
48 (Alcock, 1902), *Solenosmilia variabilis* Duncan, 1873, *Oculina varicosa* (Alcock,
49 1902) and *Enallopsammia profunda* (Pourtalès, 1867). While other deep-sea
50 scleractinians are also considered reef-forming species (Roberts et al., 2009; Henry &
51 Roberts, 2017), the above-mentioned are considered the most widespread CWC
52 within the earth's oceans, hence their consideration as the most significant reef-
53 building species (Roberts et al., 2009). Nevertheless, while widespread, these species
54 show clear regional differences in abundance (Henry & Roberts, 2017), with *L.*
55 *pertusa* being mostly reported from North Atlantic waters, and *O. varicosa* and *G.*
56 *dumosa* being restricted to the Caribbean and East Atlantic and the Indic and Pacific
57 Oceans respectively (Roberts et al., 2009).

58 As it happens with tropical reef-building corals, CWC are considered hotspots of
59 benthic diversity (Henry & Roberts, 2017), as they harbor a unique and diverse
60 associated fauna (Jensen & Frederiksen, 1992, van Soest et al., 2007; Rueda et al.,
61 2019). This, paired with their long lifespan and susceptibility to anthropogenic
62 impacts, has prompted their listing as Vulnerable Marine Ecosystems (VMEs) by the
63 Food and Agriculture Organization (FAO, 2009). Moreover, all CWC ecosystems
64 (EUNIS codes A5.631 and A6.611) are listed as "Threatened and/or Declining
65 Habitats" by the OSPAR commission (OSPAR commission 2008; 2010). Yet, despite
66 their listing as VMEs, and the acknowledgement of CWC being reservoir of
67 biodiversity (OSPAR commission 2010), our current knowledge regarding its
68 associated fauna is still fragmentary.

69

70 Furthermore, our knowledge of CWC associated fauna greatly varies across
71 the globe, with most studies on CWC associated fauna concentrating on North
72 Atlantic and Caribbean waters (Henry & Roberts, 2017), with studies outside this area
73 being far more scarce (Etnoyer & Morgan, 2005; Baco, 2007; Miyamoto et al.,

74 2017). Specifically, *L. pertusa* reefs along the Atlantic and Mediterranean waters have
75 been intensively explored during the past years (e. g. Jensen & Frederiksen, 1992;
76 Longo et al., 2005; Schroeder et al., 2005; van Soest et al., 2007; Buhl-Mortensen et
77 al., 2010; Taviani et al., 2017; Bertolino et al., 2019b; Corbera et al., 2019), revealing
78 over 1.300 associated species within CWC reefs (Roberts et al., 2006). From all these
79 taxa, Porifera stand out as one of the major components of CWC reefs associated
80 fauna (van Soest et al., 2007; van Soest & De Voogd, 2015; Bertolino et al., 2019b;
81 Rueda et al., 2019). Moreover, sponges are known to play a major role in CWC reefs
82 through the “sponge loop” by recycling dissolved organic matter (DOM) expelled by
83 the corals (Rix et al., 2016). In addition, excavating sponges are one of the main
84 bioeroding components within CWC (Beuck et al., 2007; van Soest & Beglinger,
85 2009), being considered as one of the main drivers for coral rubble generation
86 (Freiwald & Wilson, 1998). Regarding their biodiversity, studies within the Irish
87 bathyal CWC reefs reported over 150 different species, being in range with values for
88 shallow-water corals reefs (van Soest et al., 2007). Nevertheless, actual values for
89 CWC sponge biodiversity are considered to be underestimated (van Soest et al., 2007;
90 Reveillaud et al., 2011), as dozens of new species are recorded every year from CWC
91 reef communities (van Soest & Beglinger, 2009; Goodwin et al., 2011; Reveillaud et
92 al., 2010; 2011; Bertolino et al., 2019b). This remains particularly true for less
93 explored CWC ecosystems around the globe, as the discovery and exploration of new
94 seamounts and CWC reefs in these areas is expected to greatly increase the total
95 number of Porifera species in said regions (Lopes et al. 2005; Lopes & Hadju, 2014).
96 In this regard, the poriferan fauna around New Zealand had been historically poorly
97 studied in comparison to other areas of the world (Kelly, et al., 2009). While this isn't
98 true anymore for shallow and costal environments, the sponge fauna associated with
99 deep-sea communities in the region is still underexplored (Kelly, et al., 2009), thus
100 being a suitable area for the discovery of new species (Kelly & Cárdenas, 2016; Kelly
101 & Rowden, 2019).

102

103 The sponge genus *Hamigera* Gray, 1867 is currently represented by 6 species from
104 shallow tropical and subtropical regions (van Soest, 2002b), with a single species
105 (*Hamigera strongylata*) being known to occur in tropical coral reefs (Burton, 1934).
106 However, the recent discovery of *Hamigera cleistochela* from cold-water

107 environments of the Chilean Fjords (Bertolino et al., 2019a) and of a new *Hamigera*
108 sp. associated with deep-sea CWC from the North Atlantic deep-sea (Ríos et al.,
109 2017), alongside the occurrence of *Hamigera* representatives in both the North
110 Atlantic and the Pacific (van Soest, 2002b), hinted the possible existence of antipodal
111 cold-water *Hamigera* species unbeknownst to science.

112

113 In this context, this paper describes two new species of *Hamigera* associated with
114 CWC from opposing sides of the world: (1) *Hamigera bibiloniae* sp. nov. from the
115 Blanes Canyon (north-western Mediterranean Sea) and (2) *Hamigera kellyae* sp. nov.
116 from the Clementsville Seamount (Macquarie Ridge, New Zealand), and (3) discusses
117 the paleogeographical implications of the discovery of deep-sea records for this
118 previously considered shallow-water exclusive genus.

119

120 2. Material and Methods

121 2.1 Blanes Canyon:

122 Individuals of *Hamigera bibiloniae* sp. nov. were collected during the “ABIDES”
123 cruise, from 9 to 19 of September 2017, on board of the R/V *Sarmiento de Gamboa*,
124 using the articulated arm of the ROV (Remotely Operated Vehicle) *Liropus 2000*. The
125 main goal of this cruise was to evaluate the impacts of bottom trawling activities on
126 submarine canyon flanks of the Catalan continental margin (north-western
127 Mediterranean Sea). During the exploration of the Blanes submarine canyon (Fig. 1) a
128 vertical wall expanding from 860 to 670 m depth was recorded. The wall was densely
129 covered by colonies of the reef building scleractinians *Lophelia pertusa*, *Madrepora*
130 *oculata*, the solitary coral *Desmophyllum dianthus* (Esper, 1794), found along with
131 scattered colonies of the antipatharians *Parantipathes larix* (Esper, 1788) and the
132 gorgonian *Acanthogorgia hirsuta* Gray, 1857.

133

134 2.2 Clementsville Seamount:

135 Samples for *Hamigera kellyae* sp. nov. are part of the NIWA collection, and were
136 obtained from the Clementsville Seamount (Fig. 2), located at the Macquarie Ridge,
137 south of New Zealand, at 1070–1121 m depth. The Macquarie Ridge spans for 1600
138 kilometres from the southern part of New Zealand to the Australia-Pacific-Antarctic
139 triple junction halfway to Antarctica, being one the southernmost seamount ridges on

140 the Earth (Ahyong et al., 2015), with some of its seamounts having been object of
141 deep-sea exploration during this past decade (Rowden, 2008). Regarding the main
142 dominant habitat-forming scleractinians in the New Zealand area, those are
143 *Madrepora oculata*, *Goniocorella dumosa* (Alcock, 1902), the endemic *Oculina*
144 *virgosa* Squires, 1958, *Solenosmilia variabilis* Duncan, 1873 and *Enallopsammia*
145 *rostrata* (Pourtalès, 1878) (Tracey et al., 2011). From the above-mentioned species, *S.*
146 *variabilis* and *E. rostrata* are considered the most abundant reef-forming species in
147 the Macquarie Ridge area (O'Hara et al., 2008; Miller et al., 2010; Zeng et al., 2017).
148 Interestingly, *L. pertusa* in New Zealand was exclusively reported for the Macquarie
149 Ridge area, but such records are nowadays considered invalid (Tracey et al., 2011).

150

151 2.3 Museum Material:

152 Material corresponding to *Hamigera bibiloniae* sp. nov, including the holotype, have
153 been levelled and deposited in the Museu de Ciències Naturals de Barcelona (MZB),
154 whereas samples for *Hamigera kellyae* sp. nov., including the holotype are located in
155 the National Institute of Water and Atmospheric Research, New Zealand (NIWA)
156 following the reference number specified in the species' examined material. Lastly,
157 additional *Hamigera* material from the Mediterranean Sea and New Zealand,
158 including material from the Natural History Museum, United Kingdom (NHMUK,
159 before BMNH), the Queensland Museum (QM), Australia; the National Institute of
160 Water and Atmospheric Research, New Zealand (NIWA); Prof. Jean Vacelet personal
161 collections (J.V. *pers. coll.*) and *Hamigera hamigera* individuals sampled in Cap de
162 Creus coast (north-western Mediterranean Sea, Spain) has been examined for
163 comparison.

164

165 2.4. Spicule preparation:

166 To obtain spicule preparations for both optical and scanning electron microscopy
167 (SEM) fragments of the sponges were dissolved with nitric acid (HNO₃) following the
168 procedures described in Cristobo et al. (1993) and Uriz et al. (2017). The SEM
169 observation was conducted through a HITACHI TM3000 TableTop Scanning
170 Electron Microscope from the Center for Advanced Studies of Blanes (CEAB).
171 Spicule dimensions are given as maximum and minimum length and width for each
172 spicule category with the average values being given in between in italics followed by

173 \pm the Standard Deviation (i.e.. MIN. – *MEAN* \pm SD – MAX.). Otherwise stated, all
174 spicule measurements were based on 40 spicules.

175 Species classification has followed the current proposed classification for sponges in
176 the World Porifera Database (van Soest et al., 2020).

177

178 3. Results

179 Systematic Description

180

181 Phylum PORIFERA Grant, 1836

182 Class DEMOSPONGIAE Sollas, 1885

183 SubClass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

184 Order POECILOSCLERIDA Topsent, 1928

185 Family HYMEDESMIIDAE Topsent, 1928

186 Genus *Hamigera* Gray, 1867

187

188 Type species:

189 *Hamigera hamigera* (Schmidt, 1862) (as *Cribrella*).

190

191 Definition:

192 Encrusting to massive sponges; oscules slightly elevated, rounded, pores in
193 characteristic and conspicuous areolate porefields; bundles of ectosomal diactinal
194 spicules form a ring around the areolae areas; choanosomal skeleton composed of
195 plumose tracts of smooth strongyles or strongylote-tornotes, exclusively, which may
196 be mixed with smooth styles or subtylostyles with echinating smooth styles or
197 subtylostyles; microscleres are arcuate isochelae and more rarely, cleistochelae. Half
198 a dozen species. Mostly known from shallow waters of temperate seas, yet a few
199 species also occur on deep-waters habitats (amended from van Soest, 2002b;
200 Bertolino et al., 2019a).

201

202 *Hamigera bibiloniae* Santín, Grinyó, Uriz, & Gili sp. nov.

203 (Fig. 3)

204 Material examined:

205 Holotype: MZB 2019-1740 – Blanes Canyon, north-western Mediterranean Sea
206 (41°30'26"N 2°56'02"E), 'ABIDES' survey, 684 m depth, 2018;

207 Paratype: MZB 2019-2019 – Blanes Canyon, north-western Mediterranean Sea
208 (41°30'26"N 2°56'02"E), 'ABIDES' survey, 684 m depth, 2018 (slide; whole
209 individual used for spicule preparation)

210

211 Comparative material examined:

212 *Hamigera hamigera* (Schmidt, 1862) J. V. pers. coll., Sac2 – Île Grosse, Banyuls
213 (France), 10 m depth, 13th of October 1982; J. V. pers. coll. ST38 – Banyuls (France);
214 J. V. pers. coll. Sm3 – Marseille (France); J. V. pers. coll. JV365(32) – Djerba
215 (Tunisia) 0.7 m depth, 29th of September 1989. Several unregistered specimens from
216 Caials (42°17'06.3"N 3°17'48.6"E), Cadaqués (Spain), 2 m depth, July 2018 and Maó
217 (39°52'31.2"N 4°18'11.3"E), Menorca (Spain) 0–5 m depth, May 2019.

218

219 Description:

220 Shape:

221 Small encrusting sponge (ca. 1cm²), with a translucent ectosome, firmly attached to the
222 choanosome. Color is grey after drying.

223

224 Skeleton (Fig. 5A):

225 Plumose choanosomal skeleton made of paucispiculate tracts of strongyles, with
226 styles of two categories in an echinating position. The tracts occur perpendicular to
227 the base of the sponge. The ectosome is exclusively formed by the strongyles, which
228 are arranged in tracts tangentially to the surface. Arcuate isochelae occur at the
229 ectosomal and choanosomal areas without any apparent organization.

230

231 Spicule complement:

232 Strongyles, two categories of styles, and isochelae.

233

234 Strongyles (Fig. 3C): Straight and slightly asymmetric, with one end slightly wider
235 than the other; both ends with a subtle swelling or, rarely, a well-formed tyle (Fig.
236 3F), giving them the appearance of tylostrongyles or tylotes.

237 Size range: 284.1 – 315.7 – 337.4 ± 17.8 x 7.1 – 8.7 – 9.7 ± 0.8 µm

238

239 Style I (Fig. 3B): Slightly bent (one third), with an acerate end (Fig. 3D); the head is
240 unequally inflated, giving them the appearance of true styles to subtylostyles (Fig.
241 3E). Always in an echinating position on the choanosomal tracts.

242 Size range: $293 - 327.1 \pm 22.6 - 355.2 \times 5.3 - 7.25 \pm 1.2 - 8.9 \mu\text{m}$

243

244 Style II (Fig. 3A): Identical to the styles I, but bigger in size, yet they appear in lower
245 proportion, also echinating the choanosomal tracts.

246 Size range: $532.8 - 614.2 \pm 29.8 - 648.24 \times 10.7 - 16 \pm 2.2 - 17.8 \mu\text{m}$

247

248 Isochelae (Fig. 3G; a'): Stout arcuate isochelae, with short and stout alae. Mostly
249 occurring on the ectosome.

250 Size range: $35.5 - 43 \pm 4.3 - 48.9 \mu\text{m}$

251

252 Geographical and bathymetrical distribution:

253 So far, the species is only known from its type locality in the Blanes Canyon, at 684
254 m depth (Fig.1), occurring associated with CWC assemblages.

255

256 Etymology:

257 The name *bibiloniae* is chosen in honor of Dr. Maria Antonia Bibiloni i Rotger, in
258 recognition of her valuable contributions to the knowledge of Mediterranean sponges,
259 especially of the Catalan and the Balearic Islands coasts.

260

261 Remarks:

262 From all known Hymedesmiidae, only *Hamigera* and *Hemimycale* Burton, 1934
263 genera are known to exclusively possess smooth megascleres, yet both genera are
264 easily told apart by the lack of microscleres in *Hemimycale* (van Soest, 2002b; Uriz et
265 al., 2017). From all current known *Hamigera* species, only *Hamigera hamigera*
266 (Schmidt, 1862), a shallow water Mediterranean endemic species, co-occurs with
267 *Hamigera bibiloniae* sp. nov., while the other representatives of the genus only occur
268 in waters of the southern hemisphere (Shaw, 1927; Burton, 1934; Bergquist &
269 Fromont, 1988; Bertolino et al., 2019a).

270

271 While both *Hamigera bibiloniae* sp. nov. and *Hamigera hamigera* share their spicule
272 types and skeletal organization, *H. hamigera* styles could not be clearly split in two

273 clear categories as in *H. bibiloniae* sp. nov., with this second style category found in
274 *H. bibiloniae* sp. nov. doubling in size the styles from *H. hamigera* (Table 1).
275 Additionally, *H. hamigera* shows abundant areolate porefields across its surface,
276 which are lacking from *H. bibiloniae* sp. nov., yet most likely this is due to the small
277 size and encrusting morphology of the specimens examined. Thus, the possibility of
278 said species possessing areolate porefields cannot be ruled out. Finally, both species
279 occur in contrasting habitats, with *H. hamigera* being a shallow species, barely
280 recorded below 20 m, whereas *H. bibiloniae* sp. nov. was found below 650 m depth in
281 association with the CWC *Madrepora oculata*. Consequently, the spicule types of *H.*
282 *bibiloniae* sp. nov. match those of the genus, yet the possession of a second, bigger
283 style category for *H. bibiloniae* sp. nov. which is lacking in *H. hamigera* (Table 1),
284 alongside their contrasting habitats, confirmed that *H. bibiloniae* sp. nov. is a new
285 species clearly apart from other species.

286

287

288 *Hamigera kellyae* Santín, Grinyó, Uriz, & Gili sp. nov.

289 (Fig. 4)

290

291 Material examined:

292 Holotype: NIWA 39837, Clementsville Seamount, Macquarie Ridge, southern Pacific
293 Ocean, Station TAN0803/38 (50°05'49"S 163°28'27"E), 1070 – 1123 m depth, 2008.

294

295 Comparative material examined:

296 *Hamigera macrostrongyla* Bergquist & Fromont, 1988 QM G310712 –
297 Motuwharariki Island, near Rimariki Island, Mimiwhabgata Bay, New Zealand
298 (35°25'30"S 174°26'60"E) 20 m, 12th December 1988, Coll. C.N. Battershill,
299 Australian Institute of Marine Science NCI Contract Collection; NIWA 51458 –
300 North of Cape Reinga, New Zealand, Station Z9700 (34°22'48"S 179°32'49"E) 54 m,
301 1999; NIWA 100938 – Archway on the SE headland of Tasman Bay, Great Island,
302 Three Kings Islands, New Zealand, Station Z15582 (34°22'48"S 179°39'36"E) 10 m,
303 2002; NIWA 101002 – North Cape, New Zealand, Station Z15758 (34°23'60"S
304 173°01'48"E) 3 – 21 m, 1999.

305 *Hamigera strongylata* Burton, 1934 NHMUK 1930.8.13.80.a – Great Barrier Reefs,
306 Australia (2 slides, holotype).

307 *Hamigera dendyi* Shaw, 1927 NHMUK 1925.11.1.731 – Tasmania, Australia
308 (holotype, as *Hamigera stillopora*); NHMUK 1925.11.1.731 –Tasmania, Australia (5
309 slides, holotype, as *Hamigera stillopora*).

310 *Lissodendoryx* spp. NIWA 62179, Kahuwhera Bay, Bay of Islands, New Zealand,
311 Station KWB_Feb (35°15'45"S 174°10'54"E), 5.5 m depth, 2010; NIWA 51226,
312 Kahuwhera Bay, Bay of Islands, New Zealand, Station Z9681 (34°18'54"S
313 172°49'05"E), 63 m depth, 1999; NIWA 101904, Kahuwhera Bay, Bay of Islands,
314 New Zealand, Station Z9681 (34°18'54"S 172°49'05"E), 5.5 m depth, 1999.

315 *Crella incrustans* (Carter, 1885) NIWA 101066, Evans Bay, Wellington, New
316 Zealand, Station Z9681 (41°18'36"S 174°48'06"E), 5 – 10 m depth.

317

318 Description:

319 Shape:

320 Thick encrusting clathrate sponge, with ca. 1 mm in high in the mesh's connecting
321 tissue and covering an area of ca. 1cm². The ectosome is not easily torn apart from the
322 choanosome but firmly attached to it. Color creamy, in alcohol.

323

324 Skeleton (Fig. 5B):

325 Loose plumose choanosomal skeleton, made of strongyles and styloids in
326 paucispiculate tracts. These tracts go in parallel one to another, sometimes splitting
327 here and there without a clear discernible pattern. The ectosomal skeleton consists of
328 tangential tracts of strongyles. The connecting tissue between the clathrate mass is
329 devoid of spicules. Arcuate isochelae occur in high proportion, mostly concentrating
330 along the tracts, yet they can also be found scattered through the choanosome and
331 ectosome.

332

333 Spicule complement:

334 Strongyles, styloids, and isochelae.

335

336 Strongyles (Fig. 4B): Straight, greatly vary in size (Fig. 4B). Nevertheless, no clear
337 categories can be distinguished, nor a clear position in the skeleton allows to discern
338 them, as they occur altogether in the paucispiculate tracts.

339 Size range: 461.8 – 593.3 ± 67.1 – 666 x 8.9 – 11 ± 1.3 – 13.3 µm

340

341 Styloids (Fig. 4A): Smooth, slightly bent, with asymmetrical blunt ends (Fig. 4A; 4C;
342 4D), resulting in-between a style and a strongyle in shape; the head might sometimes
343 present poly- or tyloid processes (Fig. 4D).

344 Size range: $435.1 - 562.3 \pm 83.6 - 900 \times 7.2 - 8.88 \pm 1.7 - 11 \mu\text{m}$

345

346 Isochelae (Fig. 4E; 4a'): Arcuate isochelae, curved but elongate shaft and slightly
347 acerate alae. The fimbriae are greatly reduced (4f), only being observable through
348 SEM microscopy. Malformed or development stages with reduced alae might also be
349 observed (Fig. 4E). Highly abundant.

350 Size range: $57.8 - 75 \pm 8 - 89 \mu\text{m}$

351

352 Geographical and bathymetrical distribution:

353 The species is only known from its type locality in the Clementsville Seamount (Fig.
354 2), located at the Macquarie Ridge, south of New Zealand, at a 1070–1121 m depth,
355 occurring associated with Cold Water Corals.

356

357 Etymology:

358 The species *kellyae* is devoted to Dr. Kelly, in recognition of her invaluable
359 contribution to the knowledge of New Zealand sponge fauna.

360

361 Remarks:

362 From all *Hamigera* species known to date, four of them occur within Australian and
363 New Zealand waters, them being *Hamigera dendyi* Shaw, 1927 (Tasmania),
364 *Hamigera strongylata* Burton, 1934 (Great Barrier Reef, Australia) and *Hamigera*
365 *macrostrongyla* Bergquist & Fromont, 1988 and *Hamigera tarangaensis* Bergquist &
366 Fromont, 1988 (New Zealand). However, all the mentioned species occur at shallow
367 depths (Roberts & Davis 1996; Bergquist & Fromont, 1988), and only *H. strongylata*
368 occurs frequently associated with coral reefs. Conversely, *Hamigera kellyae* sp. nov.
369 occurs below 1000 m depth, in association with CWC. As for its spicule complement,
370 *Hamigera kellyae* sp. nov. has styloids or style-like spicules, as the other Pacific
371 species, and shows considerably bigger spicules, almost duplicating in size those of
372 all other representatives of the genus, (Table 1). Apart from the clear differences in
373 spicule size, the species differs from *H. tarangaensis* in the lack of polytylotoid
374 strongyles and the possession of chelae with well-formed alae, whereas in *H.*

375 *tarangaensis*, chelae have its alae heavily reduced. The new species differs from *H.*
376 *dendyi* in the lack of true, acerate styles and from *H. strongylata* and *H.*
377 *macrostrongyla* in the strongyle width and the possession of considerably larger
378 styloid spicules. Outside from the Australian-New Zealand area, there is another
379 southern hemisphere species from Chile, *Hamigera cleistochela* Bertolino, Costa &
380 Pansini, 2019, yet this species possesses unique, modified chelae, and its megascleres
381 are also considerably smaller in size than those observed in *Hamigera kellyae*. sp.
382 nov.

383 The unique external morphology of *Hamigera kellyae* sp. nov., with a smooth
384 megascleres, clathrate body and the lack of areolate porefields, makes its genus
385 assignment somewhat challenging. Said combination of smooth choanosomal
386 megascleres and arcuate isochelae are shared characteristic with the genus
387 *Lissodendoryx* (family Coelosphaeridae), a genus with a rather complicated
388 taxonomical history (Bergquist & Fromont, 1988; van Soest, 2002a; Tompkins et al.,
389 2017; Ott et al., 2019). Currently, Coelosphaeridae is defined as never presenting
390 areolate porefields (van Soest, 2002a), which would place our species closer to
391 *Lissodendoryx* than to *Hamigera*, as such porefields are lacking in *H. kellyae* sp. nov.
392 but present in most *Hamigera* (Bergquist & Fromont, 1988). In this sense, porefields
393 had been used as a reliable character to distinguish Hymedesmiidae and Crellidae
394 from other Poecilosclerida (van Soest, 2002b), which would exclude the present
395 material from Hymedesmiidae. Nevertheless, while current phylogenetic analyses
396 support the monophyly of pore-boring species in a single clade, they also cluster
397 together with several non- pore-bearing species (Morrow et al., 2013; Redmond et al.,
398 2013; Ríos et al., 2020). As so, while the absence of porefields would not support the
399 inclusion of the presence species in *Hamigera*, this character alone cannot be used for
400 its exclusion.

401 Looking into the spicular complement, only the subgenus *Lissodendoryx*
402 (*Lissodendoryx*) allocates species with smooth choanosomal megascleres, in addition
403 to ectosomal tylotornotes and arcuate isochelae and sigmas, which may be absent (van
404 Soest, 2002a). From all the currently 69 accepted *Lissodendoryx* (*L.*) species (van
405 Soest et al., 2020), only 7 species are said to lack sigmas and possess smooth
406 choanosomal styles (Ott et al., 2019). After reviewing their original descriptions, *L.*
407 (*L.*) *kyma* de Laubenfels, 1930, *L. (L.) papillosa* Koltun 1958 and *L. (L.) tubicola*
408 Burton, 1959 all are said to possess slightly acanthose styles and/or tylotornotes (de

409 Laubenfels, 1932; Koltun, 1959; Burton 1959), leaving *L. (L.) simplex* Topsent, 1904,
410 *L. (L.) stipitata* (Arnsen, 1903), *L. (L.) ciocalyptoides* Burton, 1959 and *L. (L.)*
411 *flabellata* Burton 1929 as the only true *Lissodendoryx* with smooth styles. From this
412 last four, *L. (L.) simplex* and *L. (L.) ciocalyptoides* are ill-described species, based
413 upon fragmentary material (Topsent, 1904; Burton, 1959), whereas *L. (L.) stipitata*
414 and *L. (L.) flabellata* correspond to stipitate-flabellate sponges, all possessing smooth
415 choanosomal styles, ectosomal tornotes and arcuate chelae (Burton, 1929; Tompkins
416 et al., 2017), the later modified into chleistocheleae in *L. (L.) flabellata* (Burton, 1929).
417 While these 3 species could be arguably close to Hymedesmiidae, *H. kellyae* sp. nov.
418 differs in the possession of strongyles as ectosomal megascleres, as opposed to
419 tornotes. While tornotes and tylotes might be common in some other Hymedesmiidae
420 as ectosomal megascleres (van Soest, 2002b), all *Hamigera* species known to date
421 possess exclusively smooth ectosomal strongyles (Bergquist & Fromont, 1988; Uriz
422 et al., 2017). In contrast, *Lissodendoryx* is characterized by the possession of tylote or
423 tornote ectosomal spicules (Fernandez et al., 2016; Ott et al., 2019). Additionally,
424 *Lissodendoryx* exhibits a clear distinction between ectosomal and choanosomal
425 spicules, (van Soest, 2002a), whereas several Pacific *Hamigera* possess strongyles as
426 ectosomal en choanosomal megascleres, as it happens in *H. kellyae* sp. nov. (Burton,
427 1934; Bergquist & Fromont, 1988). Finally, *Lissodendoryx* is usually defined as
428 possessing a reticulate choanosomal skeleton (van Soest, 2002a), with *Hamigera*
429 possessing a plumose one (van Soest, 2002b). In this sense, it is noteworthy noticing
430 that upon reexamination of samples from most *Hamigera* species, Mediterranean
431 representatives possess plumose tracts of strongyles with echinating styles, whereas
432 all Pacific representatives of the genus lack echinating spicules, incorporating the
433 styles as part of the tracts, as it is the case in *H. kellyae* sp. nov.

434 In conclusion, the new species differs from *Hamigera* in terms of external
435 appearance, as no areolate porefields could be identified on the holotype, yet its
436 spicular complement and skeletal arrangement fits well within the genus, especially
437 when compared with other Pacific species. Nevertheless, the species remains close to
438 *Lissodendoryx*, especially regarding its external morphology. Nevertheless,
439 *Lissodendoryx* is a poorly resolved polyphyletic genus (Morrow et al., 2013;
440 Redmond et al., 2013; Fernandez et al., 2016; Ríos et al., 2020), and it would be
441 unwise to add another atypical species to it, yet it is also possible that once further

442 material for the species becomes available, *Hamigera kellyae* sp. nov. would
443 ultimately be relocated to another genus.

444

445 4. Discussion

446 4.1 Poecilosclerida on antipodal CWC reefs

447 Representatives of the family Hymedesmiidae (Demospongiae: Poecilosclerida) have
448 been reported to be one of the main components of the sponge fauna living in
449 association with CWC (Goodwin et al., 2011), yet not a single *Hamigera* species had
450 been reported so far associated with CWC. In this regard, both the Catalan and New
451 Zealand CWC communities represented suitable areas for the discovery of new deep-
452 sea *Hamigera* species, as CWC sponge fauna in both zones had been poorly studied
453 (Kelly et al., 2009; Rueda et al., 2019) and present shallow-water representatives of
454 the genus.

455 Hymedesmiids, as with many other sponge taxa, generally present an encrusting
456 morphology, which paired with the intrinsic scarcity of material associated with deep-
457 sea sampling (Reveillaud et al., 2011), might make classification at a genus level even
458 tentative in some cases (Vacelet, 1969). In addition, in highly diverse genera, such as
459 *Hymedesmia* or *Phorbas*, species are mostly told apart from their congeneric ones by
460 small differences in spicule's shape or size, which has likely resulted in
461 misidentifications and the adscription of samples to their closest available name
462 (Goodwin & Picton, 2009; Goodwin et al., 2011). This might be the case for the
463 occasional deep-sea records of common littoral species (Table 2), such as *Phorbas*
464 *fictitius* or *Hymedesmia peachi* (Uriz & Rosell, 1990), yet it seems it is not
465 uncommon for deep-sea species to also be found in shallower environments
466 (Bertolino et al., 2019). Comparing the Poecilosclerida fauna known from both the
467 Mediterranean and New Zealand CWC, the later is considerably less known, with just
468 five species (Table 2). In this sense, the New Zealand sponge fauna has been
469 historically underexplored compared to other areas of the world (Kelly et al., 2009),
470 whereas the Mediterranean possesses as one of the most explored areas (van Soest et al.,
471 2012). As so, one possible explanation for such disparity between regions could be a
472 difference in exploration effort between areas. Nevertheless, both CWC in the
473 Mediterranean and New Zealand have been intensely studied during these past years

474 (see Orejas & Jiménez, 2019 for the Mediterranean and Tracey et al., 2011 for New
475 Zealand), which would weaken such idea.

476 On the other hand, in the Mediterranean region several articles have been published
477 dealing exclusively with CWC sponge fauna (Longo et al., 2005; Calcinai et al., 2013;
478 Bertolino et al., 2019), whereas in in New Zealand waters most taxonomic articles
479 have dealt with just a few specific species each (Vacelet et al., 2009; Kelly & Vacelet,
480 2011; Sim-Smith & Kelly, 2011; Kelly et al., 2015; this work), implying said
481 differences might arise from the different research approach between both areas.
482 Furthermore, contemporary New Zealand authors have mostly focused on other
483 Porifera groups such as horny sponges (Bergquist, 1961; 1980; 1996; Cook &
484 Bergquist, 1996; 1998; 1999; 2000; 2001 Bergquist et al., 1998; 1999) or lithistids
485 (Kelly-Borges & Pomponi, 1994; Kelly-Borges et al., 1994; Kelly, 2003; 2007; Kelly
486 et al., 2007), with most information regarding Poecilosclerida coming from just two
487 publications in an almost 100 year time span (Dendy 1924; Bergquist & Fromont,
488 1988). Moreover, even within Poecilosclerida the research effort has been unequal
489 between groups, with carnivorous sponge (Vacelet et al., 2009; Vacelet & Kelly,
490 2008; Kelly & Vacelet, 2011; Hestetun et al., 2016) and 'latrunculids' *sensu lato*
491 (Miller et al., 2001; Alvarez et al., 2002; Sim-Smith & Kelly, 2011; Kelly et al., 2016)
492 having received almost all attention when compared to other Poecilosclerida in recent
493 years. As so, New Zealand waters, and more specifically its CWC reefs should be
494 expected to harbor a way more diverse poecilosclerid fauna, making it a proper area
495 for the discovery of new poecilosclerid species (Kelly et al., 2009).

496 Finally, while the Mediterranean poecilosclerid sponge fauna is considerably better
497 known than its New Zealand counterpart, it still trails behind that of the Atlantic
498 CWC reefs (van Soest et al., 2007; van Soest & De Voogd, 2015), which considering
499 the strong relationship between the sponge fauna in both areas (Maldonado & Uriz,
500 1995; Xavier & van Soest, 2012), it could also be expected that several of this North
501 Atlantic species are to be found in Mediterranean CWC reefs.

502

503 4.2 Palogeography of *Hamigera*

504 The discovery of these new *Hamigera* species in the Mediterranean and New Zealand
505 waters poses a very similar situation than the one observed with other sponge genera,
506 such as *Discorhabdella* (Boury-Esnault et al., 1992) or *Vetulina* (Pisera et al., 2018).

507 All the mentioned genera are present in both the Atlanto-Mediterranean and the Indo-
508 Pacific areas, yet some of the Mediterranean species show higher affinity with Indo-
509 Pacific species rather than with Atlantic ones, as reported for *Discorhabdella hindei*
510 Boury-Esnault, Pansini & Uriz, 1992 (Boury-Esnault et al., 1992). It has been
511 hypothesised that these biogeographic relationships derive from a common Tethyan
512 ancestry (Ekman, 1953) that underwent speciation after the closure of the connection
513 with the Indo-Pacific Ocean during the Early Miocene period, 20 million years ago
514 (Kennett et al 1985). The discovery of these genera in deep-sea waters of the
515 Mediterranean reinforces the hypothesis that the Tethyan component of deep
516 Mediterranean fauna is more important than previously reported (Pérès, 1985).
517 Indeed, it has been suggested that during the Messinian Salinity crisis the
518 Mediterranean did not completely dry leaving vast areas of the basin flooded
519 preserving marine conditions (Hsü, 1973). In this regard, several studies support the
520 hypothesis of the existence of “refuge areas” in the Mediterranean during the
521 Messinian salinity crisis, either as brackish or hypersaline areas (Xavier & van Soest,
522 2012) or even with almost normal salinity values (Por, 1989), which could have led to
523 the confinement and survival of several marine species in those areas. Further
524 strengthening this view, during the second half of the XXth century the study of fossil
525 record confirmed the presence of living ostracodes, scleractinians, bryozoans and
526 sponge species of Tethyan origin in the Mediterranean (Vacelet, 1967; Benson et al.,
527 1976). In this line, other researches have recorded the presence of several species with
528 a marked Tethyan affinity, such as copepods occurring in anchihaline caves (Jaume &
529 Boxshall 1996; Kršinić, 2017) or hydromedusae dwelling in Mediterranean canyons
530 (Gili et al., 1998; 2000). But, perhaps, the most emblematic Tethyan relict species is
531 the seagrass *Posidonia oceanica* (Aires et al., 2011), considered a survivor of the
532 Messinian salinity crisis even if no fossil evidence has been found yet (Aguirre et al.,
533 2006). Focusing on deep Mediterranean environments, several sessile taxa have been
534 identified as Tethyan relicts, such as the soft coral *Chironophthya mediterranea*
535 López-González, Grinyó & Gili, 2014 or several sponge species (Vacelet et al., 1989;
536 Maldonado & Uriz, 1995; López-González et al 2014), reinforcing the hypothesis of
537 the Tethyan component of deep Mediterranean fauna.

538 Finally, most Mediterranean Tethyan relicts have been so far found in cave
539 environments (See Manconi et al., 2009), with just a handful being signalled from
540 deep-sea environments (Boury-Esnault et al., 1992; López-González et al 2014).

541 Nonetheless, and due to their unique environmental setting (Harmelin, 1997), caves
542 have been demonstrated to harbour once thought to be deep-sea exclusive species
543 (Vacelet et al., 1994), with and ever-increasing evidence of an existing connection
544 between cave and deep-water fauna (Harmelin & Vacelet, 1997; Gerovasileiou &
545 Voultsiadou, 2012; Grenier et al., 2018; Santín et al., 2019). As so, considering the
546 substantial research increase that is currently taking place in deep-sea Mediterranean
547 environments, it is likely that this will lead to the discovery of additional Tethyan
548 relicts in Mediterranean waters, confirming that the percentage of Mediterranean
549 species with Tethyan ancestry is more important than is currently known today.

550

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578

579 6. References

580 Aguirre J., Pérez-Muñoz A. B., & Sánchez-Almazo I. (2006). Benthic
581 foraminifera assemblages on the lower Pliocene deposits of the Almería-Níjar
582 Basin (SE Spain). *Revista Española de Micropaleontología*, 38(2–3), 411–428.

583 Ahyong, S. T., Schnabeland K. E., & Baba, K. (2015). Southern high latitude
584 squat lobsters: Galatheoidea and Chirostyloidea from Macquarie Ridge with
585 description of a new species of *Uroptychus*. *Records of the Australian Museum*
586 67(4), 109–128.

587 Aires, T., Marbà, N., Cunha, R. L., Kendrick, G. A., Walker, D. I., Serrão, E. A.,
588 ... & Arnaud-Haond, S. (2011). Evolutionary history of the seagrass genus
589 *Posidonia*. *Marine Ecology Progress Series*, 421, 117–130.

590 Alvarez, B., Bergquist, P. R., & Battershill, C. N. (2002). Taxonomic revision of
591 the genus *Latrunculia* Du Bocage (Porifera: Demospongiae: Latrunculiidae) in
592 New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 36(1),
593 151–184.

594 Baco, A. R. (2007). Exploration for deep-sea corals on North Pacific seamounts
595 and islands. *Oceanography*, 20(4), 108–117.

596 Benson, R. H. (1976). Changes in the Ostracodes of the Mediterranean with the
597 Messinian salinity crisis. *Paleogeography, Paleoclimatology, Paleoecology*, 20(1–
598 2), 147–170.

599 Bergquist, P. R. (1961). Biological Results of the Chatham Islands 1954
600 Expedition. Part 5. The Keratosa (Porifera) collected by the Chatham Islands 1954
601 Expedition. *New Zealand Oceanographic Institute Memoir* 13, 207–219.

602 Bergquist, P. R. (1980). A revision of the supraspecific classification of the orders
603 Dictyoceratida, Dendroceratida, and Verongida (class Demospongiae). *New*
604 *Zealand Journal of Zoology* 7, 443–503.

- 605 Bergquist, P. R. (1996). The marine fauna of New Zealand: Porifera,
606 Demospongiae, Part 5. Dendroceratida and Halisarcida. New Zealand
607 Oceanographic Institute Memoir 107, 1–53.
- 608 Bergquist, P. R., & Fromont, P. J. (1988). The Marine Fauna of New Zealand:
609 Porifera, Demospongiae, Part 4 Poecilosclerida. New Zealand Oceanographic
610 Institute Memoir, 96, 1–197.
- 611 Bergquist, P. R., Walsh, D., & Gray, R. D. (1998). Relationships within and
612 between orders of Demospongiae that lack a mineral skeleton. In: Watanabe, Y.;
613 Fusetani, N. (Eds.), *Sponge Sciences: Multidisciplinary Perspectives* (pp. 31–40).
614 Springer–Verlag, Tokyo.
- 615 Bergquist, P. R., Sorokin, S., & Karuso, P. (1999). Pushing the boundaries: a new
616 genus and species of Dictyoceratida. *Memoirs of the Queensland Museum* 44, 57–
617 62.
- 618 Bertolino, M., Costa, G., Reboa, A., Bavestrello, G., Pansini, M., Betti, F., Bo, &
619 M., Daneri, G. (2019a). The sponge fauna of the Seno Magdalena and Puyuhuapi
620 Fjord (Chile), with a description of two new species. *Zootaxa*, 4623(2), 306–320.
- 621 Bertolino, M., Ricci, S., Canese, S., Cau, A., Bavestrello, G., Pansini, M., & Bo,
622 M. (2019b). Diversity of the sponge fauna associated with white coral banks from
623 two Sardinian canyons (Mediterranean Sea). *Journal of the Marine Biological*
624 *Association of the United Kingdom*, 99(8), 1735–1751.
- 625 Boury-Esnault, N., Pansini, M., & Uriz, M. J. (1992). A new *Discorhabdella*
626 (Porifera, Demospongiae), a new Tethyan relict of pre-Messinian biota. *Journal of*
627 *Natural History*, 26, 1–7.
- 628 Beuck, L., Vertino, A., Stepina, E., Karolczak, M., & Pfannkuche, O. (2007).
629 Skeletal response of *Lophelia pertusa* (Scleractinia) to bioeroding sponge
630 infestation visualised with micro-computed tomography. *Facies*, 53(2), 157–176.
- 631 Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. A., Priede, I. G.,
632 Buhl-Mortensen, P., Gheerardyn, H., King, N. J., & Raes, M. (2010). Biological
633 structures as a source of habitat heterogeneity and biodiversity on the deep ocean
634 margins. *Marine Ecology*, 31(1), 21–50.

- 635 Burton, M. (1929). Porifera. Part II. Antarctic sponges. British Antarctic ('Terra
636 Nova') Expedition, 1910. Natural History Report, London, British Museum
637 (Natural History). *Zoology*, 6 (4), 393–458.
- 638 Burton, M. (1934). Sponges. Scientific Reports of the Great Barrier Reef
639 Expedition 1928–29, 4(14), 513–621.
- 640 Burton, M. (1959). Sponges. Scientific Reports. John Murray Expedition 1933–
641 34, 10(5), 151–281.
- 642 Calcinai, B., Moratti, V., Martinelli, M., Bavestrello, G., & Taviani, M. (2013).
643 Uncommon sponges associated with deep coral bank and maerl habitats in the
644 Strait of Sicily (Mediterranean Sea). *Italian Journal of Zoology*, 80(3), 412–423.
- 645 Corbera, G., Lo Iacono, C., Gràcia, E., Grinyó, J., Pierdomenico, M., Huvenne, V.
646 A., Aguilar, R., & Gili, J. M. (2019). Ecological characterisation of a
647 Mediterranean cold-water coral reef: Cabliers Coral Mound Province (Alboran
648 Sea, western Mediterranean). *Progress in Oceanography*, 175, 245–262.
- 649 Cook, S. de C., & Bergquist, P. R. (1996). New species of dictyoceratid sponges
650 (Porifera: Demospongiae: Dictyoceratida) from New Zealand. *New Zealand
651 Journal of Marine and Freshwater Research* 30, 19–34.
- 652 Cook, S. de C., & Bergquist, P. R. (1998). Revision of the genus *Psammocinia*
653 (Porifera: Demospongiae: Dictyoceratida), with six new species from New
654 Zealand. *New Zealand Journal of Marine and Freshwater Research* 32: 399–426.
- 655 Cook, S. de C., & Bergquist, P. R. (1999). New species of dictyoceratid sponges
656 from New Zealand: Genus *Ircinia* (Porifera: Demospongiae: Dictyoceratida). *New
657 Zealand Journal of Marine and Freshwater Research* 33: 545–563.
- 658 Cook, S. de C., & Bergquist, P. R. (2000). Two new genera and five new species
659 of the '*Cacospongia*' group. *Zoosystema* 22: 383–400
- 660 Cook, S. de C., & Bergquist, P. R. (2001). New species of *Spongia* (Porifera:
661 Demospongiae: Dictyoceratida) from New Zealand, and a proposed subgeneric
662 structure. *New Zealand Journal of Marine and Freshwater Research* 35, 33–38.
- 663 Cristobo, F. J. Urgorri, V., Solórzano, M. R., & Ríos, P. (1993). Métodos de
664 recogida, estudio y conservación de las colecciones de poríferos. In: Thomas B.,
665 Palacios F., & Martínez-López, M. C. (coord.) Simposio Internacional sobre

- 666 Preservación y Conservación de Colecciones de Historia Natural
667 (Comunicaciones sobre la situación, preservación y conservación de colecciones
668 de Historia Natural), 2, 277–287. ISBN 84-7483-908-4.
- 669 Dendy, A. (1924). Porifera. Part I. Non-Antarctic sponges. Natural History
670 Report. British Antarctic (Terra Nova) Expedition, 1910 (Zoology). 6(3), 269–
671 392.
- 672 Ekman S. (1953). Zoogeography of the Sea. London: Sidgwick and Jackson.
- 673 Etnoyer, P., & Morgan, L. E. (2005). Habitat-forming deep-sea corals in the
674 Northeast Pacific Ocean. In: Freiwald, A. & Roberts, J. M. (Eds.). *Cold-Water*
675 *Corals and Ecosystems* (pp. 331–343). Springer, Berlin, Heidelberg.
- 676 FAO (2009). International Guidelines for the Management of Deep-sea Fisheries
677 in the High Seas. Rome, Italy, 73pp.
- 678 Fernandez, J. C., Cárdenas, C. A., Bravo, A., Lôbo-Hajdu, G., Willenz, P., &
679 Hajdu, E. (2016). *Lissodendoryx (Ectyodoryx)* Lundbeck, 1909 (Coelosphaeridae,
680 Poecilosclerida, Demospongiae) from Southern Chile: new species and a
681 discussion of morphologic characters in the subgenus. *Zootaxa*, 4092(1), 69–89.
- 682 Freiwald, A., & Wilson, J. B. (1998). Taphonomy of modern deep, cold -
683 temperate water coral reefs. *Historical biology*, 13(1), 37–52.
- 684 Freiwald, A., & Roberts, M. (2006) Cold-Water Corals and Ecosystems. *Springer*,
685 *Berlin, Heidelberg*. Erlangen Earth Conference Series, 3, 1–1243.
- 686 Gerovasileiou, V., & Voultsiadou, E. (2012). Marine caves of the Mediterranean
687 Sea: a sponge biodiversity reservoir within a biodiversity hotspot. *PLoS One* 7
688 (7), e39873.
- 689 Gili J. M., Bouillon J., Pagès F., Palanques A., Puig P., & Heussner S. (1998).
690 Origin and biogeography of the deep-water Mediterranean Hydromedusae
691 including the description of two new species collected in submarine canyons of
692 Northwestern Mediterranean. *Scientia Marina*, 62, 113–134.
- 693 Gili, J. M., Pagès, F., Bouillon, J., Palanques, A., Puig, P., Heussner, S., Calafat,
694 A., Canals, M., & Monaco, A. (2000). A multidisciplinary approach to the
695 understanding of hydromedusan populations inhabiting Mediterranean submarine

- 696 canyons. *Deep Sea Research Part I: Oceanographic Research Papers*, 47(8), 1513–
697 1533.
- 698 Goodwin C. E., & Picton B. E. (2009). Demosponges of the genus *Hymedesmia*
699 (Poecilosclerida: Hymedesmidae) from Rathlin Island, Northern Ireland, with a
700 description of six new species. *Zoological Journal of the Linnean Society*, 156,
701 896–912.
- 702 Goodwin, C. E., Picton, B. E., & van Soest, R. W. M. (2011). *Hymedesmia*
703 (Porifera: Demospongiae: Poecilosclerida) from Irish and Scottish cold-water
704 coral reefs, with a description of five new species. *Journal of the Marine*
705 *Biological Association of the United Kingdom*, 91(5), 979–997.
- 706 Gray, J. E. (1867). Notes on the Arrangement of Sponges, with the Descriptions
707 of some New Genera. *Proceedings of the Zoological Society of London*. 1867(2):
708 492–558.
- 709 Grenier, M., Ruiz, C., Fourt, M., Santonja, M., Dubois, M., Klautau, M., ... &
710 Perez, T. (2018). Sponge inventory of the French Mediterranean waters, with an
711 emphasis on cave-dwelling species. *Zootaxa*, 4466(1), 205–228.
- 712 Harmelin, J. G. (1997). Diversity of bryozoans in a Mediterranean sublittoral cave
713 with bathyal-like conditions: role of dispersal processes and local factors. *Marine*
714 *Ecology Progress Series*, 153, 139–152.
- 715 Harmelin, J. G., & Vacelet, J. (1997). Clues to deep-sea biodiversity in a
716 nearshore cave. *Vie Milieu*, 47(4), 351–354.
- 717 Henry, L. A. & Roberts, M. (2017). Global Biodiversity in Cold-Water Coral Reef
718 Ecosystems. In: Rossi, S., Bramanti, L., Gori, A., & Orejas, C. (Eds.) *Marine*
719 *Animal Forests: The Ecology of Benthic Biodiversity Hotspots*, Springer Nature,
720 Cham. Vol I, 235–256. ISBN 978-3-319-21011-7
- 721 Hestetun, J. T., Vacelet, J., Boury-Esnault, N., Borchiellini, C., Kelly, M., Ríos,
722 P., ... & Rapp, H. T. (2016). The systematics of carnivorous sponges. *Molecular*
723 *phylogenetics and evolution*, 94, 327–345.
- 724 Hsü K. J. (1973). The Desiccated Deep-Basin model for the Messinian events. In:
725 Drooger, C. W. (Ed.), *Messinian Events in the Mediterranean*. North-Holland,
726 Amsterdam, 60–67.

- 727 Jaume D., & Boxshall G. A. (1996). The persistence of an ancient marine fauna in
728 Mediterranean waters: new evidence from misophrioid copepods living in
729 anchihaline caves. *Journal of Natural History*, 30, 1583–1595.
- 730 Jensen, A., & Frederiksen, R. (1992). The fauna associated with the bank-forming
731 deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. *Sarsia*,
732 77(1), 53–69.
- 733 Kelly, M. (2003). Revision of the sponge genus *Pleroma* Sollas (Lithistida:
734 Megamorina: Pleromidae) from New Zealand and New Caledonia, and
735 description of a new species. *New Zealand Journal of Marine and Freshwater*
736 *Research* 37, 113–127.
- 737 Kelly, M. (2007). The marine fauna of New Zealand: Porifera: lithistid
738 Demospongiae (rock sponges). NIWA Biodiversity Memoir 121, 1–100.
- 739 Kelly, M., & Vacelet, J. (2011). Three new remarkable carnivorous sponges
740 (Porifera, Cladorhizidae) from deep New Zealand and Australian (Macquarie
741 Island) waters. *Zootaxa*, 2976(1), 55–68.
- 742 Kelly, M., & Cárdenas, P. (2016). An unprecedented new genus and family of
743 Tetractinellida (Porifera, Demospongiae) from New Zealand's Colville Ridge,
744 with a new type of mitochondrial group I intron. *Zoological Journal of the*
745 *Linnean Society*, 177(2), 335–352.
- 746 Kelly, M., & Rowden, A. A. (2019). New sponge species from hydrothermal vent
747 and cold seep sites off New Zealand. *Zootaxa*, 4576(3), 401–438.
- 748 Kelly, M., Ellwood, M., Tubbs, L., & Buckeridge, J. (2007). The ‘lithistid’
749 Demospongiae in New Zealand waters: species composition and distribution. In:
750 Custódio, M. R., Lôbo-Hajdu, G., Hajdu, E., & Muricy, G. (Eds.), *Porifera*
751 *Research – Biodiversity, Innovation and Sustainability*. Museu Nacional, Rio de
752 Janeiro. Série Livros 28, 393–404.
- 753 Kelly, M., Edwards, A. R., Wilkinson, M. R., Alvarez, B., Cook, S. de C.,
754 Bergquist, P. R., Buckeridge, St J., Campbell, H. J., Reiswig, H. M., Valentine,
755 C., & Vacelet, J. (2009). Phylum Porifera: sponges. In: Gordon, D. P. (Ed.)
756 (2009). *New Zealand inventory of biodiversity: 1. Kingdom Animalia: Radiata,*
757 *Lophotrochozoa, Deuterostomia*, 23–46.

- 758 Kelly, M., Erpenbeck, D., Morrow, C., & Van Soest, R. W. M. (2015). First
759 record of a living species of the genus *Janulum* (Class Demospongiae) in the
760 Southern Hemisphere. *Zootaxa*, 3980(2), 255–266.
- 761 Kelly, M., Sim-Smith, C., Stone, R., Samaai, T., Reiswig, H., & Austin, W.
762 (2016). New taxa and arrangements within the family Latrunculiidae
763 (Demospongiae, Poecilosclerida). *Zootaxa*, 4121(1), 1–48.
- 764 Kelly-Borges, M., & Pomponi, S. A. (1994). Phylogeny and classification of
765 lithistid sponges (Porifera: Demospongiae): an assessment using ribosomal DNA
766 sequence comparisons. *Molecular Marine Biology and Biotechnology* 3, 87–103.
- 767 Kelly-Borges, M., Robinson, E. V., Gunasekera, S. P., Gunasekera, M., Gulavita,
768 N. K., & Pomponi, S. A. (1994). Species differentiation in the marine sponge
769 genus *Discodermia* (Demospongiae: Lithistida): the utility of ethanol extract
770 profiles as species-specific chemotaxonomic markers. *Biochemical systematics
771 and ecology*, 22(4), 353–365.
- 772 Kennett J. P., Keller G., & Srinivasan M. S. (1985). Miocene planktonic
773 foraminiferal biogeography and pale-oceanographic development of the Indo-
774 Pacific region. In: Kennett J. P. (Ed.), *The Miocene Ocean: Paleoceanography
775 and biogeography*. Boulder, Colorado Geologic Society of America Memoir,
776 197–236.
- 777 Koltun, V.M. (1959 [1971]). Cornosiliceous sponges of the northern and far
778 eastern seas of the U.S.S.R. *Opredeliteli po faune SSR, izdavaemye
779 Zoologicheskim muzeem Akademii nauk*, 67, 1–236. [Translated from Russian to
780 English by the Fisheries Research Board of Canada, Translation Series, 1842, 1–
781 442].
- 782 Kršinić, F. (2017). A new species of *Speleophriopsis* (Copepoda: Misophrioida)
783 from an anchialine cave in the Adriatic Sea, Mediterranean. *Marine Biodiversity*,
784 47(3), 941–947.
- 785 Laubenfels, M.W. de. (1932). The marine and fresh-water sponges of California.
786 *Proceedings of the United States National Museum*. 81(2927), 1–140.

- 787 Longo, C., Mastrototaro, F., & Corriero, G. (2005). Sponge fauna associated with
788 a Mediterranean deep-sea coral bank. *Journal of the Marine Biological*
789 *Association of the United Kingdom*, 85(6), 1341–1352.
- 790 Lopes, D. A., & Hajdu, E. (2014). Carnivorous sponges from deep-sea coral
791 mounds in the Campos Basin (SW Atlantic), with the description of six new
792 species (Cladorhizidae, Poecilosclerida, Demospongiae). *Marine Biology*
793 *Research*, 10(4), 329–356.
- 794 Lopes D. A., Hajdu E., & Reiswig H. M. (2005). Redescription of two
795 Hexactinosida (Porifera, Hexactinellida) from the southwestern Atlantic, collected
796 by Programme REVIZEE. *Zootaxa* 1066:43–56.
- 797 López-González, P. J., Grinyó J. & Gili J. M. (2014). *Chironephthya*
798 *mediterranea* n. sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the
799 genus discovered in the Mediterranean Sea. *Marine Biodiversity*, 45, 667–688.
- 800 Maldonado, M., & Uriz, M. J. (1995). Biotic affinities in a transitional zone
801 between the Atlantic and the Mediterranean: a biogeographical approach based on
802 sponges. *Journal of Biogeography*, 22(1), 89–110.
- 803 Manconi, R., Ledda, F. D., Serusi, A., Corso, G., & Stocchino, G. A. (2009).
804 Sponges of marine caves: Notes on the status of the Mediterranean palaeoendemic
805 *Petrobiona massiliana* (Porifera: Calcarea: Lithonida) with new records from
806 Sardinia. *Italian Journal of Zoology*, 76, 306–315.
- 807 Miller, K., Alvarez, B., Battershill, C., Northcote, P., & Parthasarathy, H. (2001).
808 Genetic, morphological, and chemical divergence in the sponge genus *Latrunculia*
809 (Porifera: Demospongiae) from New Zealand. *Marine Biology*, 139(2), 235–250.
- 810 Miller, K., Williams, A., Rowden, A. A., Knowles, C., & Dunshea, G. (2010).
811 Conflicting estimates of connectivity among deep-sea coral populations. *Marine*
812 *Ecology*, 31, 144–157.
- 813 Miyamoto, M., Kiyota, M., Hayashibara, T., Nonaka, M., Imahara, Y., &
814 Tachikawa, H. (2017). Megafaunal composition of cold-water corals and other
815 deep-sea benthos in the southern Emperor Seamounts area, North Pacific Ocean.
816 *Galaxea, Journal of Coral Reef Studies*, 19(1), 19–30.

- 817 Morrow, C. C., Redmond, N. E., Picton, B. E., Thacker, R. W., Collins, A. G.,
818 Maggs, C. A., Sigwart, J. D., & Allcock, A. L. (2013). Molecular phylogenies
819 support homoplasy of multiple morphological characters used in the taxonomy of
820 Heteroscleromorpha (Porifera: Demospongiae). *Integrative and Comparative*
821 *Biology*, 53(3), 428–446.
- 822 O’ Hara, T. D., Rowden, A. A., & Williams, A. (2008). Cold - water coral
823 habitats on seamounts: do they have a specialist fauna?. *Diversity and*
824 *distributions*, 14(6), 925–934.
- 825 Orejas, C., & Jiménez, C. (2019). An Introduction to the Research on
826 Mediterranean Cold-Water Corals. In: Orejas, C., & Jiménez, C. (Eds.)
827 *Mediterranean Cold-Water Corals: Past, Present and Future* Springer, Cham.
828 *Coral Reefs of the World*, 9, 3–12.
- 829 OSPAR Commission (2008). OSPAR List of Threatened and/or Declining
830 Species and Habitats. Reference number 2008-6.
831 [http://www.ospar.org/documents/dbase/decrecs/agreements/08-](http://www.ospar.org/documents/dbase/decrecs/agreements/08-06e_ospar%20list%20species%20and%20habitats.doc)
832 [06e_ospar%20list%20species%20and%20habitats.doc](http://www.ospar.org/documents/dbase/decrecs/agreements/08-06e_ospar%20list%20species%20and%20habitats.doc).
- 833 OSPAR Commission (2010). Background document for coral gardens.
834 Publication number 486/2010. OSPAR Commission, London.
- 835 Ott, B., Reisinger, H. M., McDaniel, N., & Harbo, R. (2019). New Species of
836 *Lissodendoryx* Topsent, 1892 (Demospongiae, Poecilosclerida, Coelosphaeridae)
837 and *Myxilla* Schmidt, 1862 (Demospongiae, Poecilosclerida, Myxillidae) from the
838 Northeast Pacific. *Zootaxa*. 4700(1), 1–29.
- 839 Pérès J. M. (1985). History of the Mediterranean biota and the colonization of the
840 depths. Western Mediterranean. In: Margalef R. (Ed.) *Key environments*.
841 Pergamon Press, Oxford, 198–232.
- 842 Pisera, A., Łukowiak, M., Fromont, J., & Schuster, A. (2018). First record of the
843 genus *Vetulina* Schmidt, 1879 (Porifera: Demospongiae: Sphaerocladina) from the
844 Indian Ocean with the description of two new species: biogeographic and
845 evolutionary significance. *Marine Biodiversity*, 48(3), 1529–1539.
- 846 Por, F. D. (1989). Postface: The Legacy of Tethys—Or the Guise of a Conclusion.
847 In Por, F. D. (Ed.) *The Legacy of Tethys* Springer, Dordrecht, 165–168.

- 848 Redmond, N. E., Morrow, C. C., Thacker, R. W., Diaz, M. C., Boury-Esnault, N.,
849 Cárdenas, P., ... & Kayal, E. (2013). Phylogeny and systematics of Demospongiae
850 in light of new small-subunit ribosomal DNA (18S) sequences. *Integrative and*
851 *Comparative Biology*, 53(3), 388–415.
- 852 Reveillaud, J., Remerie, T., van Soest, R., Erpenbeck, D., Cárdenas, P., Derycke,
853 S., ... & Vanreusel, A. (2010). Species boundaries and phylogenetic relationships
854 between Atlanto-Mediterranean shallow-water and deep-sea coral associated
855 *Hexadella* species (Porifera, Ianthellidae). *Molecular Phylogenetics and*
856 *Evolution*, 56(1), 104–114.
- 857 Reveillaud, J., van Soest, R., Derycke, S., Picton, B., Rigaux, A., & Vanreusel, A.
858 (2011). Phylogenetic relationships among NE Atlantic *Plocamionida* Topsent
859 (1927)(Porifera, Poecilosclerida): Under-estimated diversity in reef ecosystems.
860 *PLoS One*, 6(2): e16533. doi: 10.1371/journal.pone.0016533
- 861 Ríos, P., Cristobo, J. & Sánchez, F. (2017). Porifera del cañón de la Gavierra
862 (sistemas de cañones de Avilés, mar Cantábrico). Cristobo J., & Ríos, P. (Coord.),
863 *Avances en estudios de biología marina: contribuciones del XVIII SIEBM GIJÓN.*
864 *Temas de Oceanografía*. Instituto Español de Oceanografía, Madrid. Spain. 10:
865 123–133.
- 866 Ríos, P., Riesgo, A., Taboada, S., & Cristobo, J. (2020). A new species of
867 *Isodictya* (Porifera: Poecilosclerida) from the Southern Ocean. *Polar Biology*, 43,
868 523–533.
- 869 Rix, L., De Goeij, J. M., Mueller, C. E., Struck, U., Middelburg, J. J., Van Duyl,
870 F. C., ... & Van Oevelen, D. (2016). Coral mucus fuels the sponge loop in warm-
871 and cold-water coral reef ecosystems. *Scientific Reports*, 6(1), 1–11.
- 872 Roberts, D. E., & Davis, A. R. (1996). Patterns in sponge (Porifera) assemblages
873 on temperate coastal reefs off Sydney, Australia. *Marine and Freshwater*
874 *Research*, 47(7), 897–906.
- 875 Rowden, A. (2008). *Voyage Report—MacRidge 2—TAN0803*. Wellington:
876 National Institute of Water and Atmospheric Research.
- 877 Rueda J. L. Urra, J., Aguilar, R., Angeletti, L., Bo, M., García-Ruiz, C., González-
878 Duarte, M. M., López, E., Madurell T., Maldonado, M., Mateo-Ramírez, A.,

- 879 Megina C., Moreira, J., Moya, F., Ramalho, L. V., Rosso, A., Sitjà, C., & Taviani,
880 M. (2019). Chapter 29: Cold-Water Coral Associated Fauna in the Mediterranean
881 Sea and Adjacent Areas. In: Orejas C., Jiménez C. (Eds.) *Mediterranean Cold-*
882 *Water Corals: Past, Present and Future*, Springer, Cham. Coral Reefs of the
883 World, 9, 295–333.
- 884 Santín, A., Grinyó, J., Ambroso, S., Uriz, M. J., Dominguez-Carrió, C., & Gili, J.
885 M. (2019). Distribution patterns and demographic trends of demosponges at the
886 Menorca Channel (Northwestern Mediterranean Sea). *Progress in Oceanography*,
887 173, 9–25.
- 888 Schroeder, W. W., Brooke, S. D., Olson, J. B., Phaneuf, B., McDonough, J. J., &
889 Etnoyer, P. (2005). Occurrence of deep-water *Lophelia pertusa* and *Madrepora*
890 *oculata* in the Gulf of Mexico. In: Freiwald, A. & Roberts, J. M. (Eds.) *Cold-*
891 *water corals and ecosystems* (pp. 297–307). Springer, Berlin, Heidelberg.
- 892 Shaw, M. E. (1927). On a Collection of Sponges from Maria Island, Tasmania.
893 *Proceedings of the Zoological Society of London*. (2), 419–439.
- 894 Sim-Smith, C., & Kelly, M. (2011). Two new genera in the family
895 Podospongiidae (Demospongiae: Poecilosclerida) with eight new Western Pacific
896 species. *Zootaxa*, 2976(1), 32–54.
- 897 Taviani, M., Angeletti, L., Canese, S., Cannas, R., Cardone, F., Cau, A., ... &
898 Tessarolo, C. (2017). The “Sardinian cold-water coral province” in the context of
899 the Mediterranean coral ecosystems. *Deep Sea Research Part II: Topical Studies*
900 *in Oceanography*, 145, 61–78.
- 901 Tompkins, G., Baker, E., Anstey, L., Walkusz, W., Siferd, T. and Kenchington, E.
902 (2017). Sponges from the 2010-2014 Paamiut Multispecies Trawl Surveys,
903 Eastern Arctic and Subarctic: Class Demospongiae, Subclass Heteroscleromorpha,
904 Order Poecilosclerida, Family Coelosphaeridae, Genera *Forcepia* and
905 *Lissodendoryx*. Canadian Technical Report of Fisheries and Aquatic Sciences,
906 3224, 1–112.
- 907 Topsent, E. (1904). Spongiaires des Açores. Résultats des campagnes
908 scientifiques accomplies par le Prince Albert I. Monaco. 25, 1–280.

- 909 Tracey, D. M., Rowden, A. A., Mackay, K. A., & Compton, T. (2011). Habitat-
910 forming cold-water corals show affinity for seamounts in the New Zealand region.
911 Marine Ecology Progress Series, 430, 1–22.
- 912 Uriz, M. J., & Rosell, D. (1990). Sponges from bathyal depths (1000–1750 m) in
913 the Western Mediterranean Sea. Journal of Natural History, 24(2), 373–391.
- 914 Uriz, M. J., Garate, L., & Agell, G. (2017). Molecular phylogenies confirm the
915 presence of two cryptic *Hemimycale* species in the Mediterranean and reveal the
916 polyphyly of the genera *Crella* and *Hemimycale* (Demospongiae: Poecilosclerida).
917 PeerJ, 5, e2958.
- 918 Vacelet, J. (1967). Descriptions d'éponges Pharétronides actuelles des tunnels
919 obscurs sous-récifaux de Tuléar (Madagascar). Recueil des travaux de la Station
920 marine d'Endoume. Fascicule Hors Série, Supplément, 6, 37–62.
- 921 Vacelet, J. (1969). Eponges de la Roche du Large et de l'étage bathyal de
922 Méditerranée (Récoltes de la soucoupe plongeante Cousteau et dragages).
923 Mémoires du Muséum national d'Histoire Naturelle. (A, Zoologie), 59(2), 145–
924 219.
- 925 Vacelet, J., & Kelly, M. (2008). New species from the deep Pacific suggest that
926 carnivorous sponges date back to the Early Jurassic. Nature Precedings, 1–1.
- 927 Vacelet, J., Boury-Esnault, N., & Zibrowius, H. (1989). Unexpected deep-water
928 records of calcareous sponges (Calcarea). Deep-sea Newsletter, 15, 24–25.
- 929 Vacelet, J., Boury-Esnault, N., Harmelin, J. G. (1994). Hexactinellid Cave, a
930 unique deep-sea habitat in the scuba zone. Deep Sea Research I, 41, 965–973.
- 931 Vacelet, J., Kelly, M., & Schlacher-Hoenlinger, M. (2009). Two new species of
932 *Chondrocladia* (Demospongiae: Cladorhizidae) with a new spicule type from the
933 deep south Pacific, and a discussion of the genus *Meliiderma*. Zootaxa, 2073(1),
934 57–68.
- 935 van Soest, R. W. M. (2002a). Family Coelosphaeridae Dendy, 1922. In: Hooper,
936 J. N. A. & van Soest, R. W. M. (Eds). Systema Porifera, a guide to the
937 classification of sponges. Pp 528–546. Kluwer Academic / Plenum Publishers,
938 New York.

- 939 van Soest, R. W. M. (2002b). Family Hymedesmiidae. In: Hooper, J. N. A. & van
940 Soest, R. W. M. (Eds). *Systema Porifera, a guide to the classification of sponges*.
941 Pp 575–593. Kluwer Academic / Plenum Publishers, New York.
- 942 van Soest, R. W. M., & Beglinger, E. J. (2009). New bioeroding sponges from
943 Mingulay coldwater reefs, north-west Scotland. *Journal of the Marine Biological*
944 *Association of the United Kingdom*, 89(2), 329–335.
- 945 van Soest, R. W. M., & De Voogd, N. J. (2015). Sponge species composition of
946 north-east Atlantic cold-water coral reefs compared in a bathyal to inshore
947 gradient. *Journal of the Marine Biological Association of the United Kingdom*,
948 95(7), 1461–1474.
- 949 van Soest, R. W. M., Cleary, D. F., de Kluijver, M. J., Lavaleye, M. S., Maier, C.,
950 & van Duyl, F. C. (2007). Sponge diversity and community composition in Irish
951 bathyal coral reefs. *Contributions to Zoology*, 76(2), 121–142.
- 952 van Soest, R. W. M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck,
953 D., De Voogd, N. J., ... & Hooper, J. N. (2012). Global diversity of sponges
954 (Porifera). *PLoS ONE*, 7(4): e35105. doi: 10.1371/journal.pone.0035105
- 955 van Soest, R. W. M., Boury-Esnault, N., Hooper, J. N. A., Rützler, K., de Voogd,
956 N. J., Alvarez, B., Hajdu, E., Pisera, A. B., Manconi, R., Schönberg, C., Klautau,
957 M., Kelly, M., Vacelet, J., Dohrmann, M., Díaz, M.-C., Cárdenas, P., Carballo, J.
958 L., Ríos, P., Downey, R., & Morrow, C. C. (2020). World Porifera Database.
959 Accessed at <http://www.marinespecies.org/porifera> on 2019-11-11.
960 doi:10.14284/359
- 961 Xavier, J. R., & van Soest, R. W. M. (2012). Diversity patterns and zoogeography
962 of the Northeast Atlantic and Mediterranean shallow-water sponge fauna.
963 *Hydrobiologia*, 687(1), 107–125.
- 964 Zeng, C., Rowden, A. A., Clark, M. R., & Gardner, J. P. (2017). Population
965 genetic structure and connectivity of deep - sea stony corals (Order Scleractinia)
966 in the New Zealand region: Implications for the conservation and management of
967 vulnerable marine ecosystems. *Evolutionary applications*, 10(10), 1040–1054.

968

969 **Figure Caption:**

970 **Fig. 1** - Location of the collection site and type locality for *Hamigera bibiloniae* sp.
971 nov. (Blanes Canyon, north-western Mediterranean Sea). Projected view (UTM Zone
972 31N (WGS84)) with geographic (WGS84) coordinates indicated for reference.
973 Geographic and bathymetric data used was obtained from
974 <http://www.naturalearthdata.com>.

975 **Fig. 2** - Location of the collection site and type locality for the NIWA material
976 regarding *Hamigera kellyae* sp. nov. (Clementsville Seamount, Macquarie Ridge,
977 New Zealand). Projected view (UTM Zone 31N (WGS84)) with geographic (WGS84)
978 coordinates indicated for reference. Geographic and bathymetric data used was
979 obtained from <http://www.naturalearthdata.com>.

980 **Fig. 3** – Spicular set for *Hamigera bibiloniae* sp. nov. A) Style II B) Style I C)
981 Strongyle D) Detail of the styles acerate end E) Detail of the styles' head F) Detail of
982 of tyle modification in some strongyles G) Arcuate isochelae a') arcuate isochelae
983 relative size compared with that of the megascleres. Scale bars for A), B), C) and a')
984 200 µm; D), E), F) 30 µm and G) 40 µm.

985 **Fig. 4** – Spicular set for *Hamigera kellyae* sp. nov. A) Styloid B) Strongyles C) Detail
986 of the styloid's end D) Detail of the polytylotid modifications of some styloid's head
987 E) Arcuate isochelae, including malformed or juvenile forms F) General view of the
988 SEM imaging. a') arcuate isochelae relative size compared with that of the
989 megascleres; f) fimbriae. Scale bars for A), B) and a') 300 µm; C) and D) 30 µm; E)
990 300 µm and F) 500 µm.

991 **Fig. 5** – Schematic representation of the skeletal arrangement of *Hamigera bibiloniae*
992 sp. nov. (A.) and *Hamigera kellyae* sp. nov. (B.). All spicules are proportionally
993 represented. The acronyms mean: *e*, ectosome; *ch*, choanosome; *St*, styloid; *St I*, Style
994 I; *St II*, Style II, *Str*, strongyle.

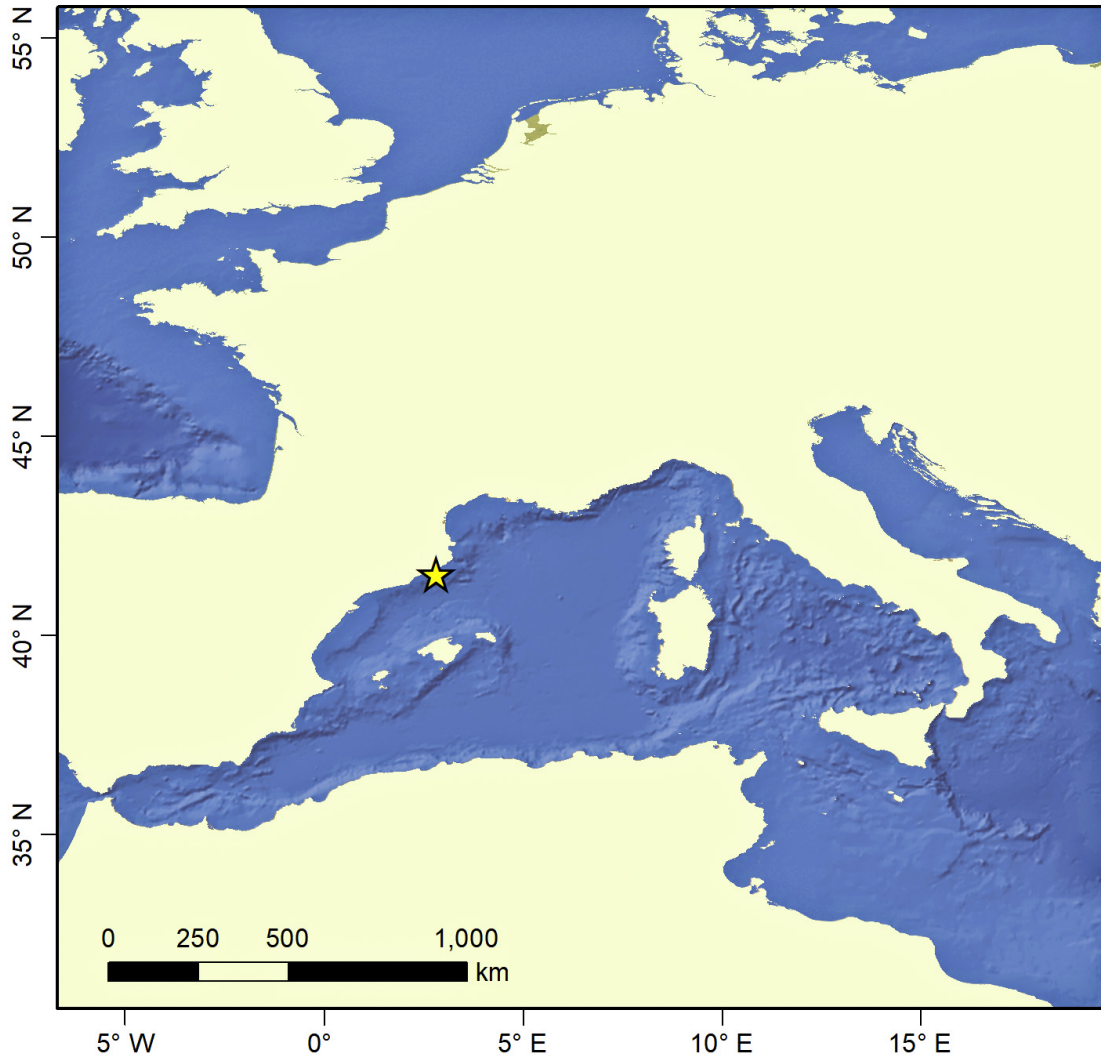
Table 1. Spicule categories and measurements of all *Hamigera* species. All measurements are in μm . Spicule measurements for *H. cleistochela* come from Bertolino et al. (2019), whereas those for *H. tarangaensis* come from Bergquist & Fromont (1988). All other measurements come from the reexamination of the type material except for, *H. macrostrongyla*, which are based on specimens from the NIWA and QM collections and *H. hamigera*, which are based on specimens from the northern area of Catalonia (north-western Mediterranean Sea).

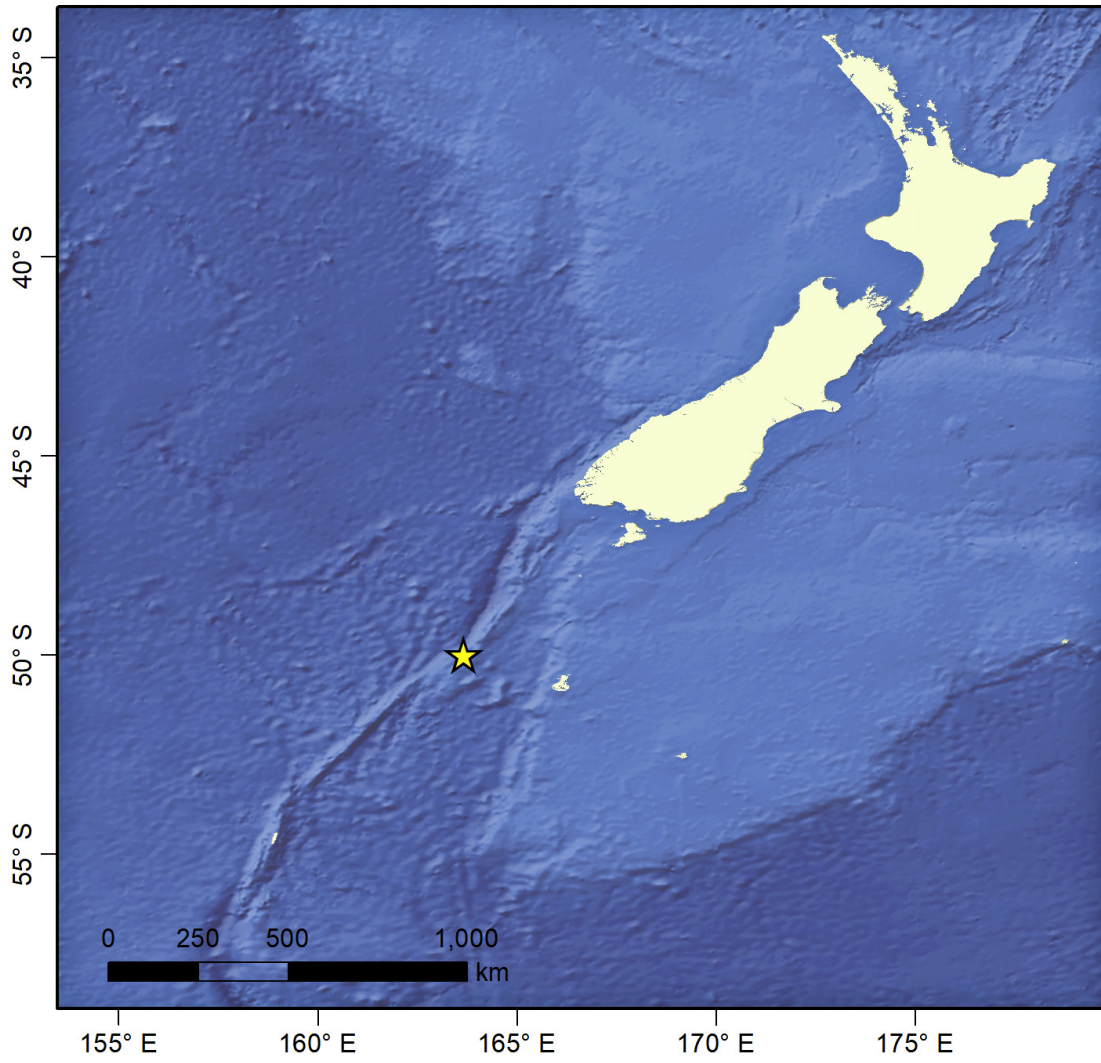
Species	Type Locality	Strongyle	Style	Arcuate isochelae
<i>Hamigera hamigera</i> (Schmidt, 1862)	Zara Canal, Croatia	230 – 300 x 3 – 7	270 – 320 x 6 – 9	15 – 22
<i>Hamigera dendyi</i> Shaw, 1927	Maria Island, Australia	260 – 400 x 3 – 5	260 – 400 x 3 – 5 (rare)	26 – 35
<i>Hamigera strongylata</i> Burton, 1934	Great Barrier Reef, Australia	235 – 297 x 1 – 4	-	17 – 22
<i>Hamigera macrostrongyla</i> Bergquist & Fromont, 1988	Slipper Island, New Zealand	390 – 500 x 5 – 7	370 – 470 x 7 – 8	44 – 62
<i>Hamigera tarangaensis</i> Bergquist & Fromont, 1988	Hen and Chickens Islands, New Zealand	210 – 440 x 3 – 7	-	23 – 60
<i>Hamigera cleistochela</i> Bertolino, Costa & Pansini, 2019	Puyuhuapi Fjord, Chile	-	I: 105 – 250 x 2.5 II: 440 – 580 x 5 – 10	Chelae: 25 – 35 Cleistochelae: 25 – 35
<i>Hamigera bibiloniae</i> sp. nov.	Blanes Canyon, Spain	280 – 340 x 7 – 9	I: 290 – 355 x 5 – 9 II: 530 – 650 x 10 – 18	35 – 48
<i>Hamigera kellyae</i> sp. nov.	Clementsville Seamount, New Zealand	460 – 670 x 9 – 14	435 – 900 x 7 – 11 (styloid)	57 – 89

Table 2. Poecilosclerida associated with CWC communities in the Mediterranean Sea and the New Zealand Waters. Species list for the Mediterranean was mainly taken from the review of the CWC associated sponge fauna in Bertolino et al. (2019) and Rueda et al. (2019), as well as some additional information from Uriz & Rosell (1990). For New Zealand species, a comprehensive review of sponge published data was undertaken (see Kelly et al., 2009 for a comprehensive list of publications up to 2009), with Dendy (1924), Sim-Smith & Kelly (2011) and Vacelet et al. (2009) being the only publications where CWC were mentioned as substrate for sponge species. All species names are listed as according to the World Porifera Database (<http://www.marinespecies.org/porifera/>). Depth range was taken from the aforementioned references, and references within.

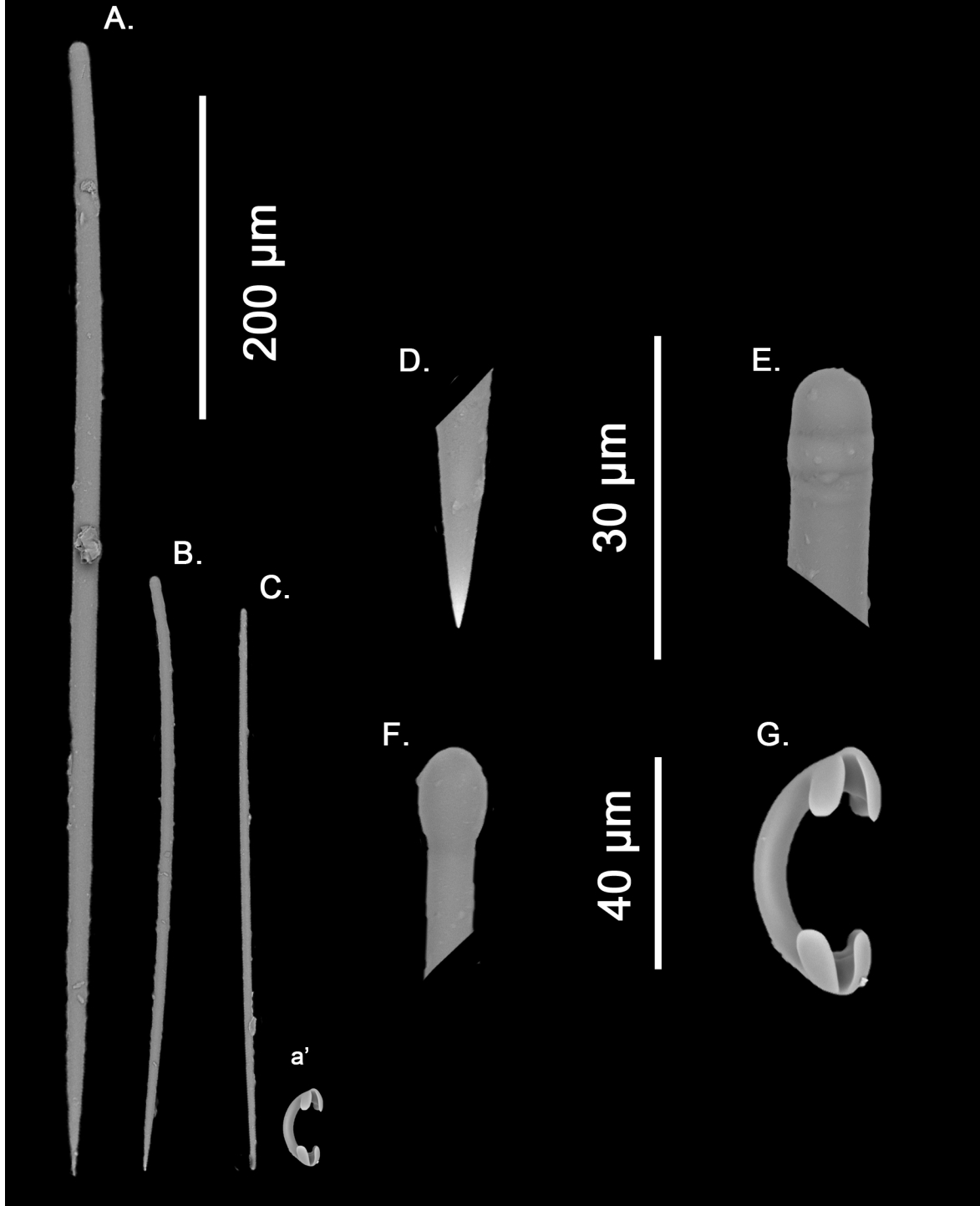
Species	Depth range	Mediterranean Sea	New Zealand
Family Acarnidae			
<i>Damiria curvata</i> (Vacelet, 1969)	180 m	X	
Family Cladorhizidae			
<i>Chondrocladia (Meliiderma) turbiformis</i> Vacelet et al., 2009	990 – 1130 m		X
<i>Lycopodina hypogea</i> (Vacelet & Boury-Esnault, 1996)	5 – 707 m	X	
Family Coelosphaeridae			
<i>Forcepia (Leptolabis) megachela</i> (Maldonado, 1992)	70 – 408 m	X	
Family Crellidae			
<i>Anisocrella hymedesmina</i> Topsent, 1927	500 – 2460 m	X	
<i>Crella (Pytheas) alba</i> (Vacelet, 1969)	180 – 235 m	X	
<i>Crellastrina alecto</i> (Topsent, 1898)	600 – 809 m	X	
Family Esperiopsidae			
<i>Esperiopsis strongylophora</i> Vacelet, 1969	500 m	X	
Family Hymedesmiidae			
<i>Hamigera bibiloniae</i> sp. nov.	684 m	X	
<i>Hamigera kellyae</i> sp. nov.	1070 – 1123 m		X
<i>Hymedesmia (Hymedesmia) gracilisigma</i> Topsent, 1928	15 – 2015 m	X	
<i>Hymedesmia (Hymedesmia) jeanvaceleti</i> van Soest & Hooper, 2020	180 m	X	
<i>Hymedesmia (Hymedesmia) lundbecki</i> Dendy, 1924	180 m		X
<i>Hymedesmia (Hymedesmia) mutabilis</i> (Topsent, 1904)	200 – 1300 m	X	
<i>Hymedesmia (Hymedesmia) peachii</i> Bowerbank, 1882	0–1750 m	X	

<i>Hymedesmia (Hymedesmia) plicata</i> Topsent, 1928	370 – 2460 m	X	
<i>Hymedesmia (Hymedesmia) pugio</i> Lundbeck, 1910	540 – 819 m	X	
<i>Hymedesmia (Hymedesmia) quadridentata</i> Cardone et al., 2019	256 – 264 m	X	
<i>Hymedesmia (Hymedesmia) serrulata</i> Vacelet, 1969	235 m	X	
<i>Phorbas fictitius</i> (Bowerbank, 1866)	0 – 2165 m	X	
<i>Plocamionida ambigua</i> (Bowerbank, 1866)	20 – 2460 m	X	
<i>Plocamionida tylotata</i> Brøndsted, 1932	180 – 480 m	X	
Family Latrunculiidae			
<i>Latrunculia (Biannulata) citharistae</i> Vacelet, 1969	103 – 477 m	X	
<i>Latrunculia rugosa</i> (Vacelet, 1969)	500 m	X	
<i>Sceptrella insignis</i> (Topsent, 1890)	200 – 2460 m	X	
Family Microcionidae			
<i>Antho (Acarnea) signata</i> (Topsent, 1904)	668 – 1360 m	X	
<i>Antho (Antho) involvens</i> (Schmidt, 1864)	0 – 280 m	X	
<i>Clathria (Microciona) armata</i> (Bowerbank, 1862)	0 – 900 m	X	
<i>Clathria (Microciona) cf. atrasanguinea</i> (Bowerbank, 1862)	4 – 264 m	X	
<i>Clathria (Microciona) gradalis</i> Topsent, 1925	0 – 350 m	X	
<i>Clathria (Paresperia) anchorata</i> (Carter, 1874)	170 – 600 m	X	
Family Mixillidae			
<i>Melonanchora emphysema</i> (Schmidt, 1875)	80 – 1438 m	X	
Family Podospongiidae			
<i>Diplopodospongia macquariensis</i> Sim-Smith & Kelly, 2011	500 – 1000 m		X
<i>Neopodospongia exilis</i> Sim-Smith & Kelly, 2011	562 – 600 m		X
<i>Podospongia lovenii</i> Barboza du Bocage, 1869	110 – 682 m	X	
Total		30	5

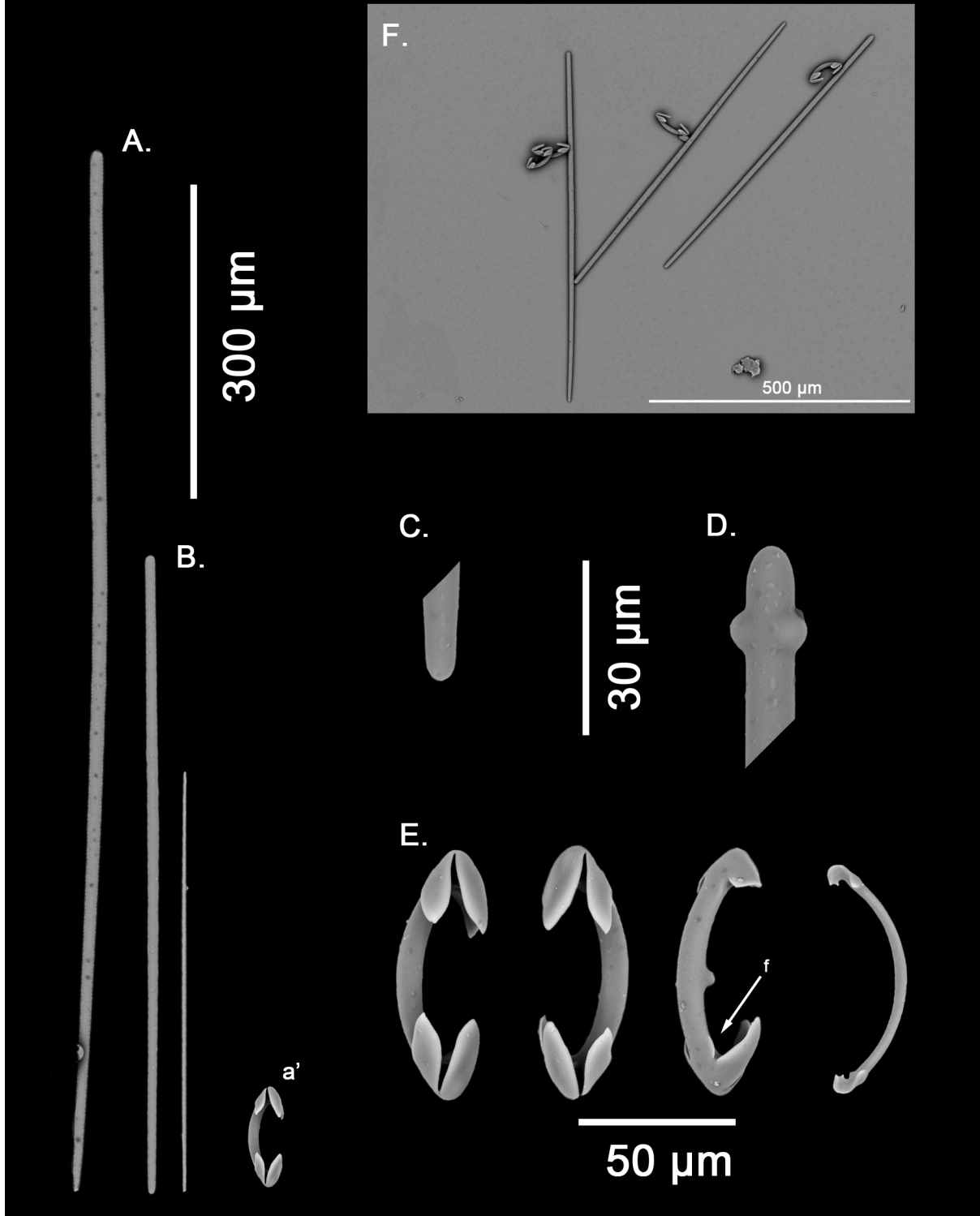


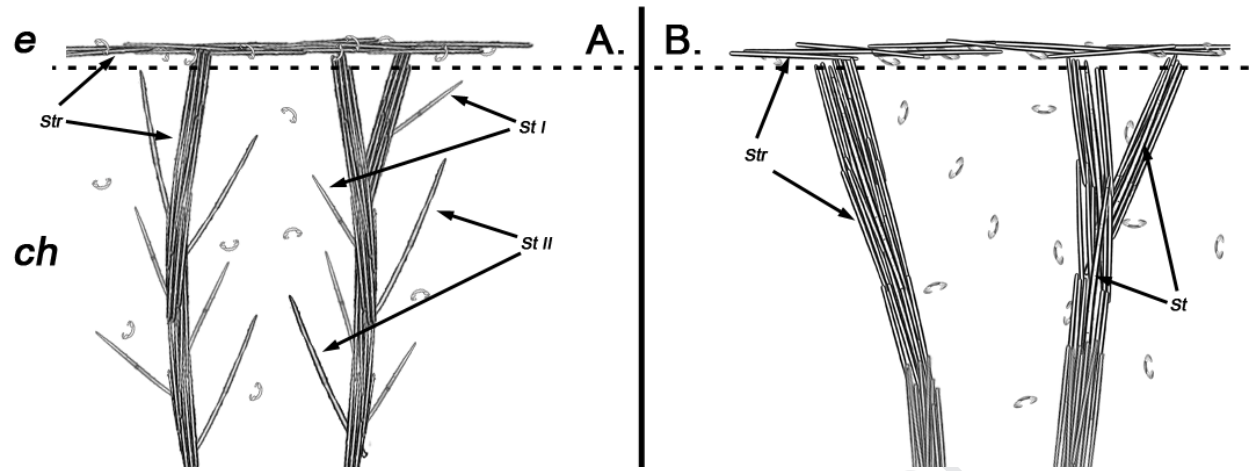


Hamigera bibiloniae sp. nov.



Hamigera kellyae sp. nov.





- Two new species of *Hamigera* (Porifera: Poecilosclerida) are here described from antipodal (Mediterranean vs. Pacific) parts of the world.
- The similitudes between *Hamigera* (family Hymedesmiidae) and *Lissodendoryx* (*Lissodendoryx*) (family Coelosphaeridae) are discussed.
- They are the first deep-sea representatives for this previously shallow-exclusive genus, both occurring in association with Cold Water Corals.
- Deep-sea ecosystems represent a unique environment for the discovery of new species.
- Sponges associated with Cold Water Corals in New Zealand waters are currently poorly studied, thus being a likely area for the discovery of new species.
- *Hamigera bibiloniae* sp. nov. (Mediterranean Sea) shows Tethyan affinities, which points towards a pre-Messinian origin, highlighting that the percentage of Mediterranean species with Tethyan ancestry might be more important than is currently known today.

Declaration of interests

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

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