

1 **A new trochoidean gastropod (Vetigastropoda: Skeneidae) discovered**  
2 **from deep-sea hydrothermal vents in the Southern Ocean**

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11  
12 **Abstract**

13  
14 Hydrothermal vents at the East Scotia Ridge (ESR) were the first vents to be visually  
15 confirmed and surveyed in the Southern Ocean. A trochoid snail was recovered from  
16 low diffuse flow venting sites of both E2 and E9 segments of the ESR. Taxonomic and  
17 systematic investigations revealed it to be a species hitherto unknown to science in the  
18 skeneid genus *Bruceiella*, which is apparently endemic to the chemosynthetic  
19 ecosystems. The new species is characterised by a large size for the genus (up to 5 mm  
20 shell width), a very broad central tooth with moderately raised horizontal basal ridge,  
21 and inner marginal teeth with one single prominent protrusion on the shaft, and is  
22 described herein as *Bruceiella indurata* sp. nov. Described members of the genus are  
23 known from the Indian and Pacific oceans, drawing interest to the biogeographic origins  
24 of the present new species. Closest relative of the present species is *Bruceiella wareni*  
25 Okutani, Hashimoto & Sasaki, 2004 from Kairei vent field, Central Indian Ridge,  
26 further indicating the close relationship between East Scotia Ridge and Indian Ocean  
27 vent fauna as has been previously suggested.

28  
29 **Keywords:** Antarctica, *Bruceiella*, East Scotia Ridge, Mollusc, New species,  
30 Trochoidea

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35 **Running Title:** New Antarctic vent snail

36

## 37 **Introduction**

38

39 Deep-sea hydrothermal vents host a great abundance of benthic animals thriving under  
40 great pressure and near extreme temperatures (Corliss et al. 1979; Van Dover 2000;  
41 Vrijenhoek 2013). These animals survive on the basis of chemosynthetic primary  
42 production of microbes, deriving energy from oxidation of compounds such as  
43 hydrogen sulfide and methane, richly contained within the vent end-member fluid  
44 (Cavanaugh et al. 1981; Felbeck 1981). Many vent fauna are endemic to vent  
45 ecosystems (Martin and Haney 2005), Wolff (2005) surveyed the distribution records of  
46 species recorded from hydrothermal vents and out of 712 recorded species and over  
47 70% of species were apparently endemic to vents. Gastropod molluscs are a major  
48 composition of such vent benthic animals and so far (Warén and Bouchet 1993; Warén  
49 and Bouchet 2001; Sasaki et al. 2010), with more than 218 species in 101 genera  
50 described, of which 138 species are limited to vents (Sasaki et al. 2010).

51

52 The first black smoking hydrothermal vents in the Southern Ocean, located in segments  
53 E2 and E9 of the East Scotia Ridge (ESR), were explored between 2009 and 2012 by  
54 the ChEsSo (Chemosynthetically driven ecosystems south of the Polar Front:  
55 Biogeography and Ecology) Consortium project (Rogers et al. 2012). The faunal  
56 community of these vent fields was significantly different from all globally known vents  
57 and a new biogeographic vent province declared (Rogers et al. 2012). The ESR vents  
58 hosted many species new to science, many of which have already been formally  
59 described (Rogers et al. 2012; Buckeridge et al. 2013; Marsh et al. 2012; Roterman  
60 et al. 2013; Chen et al. 2015; Mah et al. 2015; Thatje et al. 2015, Linse et al. 2019a,  
61 2019b). A small coiled snail collected from both E2 and E9 vents, in diffuse flow areas,  
62 was revealed by follow-up investigations to be a hitherto undescribed skeneid gastropod  
63 species of *Bruceiella*.

64

65 Skeneidae is a family of generally small (<1 cm shell diameter) vetigastropods in the  
66 superfamily Trochoidea (Sasaki et al. 2010; Williams 2012). It has been treated as its  
67 own family, but a series of anatomical and molecular investigations revealed that  
68 species traditionally classified in Skeneidae were a mixture of various small, featureless  
69 trochoids, neomphalines, caenogastropods, and even heterobranchs (Heß et al. 2008;  
70 Kano 2008; Sasaki et al. 2010). This realisation led to a reclassification of many species  
71 and genera mostly based on molecular data, with a number of genera considered to be

72 'true skeneids' including the type genus *Skenea* moved under family Turbinidae, as  
73 subfamily Skeneinae (Kano 2008; Williams et al. 2008). A further recent molecular  
74 study has, however, revealed that 'true skeneids' in fact form a separate clade outside  
75 and sister to Turbinidae, and thus Skeneidae was resurrected as a valid family (Williams  
76 2012). At present the genera *Skenea*, *Bruceiella*, *Cirsonella*, *Dillwynella*, *Dikoleps*,  
77 *Lissospira*, *Protolira* and *Skeneoides* are confirmed as skeneids by molecular analysis  
78 (Williams 2012) with another 25 genera accepted in the World Register of Marine  
79 Species. To date, only two skeneid species, *Cirsonella extrema* Thiele, 1912 and  
80 *Liotella endeavourensis* Dell, 1990 are known from the Southern Ocean (Bouchet and  
81 Rosenberg 2015).

82  
83 The genus *Bruceiella* is currently considered to be a representative of such true  
84 skeneids, although some have questioned in the past that it may require a new family of  
85 its own (Warén and Bouchet 1993). The type species *Bruceiella globulus* Warén &  
86 Bouchet, 1993 first described from the North Fiji and Lau Basins in 1750 – 2000 m  
87 depth. Then two apparently closely related species were discovered from a whale fall  
88 off New Zealand and placed in the same genus (Marshall 1994). These are *B. laevigata*  
89 Marshall, 1994 from 1242 m deep off Chatham Islands and *B. pruinosa* Marshall, 1994  
90 from the Challenger Plateau, 908 – 912 m deep. Later another species, *B. athlia* Warén  
91 & Bouchet, 2001, was recovered from a hydrocarbon seep in the Aleutian Trench, at  
92 about 4800 m deep (Warén and Bouchet, 2001). Furthermore, a further species clearly  
93 belonging to the same genus was found in Kairei hydrothermal vent field, Central  
94 Indian Ridge, Indian Ocean (Van Dover et al. 2001; Okutani et al. 2004), and was  
95 described as *B. wareni* Okutani, Hashimoto & Sasaki, 2004. *Bruceiella*, therefore,  
96 appears to be a deep-sea genus endemic to chemosynthetic ecosystems but can be found  
97 across vents, seeps, and food-falls (Sasaki et al. 2010); widely ranging from the Western  
98 Pacific to Indian Ocean.

99  
100 The purpose of the present paper is to characterise the new species both  
101 morphologically and genetically, to provide its formal description under the name  
102 *Bruceiella indurata* sp. nov., and to discuss its phylogenetic and biogeographic  
103 relationship with other closely related species.

104  
105  
106 **Materials and Methods**  
107

108 **Sample collections**

109

110 Skeneid gastropods were sampled using the suction sampler of the remote operating  
111 vehicle (ROV) *Isis* at two vent fields in the ridge segments E2 and E9 of the ESR  
112 (Rogers et al. 2012; Marsh et al. 2012) (Fig. 1, Table 1). The skeneids were collected  
113 from the sediment surfaces in diffuse flow areas when either actinostylid anemones, yeti  
114 crabs (*Kiwa tyleri*) or eolepadid barnacles (*Neolepas scotiaensis*) were actively sampled  
115 (Fig. 2). The specimens of *Bruceiella* were found sorting the sediment remainder from  
116 the bioboxes and suction sampler ends and preserved in 96% ethanol.

117

118 *In-situ* images of the vent sites and diffuse flow habitats were taken using the imaging  
119 systems of ROV *Isis*; a Scorpio digital still camera with flash unit was used as well as  
120 two high definition video cameras (1080i) (Marsh et al. 2013) (Fig. 2).

121

122 **Morphology**

123

124 Morphological investigation and dissection were carried out under a Zeiss Stemi SV6  
125 dissection microscope. Radulae were dissected from specimens preserved in 96%  
126 ethanol. Tissues around the radula were dissolved with commercial bleach solution  
127 (length varied from specimen to specimen). Both radula and dissoconch shells were air-  
128 dried overnight for Scanning Electron Microscopy (SEM). SEM imaging was  
129 undertaken using a Hitachi TM3000 SEM (British Antarctic Survey, Cambridge). Shell  
130 morphometric measurements were carried out using an eyepiece graticule in the Stemi  
131 SV6.

132

133 Materials examined, including type specimens, are deposited in the invertebrate  
134 collections at the Natural History Museum, London (NHMUK), the University Museum  
135 of Zoology, Cambridge (CAMZM), the Museum National de Historie Naturelle, Paris,  
136 France (MNHN), and the University Museum, the University of Tokyo (MNHN).

137

138 **Genetics**

139

140 Genomic DNA was extracted using whole specimens with the DNeasy Tissue  
141 Extraction Kit following the manufacturer's instructions (QIAGEN, Crawley, UK).  
142 Quality checks of extractions were carried out using a Nanodrop 2000  
143 spectrophotometer. DNA amplification was carried out using the polymerase chain

144 reaction (PCR) with standard reagents in 25 µl total volume (2.5 µl of 10x buffer  
145 containing 15 mM Mg<sup>++</sup>, 0.5 µl of 10 mM dNTPs, 2.5 µl of each 10 µM primer, 0.125  
146 µl of 2.5U Taq DNA Polymerase, 5 µl of 'Q' solution, 10.875 µl double-distilled water,  
147 1 µl genomic DNA).

148

149 The barcoding fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI)  
150 gene was amplified using the universal primer pair LCO 1490 and HCO 2198 (Folmer  
151 *et al.* 1994), with the PCR amplification carried out as follows: 94°C for 2 minutes to  
152 denature initially, followed by 94°C for 20 seconds, 50°C for 20 seconds and 72°C for  
153 1-2 minutes. After 35 cycles the reaction was held at 72°C for 7 minutes. Amplification  
154 was confirmed with 1% agarose gel electrophoresis using cyber green. PCR purification  
155 and DNA sequencing of forward and reverse strands was performed at LGC Berlin  
156 Germany from the successfully amplified PCR products.

157

158 In addition to the ESR skeneid gastropods, a specimen of *Bruceiella wareni* was also  
159 sequenced for comparison, collecting data as follows: Kairei hydrothermal vent field,  
160 25°19.2249'S 70°2.4123'E, 2434 m deep, Central Indian Ridge (CIR), DSV *Shinkai*  
161 6500 dive #1450, R/V *Yokosuka* cruise YK16-E02 (PI: Ken Takai), 2016/ii/14,  
162 preserved in 99% ethanol.

163

164 Alignment and editing of genetic sequences were carried out using the software  
165 Geneious R11 (<https://www.geneious.com/>), and reads were further manually quality-  
166 checked and corrected by eye. In downstream analyses, only those sequences with both  
167 good quality matching forward and reverse reads were used. The software MEGA X  
168 (Kumar *et al.* 2018) was used to calculate the pairwise distances of COI sequences.  
169 Prior to phylogenetic analyses the programme PartitionFinder 2 (Lanfear *et al.* 2012;  
170 2016) was used to find the most suitable evolutionary model, selected by scores for the  
171 Akaike Information Criterion. This selected the GTR+I+R model for the first and  
172 second codon positions and GTR+G model for the third codon position. Tree  
173 reconstruction was carried out with Bayesian inference using the programme MrBayes  
174 3.2 (Ronquist *et al.* 2012). The total sequence length used in the final analyses was 580  
175 bp. The Metropolis-coupled Monte Carlo Markov Chains were run for two million  
176 generations in the final analyses. Topologies were sampled once every 100 generations,  
177 with the first 20% discarded as "burnin" so to ensure the chains sampled a stationary  
178 position. TRACER v1.5 (Rambaut and Drummond 2009) was used to assess the  
179 convergence, split frequencies were less than 0.01 before the analyses were terminated.

180

181 New sequences generated from this study are deposited in GenBank under accession  
182 numbers MK533011-MK533013.

183

184

## 185 **Results**

186

### 187 ***Taxonomy***

188

189 Subclass Vetigastropoda Salvini-Plawen, 1980

190 Superfamily Trochoidea Rafinesque, 1815

191 Family Skeneidae Clark, 1851

192 Genus *Bruceiella* Warén & Bouchet, 1993

193 Type species *Bruceiella globulus* Warén & Bouchet, 1993

194

#### 195 ***Bruceiella indurata* sp. nov.**

196 (Fig. 3-4)

197

198 *Diagnosis:* A large *Bruceiella* with a shell diameter up to 5 mm. Shell skeneiform, up to  
199 3 whorls but often corroded to only 1 left. Final 0.5 whorls loosens in coiling and  
200 becoming disjunct in adults. Central tooth with very wide, triangular base and  
201 moderately raised horizontal ridge near base and inner marginal teeth with a single  
202 protrusion on shaft.

203

#### 204 *Type material:*

205 Holotype (Fig. 3a-d, NHMUK 20190515), shell width (SW) 2.9 mm, aperture  
206 height (AH) 1.6 mm, live collected, fixed and stored in 96% ethanol, 'Anemone Field',  
207 E2 segment hydrothermal vent site, 56° 5.27' S 30° 19.10' W, East Scotia Ridge, 2603-  
208 2605 m deep, RRS *James Cook* expedition JC42, ROV *Isis* Dive #134, 2010/i/24.

209 Paratype #1, (Fig. 3e-f, MNHN-IM-2014-7031), SW 2.1 mm, AH 1.2 mm, live  
210 collected, fixed and stored in 96% ethanol, E2 segment hydrothermal vent site, 56°  
211 5.33' S 30° 19.11' W, East Scotia Ridge, 2619 m deep, RRS *James Cook* expedition  
212 JC42, ROV *Isis* Dive #133, 2010/i/23.

213 Paratype #2, (Fig. 3g-h, MNHN-IM-2014-7032), SW 3.4 mm, AH 1.9 mm, live  
214 collected, fixed and stored in 96% ethanol, same lot as the holotype.

215 Paratype #3, (Fig. 3i-l, UMZC 2019.3), SW 4.6 mm, AH 2.2 mm, live

216 collected, fixed and stored in 96% ethanol, same lot as the holotype.

217 Paratype #4, (Fig. 3m-p, MNHN-IM-2014-7033), SW 5.0 mm, AH 2.8 mm,  
218 live collected, fixed and stored in 96% ethanol, same lot as the holotype.

219 Paratype #5, (Fig. 3q-r, NHMUK 20190516), SW 4.0 mm, AH 2.2 mm, live  
220 collected, fixed and stored in 96% ethanol, same lot as the holotype.

221 Paratype #6, (Fig. 4a-c, NHMUK 20190517), live collected, fixed in 96%  
222 ethanol, dissected for radula SEM and stored dry on SEM stub, same lot as the  
223 holotype.

224 Paratype #7, (Fig. 4d, NHMUK 20190518), live collected, fixed and stored in  
225 96% ethanol, dissected for operculum SEM and stored dry on SEM stub, same lot as the  
226 holotype.

227

228 *Etymology*: ‘*Indurato*’ (Latin) meaning ‘to endure’, ‘to harden’. This is in reference to  
229 how the snail endures continuous dissolution of its shell from vent fluid by persistent  
230 shell repairing. It is used as an adjective.

231

232 *Further materials used for morphometrics*:

233 6 specimens (NHMUK 20190519), live collected, fixed and stored in 96%  
234 ethanol, same lot as holotype.

235 5 specimens (MNHN-IM-2014-7034), live collected, fixed and stored in 96%  
236 ethanol, same lot as paratype #1.

237 1 specimen (UMZC 2019.4), live collected, fixed and stored in 96% ethanol,  
238 E2 segment hydrothermal vent site, 59° 5.37’ S 30° 19.06’ W, East Scotia Ridge, 2641  
239 m deep, RRS *James Cook* expedition JC42, ROV *Isis* Dive #134, 2010/i/24.

240 2 specimens (MNHN-IM-2014-7035), live collected, E9 segment hydrothermal  
241 vent site, 60° 2.81’ S 29° 58.71’ W, East Scotia Ridge, 2395 m deep, RRS *James Cook*  
242 expedition JC42, ROV *Isis* Dive #141, 2010/i/30. Both specimens fixed in 96% ethanol  
243 with one stored in 96% ethanol and one mounted dry on SEM stub.

244 1 specimen (MNHN-IM-2014-7036), live collected, fixed and stored in 96%  
245 ethanol, E9 segment hydrothermal vent site, 60° 2.81’ S 29° 58.71’ W, East Scotia  
246 Ridge, 2394 m deep, RRS *James Cook* expedition JC42, ROV *Isis* Dive #142, 2010/ii/2.

247

248 *Description*. Shell (Fig. 3). Teleoconch depressed to tall skeneiform, up to 4.5 whorls.  
249 Early whorls more tightly coiled than later ones, with ultimate 0.5 whorls in adults  
250 becoming disjunct in coiling. Surface smooth except very fine axial growth lines, often  
251 encrusted by dark coloured mineral deposits. Periostracum thin, semi-transparent and

252 greenish when present. In adults surface almost always very severely corroded with  
253 earlier whorls removed entirely and outer calcareous layers removed (Fig. 3m). In such  
254 specimens only a thin, translucent layer remain to cover volume occupied by animal (ca.  
255 1 whorl), showing numerous undulating lines resulting from corrosion of shell layers.  
256 Such shells are effectively open coiling in appearance. In extreme cases holes protrude  
257 through body whorl. Protoconch not known due to all specimens having heavily  
258 corroded apex. Umbilicus deep, moderate in width. Aperture large, circular, not  
259 interrupted by the previous whorl.

260

261 Radula (Fig. 4a-c). Rhipidoglossate, with a formula of  $n-4-1-4-n$ . Central tooth with a  
262 rectangular shaft which abruptly expands into very broad triangular, arrow-like  
263 laterobasal processes, possessing wing-like lateral projections on both sides. Cutting  
264 edge of the sole cusp triangular with smooth cutting edge, tip sharply pointed. A central  
265 ridge weakly projects out horizontally where laterobasal processes begin to expand near  
266 shaft. Four laterals similar in form with shallowly serrated cusps, shafts slightly convex,  
267 sturdy with a strong and abrupt bend near the base, shape interlocking with adjacent  
268 teeth. Basal support of laterals strongest at first or innermost tooth. Shaft of marginal  
269 teeth rather slender, flattened laterally. Cusps of inner marginals truncated, evenly  
270 serrated into ca. 7 – 8 denticles on the distal end. A prominent protrusion is present  
271 beneath cusps of a few innermost marginals. Towards outer edge outer marginals  
272 become decreased in sturdiness as well as having gradually smaller, more finely serrated  
273 cusps.

274

275 Operculum (Fig. 4). Multispiral, concentric, circular. Thin, greenish brown, semi-  
276 transparent. Often completely encrusted by dark mineral deposits.

277

278 *Dimensions:* Known specimens ranging from 2.1 – 5 mm in shell diameter and 1.1 – 2.8  
279 mm in aperture height (Fig. 6, Table 2). Shell height up to 4.4 mm with 44 whorls in  
280 specimen JC42-F-176.4 with 3.7 mm shell diameter (Table 2). Shell height is not an  
281 accurate measure for size as the apex and subsequent whorls are usually very heavily  
282 corroded.

283

284 *Distribution:* So far only known from low diffuse flow hydrothermally influenced areas  
285 of segments E2 and E9, East Scotia Ridge. Often lives in close proximity with  
286 *Provanna* sp., actinostylid anemones, and *Neolepas scotiaensis* stalked barnacles (Fig.  
287 2a-b).



288

289 *Remarks:* Although unfortunately the characteristic protoconch of the genus *Bruceiella*  
290 which carry characteristic sculptures consisting of dendric threads and granules aligned  
291 in fine spirals and also ends in a large, strong varix (Warén and Bouchet 1993; Marshall  
292 1994; Warén and Bouchet 2001) could not be observed in *Bruceiella indurata* sp. nov.,  
293 like in *B. wareni*. The radula configurations, however, strongly support the placement of  
294 *B. indurata* sp. nov. in the genus *Bruceiella*. *Bruceiella indurata* sp. nov. is  
295 morphologically distinct from all five other described *Bruceiella* species by its radular  
296 characteristics, especially the central tooth. The central tooth differs from *Bruceiella*  
297 *globulus* Warén & Bouchet, 1993 by having very broad laterobasal processes or lateral  
298 ‘wings’. The horizontal central ridge near the base of central tooth is lacking in both *B.*  
299 *globulus* and *B. wareni*. In addition, *B. wareni* has five lateral teeth (Okutani et al. 2004)  
300 but *B. indurata* sp. nov. only has four. The two New Zealand species, *B. laevigata*  
301 Marshall, 1994 and *B. pruinosa* Marshall, 1994 have very similar radular morphology,  
302 the central tooth of which is easily differentiated from that of *B. indurata* sp. nov. by  
303 being much narrower and more delicate in comparison. *Bruceiella athlia* Warén &  
304 Bouchet, 2001 is the most similar in radular morphology to *B. indurata* sp. nov., but the  
305 basal central ridge of the central tooth is much stronger and raised in *B. athlia*.  
306 Furthermore, the inner marginals of *B. athlia* are characterised by having distinct two  
307 projections halfway towards the distal end, whereas *B. indurata* sp. nov. only has one.

308

309 The shell of *Bruceiella indurata* sp. nov. also differs from the five other described  
310 *Bruceiella* species by being larger in size. The final half whorl is moderately but  
311 noticeably disjunct in growth from the previous whorls, which is also seen in various  
312 degrees in other *Bruceiella* species. The suture of *B. indurata* sp. nov. is deeper than all  
313 species except *B. wareni*. These, however, may not be as useful as the radular  
314 characteristics in identification as the shell of *Bruceiella* species is often heavily  
315 corroded leaving only the final whorl (Warén and Bouchet 2001). Furthermore, *B.*  
316 *indurata* sp. nov. is geographically isolated from all other known *Bruceiella* species and  
317 only known from the East Scotia Ridge in the Southern Ocean.

318

319 *Molecular phylogeny:* *Bruceiella indurata* sp. nov. was recovered as nesting within the  
320 genus *Bruceiella* with three other congeners in the Bayesian phylogenetic reconstruction  
321 using 580 bp of the mitochondrial COI gene (Fig. 6), confirming its placement in genus  
322 *Bruceiella*. The two sequences of *Bruceiella indurata* sp. nov. obtained were identical  
323 haplotypes, and together were recovered as a well-supported lineage (Bayesian

324 Posterior Probability, PP=1) clearly distinct from *B. wareni* of the Indian Ocean vents  
325 which was recovered as its sister taxa among those sampled. The uncorrected P-distance  
326 between *B. indurata* sp. nov. and *B. wareni* was 14.9% in 580 bp of the COI gene,  
327 supporting that *B. indurata* is indeed a separate species. These two species formed a  
328 fully supported clade within Skeneidae (BPP=1), which was in turn sister to another  
329 clade consisting of *B. globulus* and *Bruceiella* sp. Lau 1925 m (*sensu* Kano 2008). The  
330 genus *Bruceiella*, containing these four taxa, was recovered as monophyletic with full  
331 support (BPP=1). Furthermore, the family Skeneidae was recovered as a strongly  
332 supported (BPP=0.99) monophyletic clade, as well as the whole superfamily Trochoidea  
333 (BPP=1).

334

335

### 336 **Discussion**

337

338 Until the present study, *Cirsonella extrema* and *Liotella endeavourensis* were the only  
339 two skeneids known from the Southern Ocean (Bouchet and Rosenberg 2015), and *B.*  
340 *indurata* sp. nov. is now the third. *Bruceiella indurata* sp. nov., from our current  
341 knowledge has a distribution restricted to two vent sites in the ESR, in comparison the  
342 other two known skeneids in the Southern Ocean show with ranging, circum-Antarctic  
343 distributions: *C. extrema* is known from the shelf to upper slope of Antarctica and the  
344 South Sandwich Islands in 15 to 870 m in depth (Aldea and Troncoso 2008) and *L.*  
345 *endeavourensis* from the Bellingshausen, Weddell and Ross Seas (Aldea and Troncoso  
346 2008; Williams 2012) in 362 to 1324 m. Although this is likely due to the fact that other  
347 Southern Ocean vent sites (e.g., Hahm et al. 2015) remain undiscovered and unsampled,  
348 it is notable that all currently discovered species of *Bruceiella* appear to have restricted  
349 distributions, and known from only a few sites within a local scale (Bouchet and Warén  
350 2001; Sasaki et al. 2010). Other known ESR vent species (Rogers et al. 2012) including  
351 the yeti crab *Kiwa tyleri* Thatje in Thatje et al., 2015, the stalked barnacle *Neolepas*  
352 *scotiaensis* (Buckeridge, Linse & Jackson, 2013), the peltospirid snail *Gigantopelta*  
353 *chessoia* Chen et al., 2015, the abyssochrysoidean snail *Provanna cooki* Linse, Nye,  
354 Copley & Chen 2019,, the vent limpet *Lepetodrilus concentricus* Linse, Roterman &  
355 Chen 2019,, and the three sea spiders in genus *Sericosura* are only known from the ESR  
356 and the nearby Kemp Caldera (Arango and Linse 2015). The sea star *Paulasterias tyleri*  
357 Mah et al., 2015 appears to have a circum-Antarctic distribution, being found at these  
358 sites but also in the Australian-Antarctic Ridge, in a location implied to be near vents  
359 (Mah et al. 2015; Hahm et al. 2015). The two polychaetes, including the siboglinid

360 *Sclerolinum contortum* Smirnov, 2000 and the maldanid *Nicomache lokii* Kongsrud &  
361 Rapp, 2012 have wide distributions to the Arctic and the Pacific (Eilertsen et al. 2018).

362

363 When describing the genus *Bruceiella*, Bouchet and Warén (1993) only placed it  
364 tentatively in Skeneidae, and suggested that it probably belongs in a separate family due  
365 to anatomical differences such as the absence of the propoial penis and the fact that the  
366 snout expanded distally. The phylogenetic reconstruction including *Bruceiella indurata*  
367 sp. nov. in the present study, however, agrees with previous phylogenetic  
368 reconstructions (Kano 2008; Williams 2012) that the genus *Bruceiella* is nested within  
369 Skeneidae and is a true skeneid. Our phylogenetic tree also shows that *Cirsonella* is  
370 paraphyletic, which was already pointed out by Williams (2012), but as the three species  
371 in the same clade other than *C. extrema* are undescribed, we make no attempt to resolve  
372 this.

373

374 Six mollusc species have been collected from the ESR vent ecosystems to date, all are  
375 gastropods and all in different families (Rogers et al. 2012; Chen et al. 2015; Roterman  
376 et al. 2016). *Bruceiella indurata* sp. nov. was only present in weak diffuse flow areas,  
377 where they co-occur mostly with *Provanna cooki* (Linse et al. 2019a), actinostolid  
378 anemones, and *Neolepas scotiaensis* stalked barnacles (Fig. 2a-b; Linse et al. 2019a).  
379 Compared to *Provanna cooki*, it was much rarer and was less visible during video  
380 surveys partly due to their small size and partly due to the black sulphide coverage on  
381 their shells. In some relatively more hydrothermally active diffuse flow localities, such  
382 as the SW field in E9 (Fig. 2c), it also co-occurred with the holobiont peltospirid snail  
383 *Gigantopelta chessoia* and the vent limpet *Lepetodrilus concentricus* (Linse et al.  
384 2019b), but in these sites, it was extremely rare with only 1-2 specimens collected per  
385 site despite intensive sampling of the fauna there. This strongly suggests that *B.*  
386 *indurata* sp. nov. prefers a weak diffuse flow environment, which corresponds also to  
387 the habitat of the closely related *B. wareni* from Indian Ocean vents (Okutani et al.  
388 2004). Perhaps this is unsurprising given that *Bruceiella* is one of few genera of  
389 gastropods that occurs across vents, seeps, and organic falls, and clearly do not require a  
390 high flow of vent fluid (Marshall 1994; Warén and Bouchet, 2001; Sasaki et al. 2010).

391

392 Despite living in a habitat relatively weakly influenced by hydrothermal fluids, the  
393 shells of *B. indurata* are usually covered in sulfide deposits and/or highly corroded, to  
394 the degree where no part of the original periostracum and shell surface remain (Fig.  
395 3m). Similar levels of corrosion are also known in *B. wareni* and *B. athlia* (Warén and

396 Bouchet 2001; Okutani et al. 2004). The shell *Provanna cooki* which often co-occurs  
397 with it usually only has corroded apex but retains a periostracum over most parts (Linse  
398 et al. 2019a), indicating that the shell of *B. indurata* sp. nov. is much more prone to  
399 corrosion. As hydrothermal vents are known to be acidic (Van Dover 2001), gastropods  
400 with a strong, thick periostracum such as *Gigantopelta chessoia*, *Lepetodrilus*  
401 *concentricus*, and *Provanna cooki* are more likely to tolerate against shell corrosion.  
402 The periostracum of *B. indurata* sp. nov. is very thin (Fig. 3a-d), which may be the  
403 reason they show a high degree of corrosion.

404  
405 The phylogeographic relationship between *Bruceiella* species sampled (Figs. 6,7) shows  
406 that *B. indurata* sp. nov. from the ESR is more closely related to *B. wareni* from the  
407 Indian Ocean, than the two western Pacific species (*B. globulus* from North Fiji and Lau  
408 basins and another undescribed species from Lau Basin). This is a similar biogeographic  
409 pattern seen with *Neolepas* stalked barnacles (Herrera et al. 2015; Watanabe et al. 2018),  
410 *Gigantopelta* snails (Chen et al. 2015), and *Kiwa* yeti crabs (Roterman et al. 2013;  
411 Roterman et al. 2018) with the ESR and Indian Ocean species being sisters while the  
412 genus itself appears to have a Pacific provenance. Future multi-locus phylogeny of  
413 *Bruceiella* with better taxon sampling would help to confirm the origin of the genus.

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440

441

442 **Conflict of interest**

443

444 The authors declare that they have no conflict of interest.

445

446 **Ethical approval**

447

448 All applicable international, national, and/or institutional guidelines for the care and use  
449 of animals were followed by the authors. All necessary permits for sampling and  
450 observational field studies have been obtained by the authors from the competent  
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453

454 **Data availability**

455

456 The datasets generated during and/or analysed during the current study are available in  
457 the NCBI GenBank repository, with accession numbers MK533011-MK533013.

458 Specimens used in the present study are deposited in the following museums: NHMUK  
459 (20190515-20190519), MNHN (MNHN-IM-2014-7031—7036), and UMZC (2019.3-  
460 2019.4).

461

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606 **Figure Legends**

607

608 **Fig. 1** Distribution map of *Bruceiella indurata* sp. nov., in the East Scotia Ridge

609

610 **Fig. 2** *In-situ* diffuse flow venting habitats of *Bruceiella indurata* sp. nov. at E2 and E9  
611 hydrothermal fields in the East Scotia Ridge: **a**, Anemone Field, 56°5.27'S 30°19.10'W,  
612 2605 m depth (type locality), E2; **b**, Diffuse flow, 56°5.33'S 30°19.11'W, 2605 m depth,  
613 E2; **c**, Deep Castle, 56°5.37'S 30°19.06'W, 2641 m depth, E2; **d**, SW Field, 60°2.82'S  
614 29°58.69'W, 2396 m depth, E9

615

616 **Fig. 3** *Bruceiella indurata* sp. nov.: **a-d**, Holotype (NHMUK 20190515), shell width  
617 (SW) 2.9 mm, aperture height (AH) 1.6 mm; **e-f**, Paratype #1 (MNHN-IM-2014-7031),  
618 SW 2.1 mm, AH 1.2 mm; **g-h**, Paratype #2 (MNHN-IM-2014-7032), SW 3.4 mm, AH  
619 1.9 mm; **i-l**, Paratype #3 (CAMZM XXXXX), SW 4.6 mm, AH 2.2 mm; **m-p**, Paratype  
620 #4 (MNHN-IM-2014-7033), SW 5.0 mm, AH 2.8 mm; **q-r**, Paratype #5 (NHMUK  
621 20190516), SW 4.0 mm, AH 2.2 mm

622

623 **Fig. 4** *Bruceiella indurata* sp. nov., SEM micrographs: **a**, Middle section of an adult  
624 radula ribbon overview (Paratype #6, NHMUK 20190517); **b**, Radula, close-up of  
625 central and lateral teeth (Paratype #6, NHMUK 20190517); **c**, Radula, close-up of  
626 marginal teeth (Paratype #6, NHMUK 20190517); **d**, Operculum (Paratype #7,  
627 NHMUK 20190518). Scale bars: **a** = 50 µm; **b-c** = 20 µm; **d** = 500 µm

628

629 **Fig. 5** Shell morphometrics of *Bruceiella indurata* sp. nov.

630

631 **Fig. 6** Bayesian phylogenetic tree of Skeneidae constructed using 580 bp of the  
632 mitochondrial COI gene showing the systematic position of *Bruceiella indurata* sp. nov.  
633 within genus *Bruceiella*. GenBank accession numbers are shown in brackets

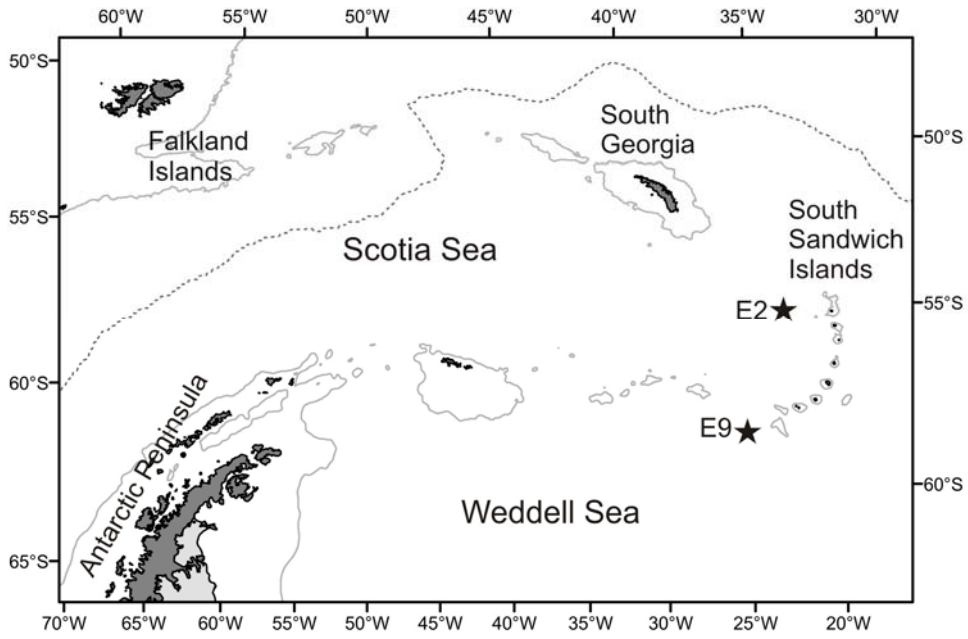
634

635 **Fig. 7** The global distribution of genus *Bruceiella*, including *Bruceiella indurata* sp.  
636 nov.

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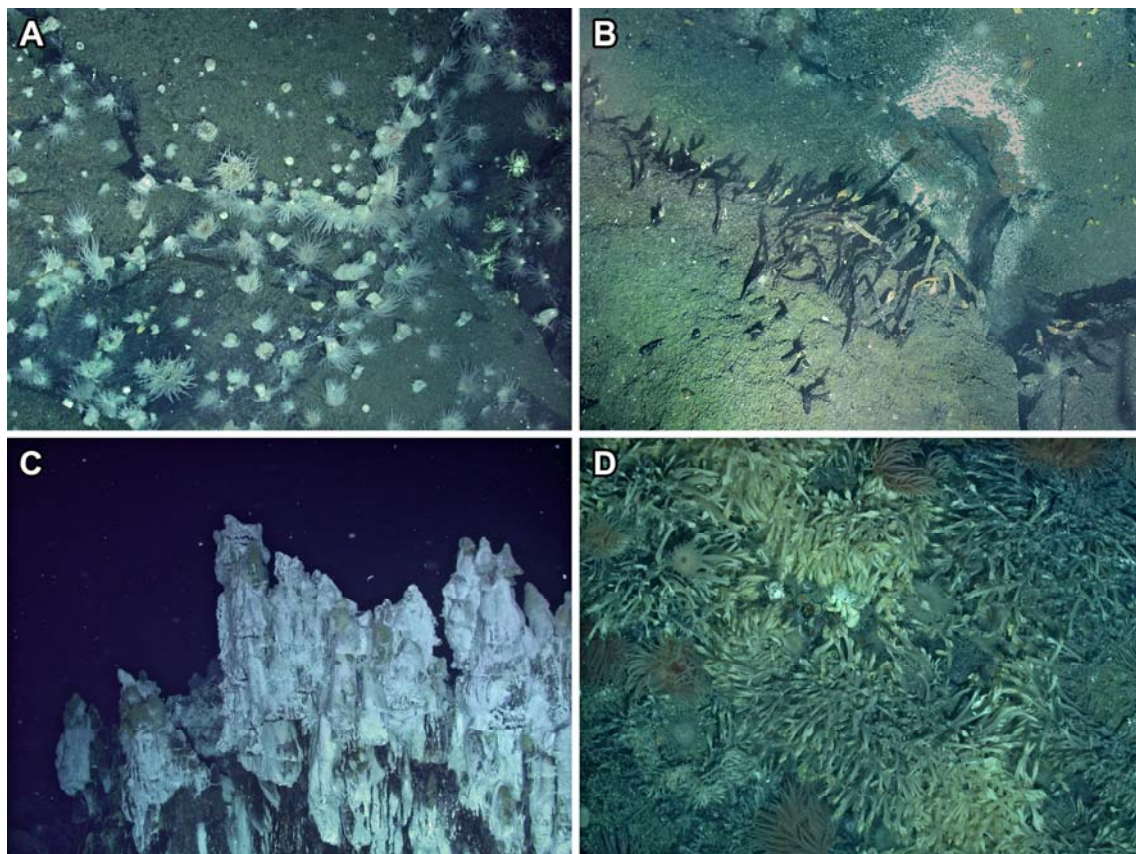


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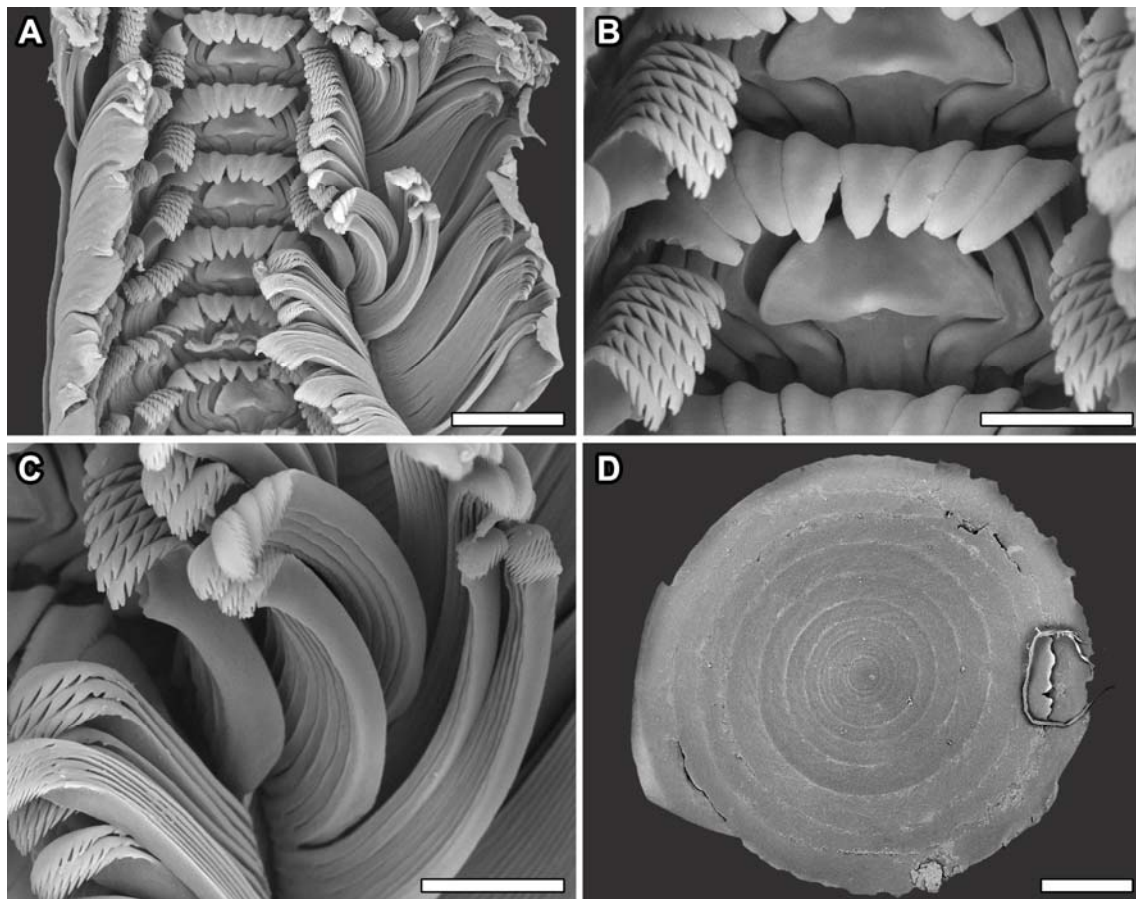
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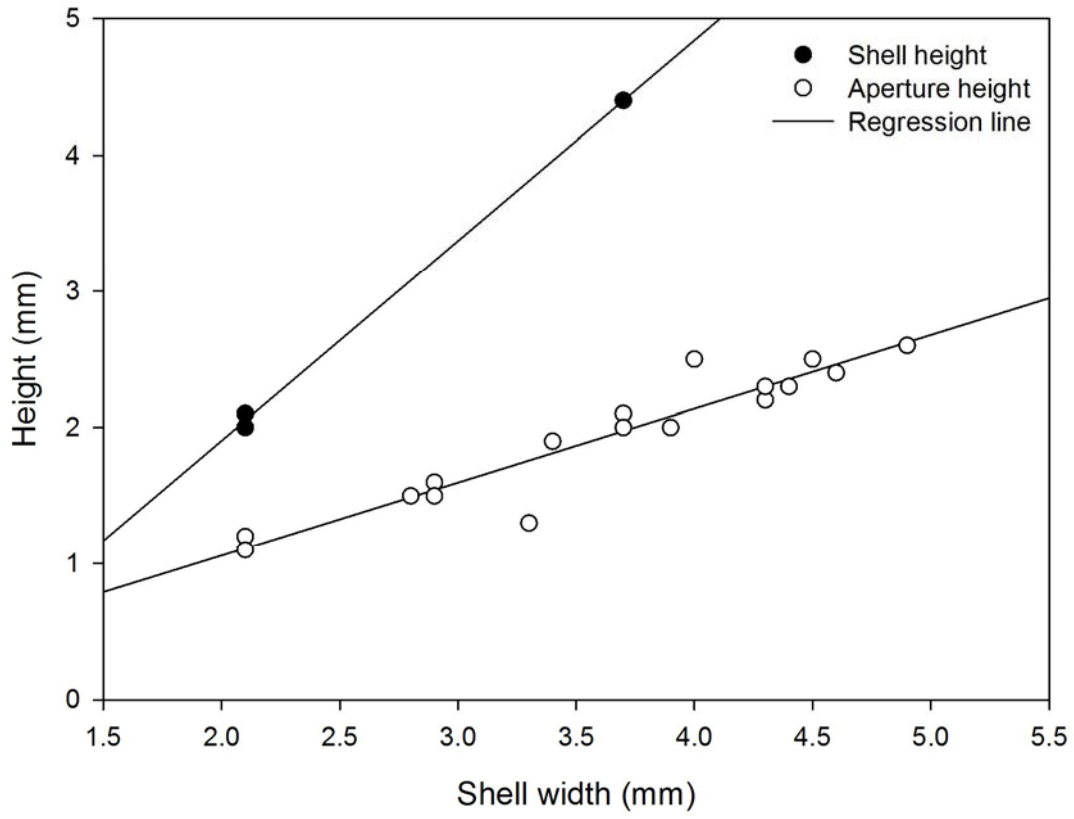
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662 marginal teeth (Paratype #6, NHMUK 20190517); **d**, Operculum (Paratype #7,  
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666 **Fig. 5** Shell morphometrics of *Bruceiella indurata* sp. nov.



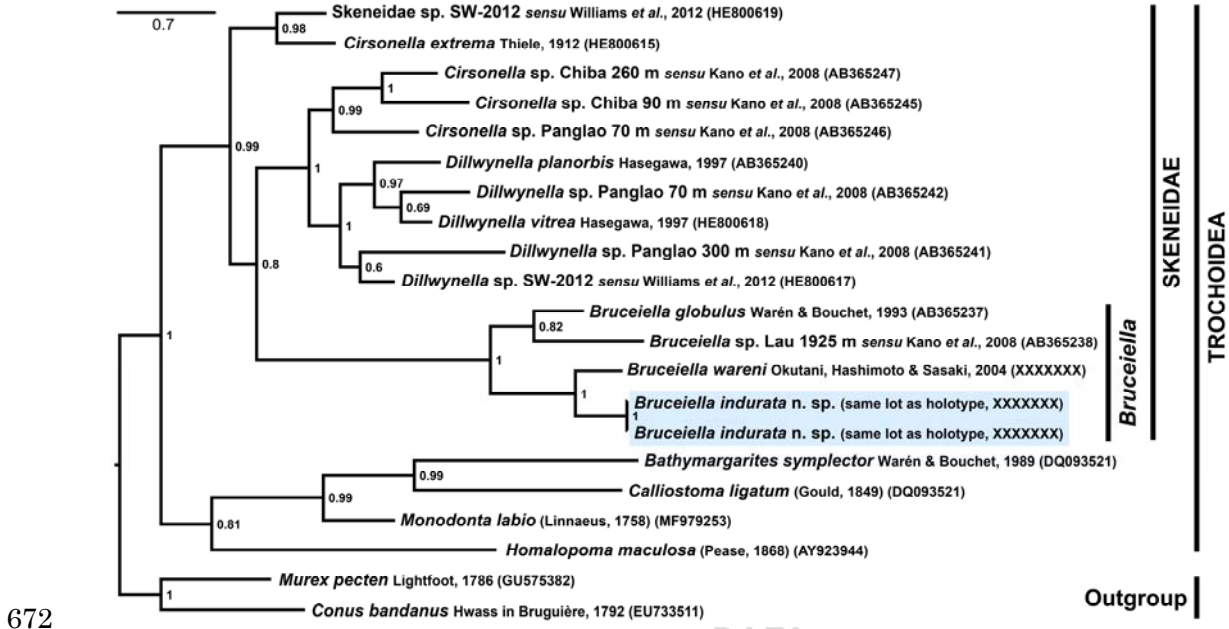
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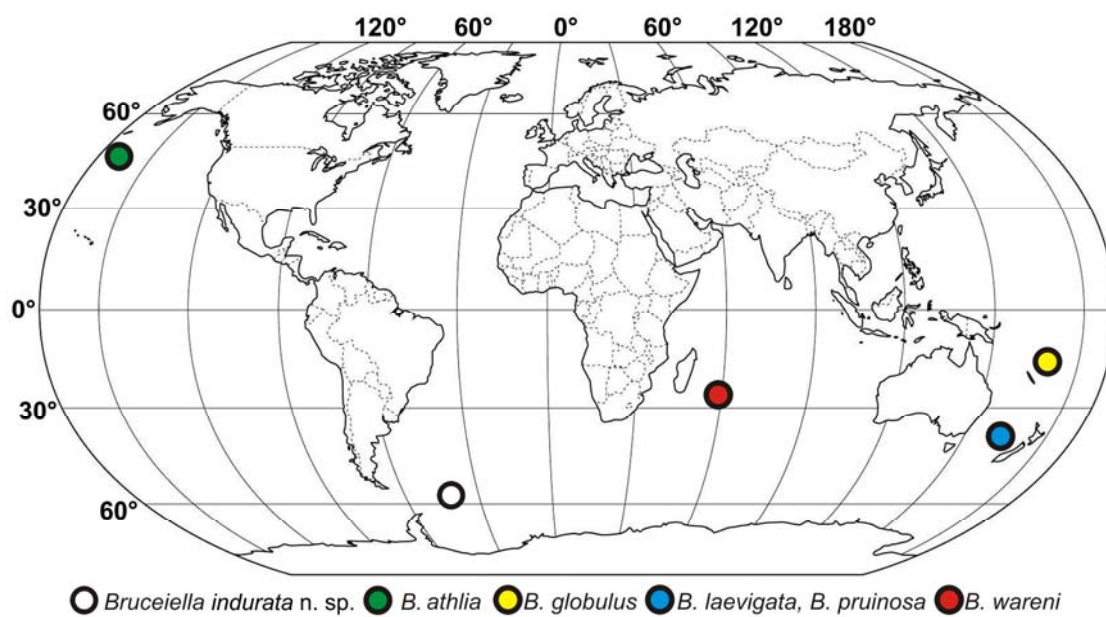
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673 **Fig. 7** The global distribution of genus *Bruceiella*, including *Bruceiella indurata* sp.  
674 nov.



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