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**A NEW MORPHOTYPE DESCRIPTION OF ARBACIA
SPATULIGERA VALENCIENNES, 1846 (ARBACIOIDA,
ECHINOIDEA) AND BATHYMETRIC RANGE EXTENSION FROM
MESOPHOTIC REEFS OF THE CENTRAL COAST OF CHILE**

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2 VALENCIENNES, 1846 (ARBACIOIDA, ECHINOIDEA) AND BATHYMETRIC
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4 CHILE

5 A NEW MORPHOTYPE OF *A. SPATULIGERA* IN MESOPHOTIC REEFS

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23
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Abstract

26 The sea urchin *Arbacia spatuligera* is an echinoid distributed in the Southeastern Pacific
27 Ocean from Peru to Chile. This species was previously reported from the subtidal zone with
28 a bathymetric distribution up to 30 m depth. In this work, 128 individuals were found in four
29 mesophotic reefs along the central coast off Chile using Closed Circuit Rebreathers in
30 technical diving at higher depths than previously, ranging from 36 to 63 meters in depth. A
31 population exhibits unexpected morphological characters, requiring an emended diagnosis
32 and description of a new morphotype for *A. spatuligera*. These morphological traits are
33 further discussed as potential ecophenotypic adaptations.

34 Keywords: echinodermata, biodiversity, rocky reef, rebreather diving, scientific diving

35 Introduction

36 Sea urchins form a large group of benthic marine invertebrates belonging to the phylum
37 Echinodermata, which comprises approximately 1,000 valid species belonging to 115 genera
38 (Mickael et al., 2016; Luparello et al., 2020), distributed at all latitudes in various marine
39 environments and ranging from the intertidal to the deep sea (Iken et al., 2001; Lebrato et al.,
40 2010). The order Arbacioida Gregory, 1900 includes 26 known extant species and eight
41 recognized genera belonging to a single family, the Arbaciidae Gray, 1855. Within the
42 family, the genus *Arbacia* Gray, 1835 is distributed from tropical to temperate and sub-
43 Antarctic regions of the Pacific, Atlantic oceans, and Mediterranean Sea and comprises five
44 valid species: *Arbacia dufresnii* (Blainville, 1825), *Arbacia lixula* (Linné, 1758), *Arbacia*
45 *punctulata* (Lamarck, 1816), *Arbacia spatuligera* (Valenciennes, 1846), and *Arbacia stellata*
46 (Blainville, 1825) (Gianguzza & Bonaviri, 2013).

47 The species *A. spatuligera* is located in the Southeastern Pacific Ocean from northern Peru
48 to Puerto Montt, in south-central Chile (Larraín, 1975; Lessios et al., 2012; Millán et al.,
49 2019). Valenciennes first described the species in 1846 with reliable and detailed drawings
50 and descriptions for that time. More recent descriptions and figures were published by
51 Koehler (1914). In 1935, Mortensen mentioned that the species easily distinguished from the
52 other southern species *Arbacia dufresnii* by its color, with “no green (patches of) nor red
53 color in the interambulacral – as also by its club-shaped aboral spines”. Larraín (1975)
54 defined neotypes for *Arbacia spatuligera* in an extensive monography focused on extant and
55 fossil echinoid species from Chile. He proposed a new detailed description of the species and
56 an extended diagnosis.

57 Bathymetric records of *A. spatuligera* indicate that the species occurs in shallow waters
58 above 30 m depth (Larraín, 1975; Lessios et al., 2012; Gianguzza & Bonaviri, 2013; Millán
59 et al., 2019). However, due to logistical limitations to recreational scuba diving, most of the
60 knowledge about the distribution and ecology of *A. spatuligera* was based on information
61 obtained from shallow areas (<30 m depth) (Kramer et al., 2019).

62 Mesophotic Reef Ecosystems (MREs) are considered a continuation of shallow reefs
63 (Hinderstein et al., 2010) with depths up to 150 m in tropical and subtropical latitudes (Rocha
64 et al., 2018). They are characterized by the presence of light-dependent organisms and their

65 associated biological communities (Eyal & Pinheiro, 2020). Along the central coast of Chile,
66 Temperate Mesophotic Reef Ecosystems (TMRE) have been poorly studied due to the
67 logistic implications of taking samples in zones that exceed the no-decompression limits for
68 recreational scuba diving (Shreeves & Richardson, 2006). These logistic limitations are
69 reflected in the little information available about species' bathymetric ranges, habitat
70 preferences, and communities' structures (Kahng et al., 2010). In order to explore and
71 generate new knowledge about these deep ecosystems, technical dives with Closed-Circuit
72 Rebreathers (CCRs) were performed for the first time over Chilean temperate reefs. As a
73 result, the present work presents novel ecological information about the presence and
74 distribution of the sea urchin *A. spatuligera* in four temperate mesophotic reef ecosystems of
75 the continental shelf off Chile, in addition to data from two shallow rocky reefs.

76 Material & Methods

77 In February 2019, April, May, August, and September 2022, photographic and video records
78 of the sea urchin *Arbacia spatuligera* were obtained from four mesophotic rocky reefs:
79 Pichidangui in the Coquimbo Region, two artificial reefs (shipwrecks), and one sandy slope
80 at Valparaíso Bay, between 36 and 63 m depth, nearby the central coast off Chile (Figure 1).
81 30-minute bottom time dives were performed to search for the target species. Photos and
82 videos were taken using a GoPro 9 and a Sony RX100 V camera with underwater housing
83 and a light system. A Shearwater Petrel dive computer recorded the depth at which organisms
84 were observed. All dives were made during the day using the JJ-CCR rebreather with
85 different gas mixtures as diluents (air and trimix) according to the maximum depth for each
86 dive (Table I).

87 We recorded 128 individuals of *Arbacia spatuligera* in four mesophotic reefs on the central
88 coast of Chile at depths ranging between 36 and 63 m. (Table I). The four reefs presented
89 differences in habitat and light conditions. Large rocks with filamentous algae (turf), sponges,
90 crustose algae (order Corallinales), and channels with sand characterized the rocky reef of
91 Pichidangui. Both wrecks in the Bay of Valparaíso lie on a bottom of fine sand and silt with
92 filamentous algae and the striped anemone *Anthothoe chilensis* (Lesson, 1830) attached to
93 the deck and hull. Light penetration at both sites is limited compared to the Pichidangui rocky
94 reef. The sandy slope presented much plastic debris and abandoned fishing gear, which was

95 used as a substrate for individuals of *A. spatuligera*. On this site, three individuals of *A.*
96 *spatuligera* were observed next to three specimens of the lobed anemone *Antholoba achates*
97 (Drayton, 1846). The highest abundance of this species was recorded in the rocky reef of
98 Pichidangui at depth ranges between 40-58 m. On this site, we found variable numbers
99 ranging from a single individual to an aggregation of 11 sea urchins on the rocky substrate
100 (Figure 2). The artificial reef with the lowest abundance (10 individuals) was the deepest
101 wreck at 63 m. The organisms with the smallest recorded size were found on the sandy slope
102 with debris, while the organisms with the largest sizes were observed on the rocky reef of
103 Pichidangui.

104 Twelve individuals were collected at 53 meters' depth off Pichidangui (Figure 1) for
105 specimen identification in May 2023. The collected specimens exhibit striking similarities in
106 all aspects to those photographed during the initial fieldwork in 2022 (Fig. 2I-O). Samples
107 were preserved in 95% ethanol and prepared for morphological observations and DNA
108 sequencing. To perform morphological observations, tests were cleaned off using a brush
109 and a diluted bleach solution, allowing removal of all spines and soft tissues to reveal the
110 plate patterns. Systematic nomenclature and terminology for morphological description
111 follow Kroh (2020). Plates are numbered according to Lovén's system (Lovén, 1874).

112 The isolation of DNA, PCR, and preparation for Sanger sequencing were performed in the
113 Molecular Ecology Laboratory of the Millennium Institute of Biodiversity of Antarctic and
114 Subantarctic Ecosystems at Universidad de Chile, Chile. DNA was extracted from the spines
115 and gonads preserved in 95% ethanol using the Dneasy Blood & Tissue Kit by QIAGEN.
116 The mitochondrial genome's Cytochrome Oxidase subunit I (COI) was amplified for seven
117 individuals. COI primers specific to the genus *Arbacia* were used, ArbaF and ArbaR (Haye
118 et al., 2014). PCR's were performed using Accustart II PCR ToughMix (ref. 95142-800)
119 following notice volumes (for a 50 µl PCR reaction, 5 µl of total genomic DNA, 1 µl of each
120 primer and 25 µl of Taq polymerase). Cycling conditions consisted of an initial denaturation
121 at 94°C for 3 min followed by 40 cycles of 1 min denaturing at 94°C, 45 sec annealing at
122 45°C, and a 1 min extension at 72°C., with a final 3min extension at 72°. Sequencing was
123 performed in one direction using automatic sequencers from MACROGEN Chile.

124

125 Results

126 **Genetic data.** All seven specimens sequenced from Pichidangui correspond to one unique
127 COI haplotype of *Arbacia spatuligera*, already recorded by Millán et al. (2019). The
128 haplotype sequence was deposited in the GenBank database (GenBank accession member
129 requested). It corresponds to the COI haplotype “AspaCN1” (GenBank accession number:
130 MK382495.1), and this haplotype corresponds to the Hap1 on the haplotype network
131 presented by Millán et al. (2019) and aligns with the most prevalent haplotype (114 out of
132 140 individuals; Millán et al., 2019) within *A. spatuligera*, found from Concepción (Chile)
133 to Lima (Peru) in shallow water (0-30 m).

134 **Morphological data.** The specimens observed along the coasts of Valparaíso (Fig. 2A-H)
135 exhibit the typical morphology of *Arbacia spatuligera* as described by Mortensen (1935) and
136 Larraín (1975): they are characterized by white, short, and club-shaped spines on the aboral
137 side and long, and slender spines at the ambitus. The test coloration is light brown, and the
138 interambulacrum is marked by a vestigial bare interambulacral area in larger specimens, in
139 accordance with previous descriptions by Mortensen (1935) and Larraín (1975). In contrast,
140 samples from Pichidangui (Fig. 2I-O) were distinguished by long and slender dark brown
141 spines extending adapically along the interambulacrum up to the apical system. The test
142 coloration in these specimens is dark green, which deviates from the typical light brown to
143 light green coloration observed in other studied specimens.

144 The morphological study of specimens from Pichidangui enabled the identification of
145 diagnostic characters of the species *A. spatuligera* (Fig. 3A-C) as described by Mortensen
146 (1935) and Larraín (1975). It includes a narrow naked interambulacral area reduced to the
147 interradius in larger specimens (Figure 3C), poorly developed aboral ambulacral tubercles
148 that do not reach the ocular plates (Figure 3A), supra-anal plates forming a pyramid shape
149 with small and narrow extensions at the tips (Figure 3A), and larger ambulacral pores
150 compared to other species of the genus (Figure 3C). However, specimens from Pichidangui
151 also show unique morphological characters that had been not reported in *Arbacia spatuligera*
152 so far (Valenciennes, 1846; Koehler, 1914; Lovén, 1887; Mortensen, 1910, 1935; L. Agassiz
153 & Desor, 1846; A. Agassiz, 1872; A. Agassiz & Clark, 1908). Interambulacral tubercles are
154 large, with usually three tubercles per plate of a subequal size above the ambitus and the same

155 size throughout the aboral surface (Figure 3A, C). The adoral area is characterized by shorter
156 phyllodes and a pentagonal peristome (Figure 3B). This population's tags are much smaller,
157 only reaching the second interambulacral plate (Figure 3B). The aboral spines are brown,
158 long and slender, even close to the apical system, and the test shows an overall dark green
159 coloration (Figure 2I-O). These morphological variations have prompted the need for an
160 amended diagnosis to describe and characterize *A. spatuligera* accurately.

161 **Systematic part**

162 Phylum Echinodermata Klein, 1778

163 Class Echinoidea Schumacher, 1817

164 Order Arbacioida Gregory, 1900

165 Family Arbaciidae Gray, 1855

166 Genus *Arbacia* Gray, 1835

167 *Arbacia spatuligera* (Valenciennes, 1846)

168 1846 *Echinus (Agarites) spatuligera* Agassiz & Desor: p. 353.

169 1872 *Arbacia spatuligera* A. Agassiz: p. 93; p. 403, pl. 35, fig 7.

170 1912 *Arbacia spatuligera* Jackson: p. 115; p. 158.

171 1914 *Arbacia spatuligera* Koehler: p. 240; pl. 12, figs. 14;19–20.

172 1935 *Arbacia spatuligera* Mortensen: p. 577–579; pl. 70, figs 1–5; pl. 71, fig 6; pl. 87, figs
173 1–6.

174 **Emended diagnosis.** *Arbacia* with ambulacral tubercles not reaching the apical system; tip
175 of supra-anal plates with a small and narrow extension; extended phyllodes, resulting in a
176 highly intricate contour of the peristome; interambulacral bare area vestigial in the largest
177 specimens ($D > 65$ mm); color brown to green; spines white to light brown.

178 **Type material.** Type specimen never established. Larraín (1975) defined a neotype, housed
179 in the Museum of the Zoological Department of the Universidad de Concepción, Chile under
180 reference number 7966.

181 **Occurrence.** *A. spatuligera* is found within the Warm Temperate Southeastern Pacific
182 Province (Spalding et al., 2007), spanning a latitude range from 42° to 6°S between Puerto
183 Montt (south-central Chile) to Chiclayo (northern Peru). Mortensen (1935) mention the

184 presence of *A. spatuligera* in Guayaquil, Ecuador, near 2°S latitude, in the Tropical Eastern
185 Pacific Province. However, none of the specimen preserved in the large, extensive collection
186 of the natural history museum comes from Ecuador and this occurrence remains doubtful.

187 It was initially reported from the subtidal zone, as documented by Mortensen (1935), Larraín
188 (1975), and Millán et al. (2019). Our study reveals its presence in deeper mesophotic
189 environments as well.

190 **Emended description.** Test circular to subpentagonal in outline at ambitus. Test large,
191 reaching 70 to 80 mm in diameter. Living specimens dark brown to dark green, with lighter,
192 usually white, spines. Denuded test light green, sometimes deep brown. Allometric
193 relationship between test height and test diameter described by linear regression model $\ln(y)$
194 $= 1.05\ln(x) - \ln(0.8554)$; $R^2 = 0.9136$.

195 *Apical system* Small, dicyclic to hemicyclic, with no tubercles. Ocular plates usually exert
196 (53%) in large specimens (TD > 40 mm), plate V often insert (47%) and plates I rarely insert
197 (5%). Plates I and IV closer to periproct margin. Juveniles always with dicyclic apical system,
198 ocular plates becoming insert with growth. Ocular and genitals free of tubercles in adults.
199 Periproct oval with maximum diameter in direction 1-IV, as it is usually the case in species
200 of the genus *Arbacia*. Gonopores small, slightly elongated. Ocular plates with numerous
201 ophicephalous pedicellariae, connected to the plate by a small, circular granule.

202 *Peristome* Relative peristome diameter large, usually close to 50% of the test diameter.
203 Buccal notches deep, tags usually long and narrow (spanning up to 3 tubercles), shorter in
204 specimens from Pichidangui (spanning < 2 tubercles). Peristome shape usually characterized
205 by extended phyllodes, resulting in a highly intricate contour of the peristome. Perignathic
206 girdle thin and long, auricles usually not in contact, forming an arch over the perradius.
207 Peristome relative size decreasing with growth. Allometric relationship between peristome
208 diameter and test diameter described by linear regression model $\ln(y) = 0.7088 \ln(x) + \ln$
209 (0.4042) ; $R^2 = 0.902$.

210 *Ambulacra* Narrow (half of the interambulacra), each plate with one imperforate and non-
211 crenulate primary tubercle of the same size as interambulacral ones at the ambitus and
212 quickly decreasing in size adapically. Tubercles spaced aborally, not reaching apical system.

213 Tubercles separated by fine granules at the perradial suture. Ambulacral plates trigeminate
214 from ambitus to apical system, of arbaciid type aborally, forming more complex compound
215 plating adorally and leading to narrow phyllodes adorally. Aborally, pores of a pair deeply
216 conjugate, and pore-pairs separated by marked ridges. Neural canal poorly developed. Close
217 to peristome, single perradial pit for sphaeridium along perradius of each ambulacrum.

218 *Interambulacra* Wide, with up to five imperforate and non-crenulate primary tubercles per
219 plate at the ambitus, all similar in size in large specimens (TD > 70 mm). Smaller specimens
220 (TD < 50 mm) bear three to four tubercles at ambitus. Tubercles decrease in size above the
221 ambitus. Inner tubercles abutting the oral suture of the plate and usually decreasing in size
222 toward interradius, except for specimens from Pichidangui with subequal tubercles aborally
223 (Fig. 3). Adradial column of large primary tubercles reaches the apical system. The second
224 column of tubercles almost reaches the apical system. Tubercles with large mamelons,
225 narrow platforms, and broad areoles, occupying most of plate width at ambitus. Except for
226 naked interradian area, plates coarsely granulated between tubercles. Bare area usually
227 restricted to interradius and vestigial in large specimens (TD > 70 mm). Number of
228 interambulacral plates high, usually between 15-16 plates (TD = 40 mm) and 17 plates (TD
229 = 50 mm). Large specimens, reaching 70 mm TD, bears up to 21 interambulacral plates.
230 Height of plates not varying along aboral surface adapically.

231 *Pedicellariae* of three types, ophicephalous, tridentate and triphyllous, abundant over the test.
232 All pedicellariae are white in adult specimens.

233 Ophicephalous pedicellariae (Fig. 5A, B) differentiated between the oral and aboral sides.
234 Aboral surface covered with numerous ophicephalous pedicellariae, including area
235 surrounding the apical system. Valves of ophicephalous pedicellariae circular, narrow, and
236 constricted in upper part, with indented and sharply serrated blade edges (Fig. 5A). Buccal
237 membrane covered by second type of ophicephalous pedicellariae (Fig. 5B) with higher,
238 elongated valves, indented blade edges, and slight serration. Upper part of the valve slightly
239 constricted.

240 Tridentate pedicellariae (Fig. 5C-D) small, being only twice as long as ophicephalous
241 pedicellariae. Abundant on both oral and aboral surface, including on ocular plates but absent
242 on buccal membrane. Valves of tridentate pedicellariae slender, elongated, and not

243 constricted in the middle. Blade edges finely serrated. Width-to-length ratio varies between
244 0.51 and 0.63 (Fig. 5C-D).

245 Triphyllous pedicellariae scarce and resemble those found in other *Arbacia* species, as noted
246 by A. Agassiz & Clark (1908) and Larrain (1975). Valves of triphyllous pedicellariae
247 elongated and constricted in middle part. Blade edges finely serrated.

248 *Spines* Two morphologies of *A. spatuligera* spines are known. Typical form with aboral
249 spines short and robust, exhibiting a distinctive "club-shaped" morphology (Mortensen,
250 1935); long, and slender at ambitus. Spines length usually equal to test diameter, up to 50
251 mm. Specimens from Pichidangui with long and slender spines over the entire aboral side,
252 up to apical system. Presence of long and sturdy aboral spines, consistently sized across the
253 aboral surface, linked to the presence of large, equally sized interambulacral tubercles.
254 Ambital and subambital spines with large "enameled" tips. Spines white in typical form, but
255 appear darker, approaching a brown hue in long-spine form.

256 **Remarks.** The presence of a well-developed epistroma, of sphaeridia positioned in adoral
257 pits in each perradius, of imperforate and non-crenulate tubercles, and of a periproct with
258 four anal plates support the assignment of the species to the order Arbacioida. The compound,
259 arbaciid-like plates of ambulacra, the occurrence of tubercles similar in size in both
260 ambulacra and interambulacra at the ambitus, and of a clear difference in tuberculation
261 between the oral and aboral side (aboral tubercles highly reduced in size and number), are
262 diagnostic of the family Arbaciidae. The presence of a straight pore-zone with tube feet not
263 arranged into in arcs of three, of ambulacral tubercles forming a regular series throughout, of
264 a large peristome (> 30% of test diameter), of interambulacra with numerous primary
265 tubercles arranged in horizontal and vertical series, of a single sphaeridial pit near the
266 peristomial edge in each interambulacrum, and of straight and finely striated spines with an
267 enameled tip are all diagnostic characters of the genus *Arbacia*.

268

269

270

271

272 Discussion

273 Specimens of *A. spatuligera* from Pichidangui depart from the typical morphology of the
274 species formerly described (Mortensen 1935, Larraín 1975), which raises questions about the
275 underlying processes at play. These morphological variations have prompted the need for an
276 amended diagnosis to describe and characterize *A. spatuligera* accurately. The absence of
277 genetic difference in COI gene between the two morphotypes suggests that morphological
278 differences observed between the specimens from Pichidangui and the typical form are not
279 the result of a genetic differentiation linked to either geographic isolation or ecological niche
280 evolution in deeper environments. Millán et al. (2019) emphasized the absence of genetic
281 structure and unexpectedly low genetic diversity in populations of *A. spatuligera* over its
282 entire distribution range. Additionally, they found evidence of a recent demographic
283 expansion of the species, estimated to have occurred 33,000 to 47,000 years ago. This is in
284 line with the unique haplotype found in the studied specimens and the absence of genetic
285 difference identified in COI sequences between the two morphologies.

286 The observed morphological variations may also result from phenotypic plasticity. The
287 differences in spine length and color are typical of ecophenotypic variations observed in
288 echinoids. Phenotypic plasticity could be defined as the environmental sensitivity of a
289 genotype to produce alternative phenotypes in response to environmental cues (Fusco &
290 Minelli, 2010). Environmental conditions, particularly water currents, frequently influence
291 spine length. The occurrence of the studied specimens in a deep and calm environment with
292 reduced tidal influence may have favored the long spine morphology. The size and density
293 of spines could also play a significant role in providing protection against predators (Smith,
294 1980). The presence of long and sturdy aboral spines, with large, equally sized
295 interambulacral tubercles, can be readily explained by the necessity of these spines to have a
296 substantial, large muscle surface area for attachment (Smith, 1980). The quantity of oral tube
297 feet significantly impacts the ability to adhere to the substrate, and the observed reduction in
298 the size of phyllodes in specimens from Pichidangui in a low-energy environment aligns with
299 the ecophenotypic interpretation.

300

301 It is important to note that a population of *A. spatuligera* with a “typical morphology” has
302 also been observed in mesophotic environments along the coasts of Valparaiso (Fig. 2A-H)
303 at the same depth as those of Pichidangui. Moreover, another specimen, in all aspects similar
304 to those from Pichidangui, was observed at 60 m depth in Algarrobo, Chile (Fig. 7), 200 km
305 away to the south (NUTME 2023 per.com.). Subsequent investigations focusing on the
306 environmental conditions of these specimens, as well as their ecology, coupled with
307 additional genetic studies, will offer further insights into which of these two hypotheses takes
308 precedence.

309 The bathymetric distribution and habitat preference of the genus *Arbacia* widely varies
310 depending on the species. For instance, the Atlantic purple sea urchin (*Arbacia punctulata*)
311 is located at a maximum depth of 255 m (Hill & Lawrence, 2003) while *A. lixula* is well
312 adapted to shallow waters of the upper infralittoral in the Mediterranean Sea and Madeira
313 Island (Roma et al., 2021). On the other hand, the green sea urchin *Arbacia dufresnii* located
314 from the Pacific Ocean from Puerto Montt (locality where the distribution area of *A.*
315 *spatuligera* ends) to the Falkland Islands (Bernasconi, 1966) has the deepest distribution of
316 the genus reaching depths of 315 m (Bernasconi, 1953).

317 The present study extends the known bathymetric range of *A. spatuligera* from 30 to 63 m
318 depth, which is within the range of other species of the genus. No data on the species' density
319 and preferred habitat were available so far. We report that the number of individuals present
320 in each mesophotic reef is low compared to shallow sites in other locations on the Chilean
321 coast (Table I). For example, in the Biobio region, located ~556 km away from our study
322 area, we have recorded up to 220 individuals in Penco and 188 organisms in Laraquete (pers.
323 obs.); both localities do not exceed 8 m depth. Habitat preference in shallow locations was
324 consistent with the presence of a rocky bottom and holdfast and blades of giant kelp
325 (*Macrosystis pyrifera*) and co-occurrence with the black sea urchin *Tetrapygyus niger* and the
326 red sea urchin *Loxechinus albus* (Fig. 6).

327 The abundance of *T. niger* in Penco was lower (55 individuals) than *A. spatuligera*. In the
328 locality of Laraquete, *A. spatuligera* co-occurred with two species of sea urchins, *T. niger*
329 (36 individuals) and *L. albus* with 12 individuals (Fig. 6). In this last locality, individuals of

330 *A. spatuligera* were also found in beds of the Magellan mussel (*Aulacomya atra*) (Molina,
331 1782).

332 Conclusions

333 The population found off the coast of Pichidangui (Chile) shows a different morphology
334 compared to all other specimens despite the lack of COI sequence divergence. This allows
335 us to amend the diagnosis and description of the species and discuss these variations as
336 potential ecophenotypic adaptation or recent geographical isolation. *Arbacia spatuligera* has
337 a bathymetric distribution ranging from 5 to 63 m in depth. The species can be found on
338 various bottom types, from rocky reefs with kelps *Macrocystis pyrifera* and *Lessonia* spp.,
339 filamentous algae, beds of the bivalve *Aulacomya atra*, to artificial reefs such as shipwrecks
340 and sandy bottoms with hard substrate. It is necessary to continue with studies in this species
341 to determine if there are differences between the feeding habits in shallow and mesophotic
342 organisms. Finally, technical diving using Closed Circuit Rebreathers (CCRs) is a
343 fundamental tool in scientific diving for generating novel ecological knowledge in deep
344 zones below 30 m depth, the recreational diving limit.

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349 Author contributions

350 Rigoberto Moreno-Mendoza: Work conception, data acquisition, analyses, data
351 interpretation, manuscript draft. Erwan Courville: taxonomic identification molecular data
352 acquisition, photography, manuscript draft. Luis Angeles Gonzalez: analyses, data
353 interpretation, manuscript draft. Julio Duarte-Gutierrez: conception, analyses, data
354 interpretation, manuscript draft. Marc Carulla: data acquisition, photography, manuscript
355 draft. Daniel Malfanti-Bravo: conception, data acquisition, manuscript draft. Andrés Mena-
356 Auladell: data acquisition, manuscript draft. Elie Poulin: molecular data acquisition,
357 manuscript draft. Thomas Saucède: taxonomic identification, manuscript draft. Nuno
358 Simões: data acquisition, analyses, data interpretation, manuscript draft.

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364 Conflict of interest

365 The authors declare none.

366 Ethical standards

367 Does not apply

368 References

369 **Agassiz A** (1872) *Revision of the Echini. Illustrated Catalogue of the Museum of*
370 *Comparative Zoölogy at Harvard College*. Cambridge [Mass.]: University Press.

371 **Agassiz A and Clark HL** (1908) *Hawaiian and other Pacific Echini. The Salenidae,*
372 *Arbaciadae, Aspidodiadematidae, and Diadematidae*. Cambridge: Printed for the Museum.

373 **Agassiz JLR and Desor PJÉ** (1846) *Catalogue Raisonné of the Families, Genera and*
374 *Species of the Class of Echinoderms: A translation of Agassiz, Louis, Desor, E. 1846.*
375 *Catalogue raisonné des familles des genres et des espèces de la Classe de Echinodermes.*
376 *Annales des sciences naturelles. Herizos Press, Tampa* **6**, 305–374.

377 **Bernasconi IM** (1953) *Monografía de los equinoideos argentinos. Anales Museo Historia*
378 *Natural de Montevideo* **6**, 23-25.

379 **Bernasconi IM** (1966) *Los equinoideos y asteroideos colectados por el buque oceanografico*
380 *R/V" Vema", frente a las costas Argentinas, Uruguayas y sur de Chile. Coni.*

381 **Blainville H-MD** (1825) *Manuel de malacologie et de conchyliologie*. Paris: F. G. Levrault.

382 **Eyal G and Pinheiro HT** (2020) *Mesophotic ecosystems: the link between shallow and*
383 *deep-sea habitats. Diversity* **12**, 411.

- 384 **Gianguzza P and Bonaviri C** (2013) *Arbacia*. In Miller Lawrence J.(ed). Elsevier, pp. 275-
385 283.
- 386 **Gray J** (1835) On the genera distinguishable in Echinus Lamarck. *Proceedings of the*
387 *Zoological Society of London* **3**, 57–60.
- 388 **Gray J** (1855) An arrangement of the families of Echinida, with descriptions of some new
389 genera and species. *Proceedings of the Zoological Society of London* **23**, 35–39.
- 390 **Gregory J** (1900) The Echinoderma. In *A Treatise on Zoology*, Lankester, E.R, pp. 237–281.
391 Adam & Charles Black, London.
- 392 **Haye PA, Segovia NI, Muñoz-Herrera NC, Gálvez FE, Martínez A, Meynard A, Pardo-**
393 **Gandarillas MC, Poulin E and Faugeron S** (2014) Phylogeographic Structure in Benthic
394 Marine Invertebrates of the Southeast Pacific Coast of Chile with Differing Dispersal
395 Potential. *PLOS ONE* **9**, e88613.
- 396 **Hill SK and Lawrence JM** (2003) Habitats and Characteristics of the Sea Urchins
397 *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) on the Florida Gulf-Coast
398 Shelf. *Marine Ecology* **24**, 15-30.
- 399 **Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, ... and**
400 **Appeldoorn R** (2010) Theme section on Mesophotic coral ecosystems: characterization,
401 ecology, and management. *Coral reefs* **29**, 247-251.
- 402 **Iken K, Brey T, Wand U, Voigt J and Junghans P** (2001) Food web structure of the benthic
403 community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progress*
404 *in Oceanography* **50**, 383-405.
- 405 **Jackson RT** (1912) Phylogeny of the Echini: with a revision of palaeozoic species. *Memoirs*
406 *of the Boston Society of Natural History* **7**, 1–491.
- 407 **Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E and Toonen**
408 **RJ** (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* **29**, 255-
409 275.

- 410 **Klein JT** (1778) *Naturalis Dispositio Echinodermatum. Accessit Lucubratiuncula de Aculeis*
411 *Echinorum Marinorum et Specilegium de Belemnitis. Edita et Descriptionibus Novisque*
412 *Inventis et Synonymis Auctorum Auca a Nathanaele Godofredo Leske. Officina*
413 *Gleditdchiana, Lipsiae (Leipzig).*
- 414 **Kramer N, Eyal G, Tamir R and Loya Y** (2019) Upper mesophotic depths in the coral
415 reefs of Eilat, Red Sea, offer suitable refuge grounds for coral settlement. *Scientific Reports*
416 **9**, 1-12.
- 417 **Koehler R** (1914) *Echinoderma I*. Hamburg: Friederichsen and Co.
- 418 **Lamarck J** (1816) *Histoire Naturelle des Animaux sans Vertèbres, présentant les caractères*
419 *généraux et particuliers de ces animaux, leur distribution, leur classes, leurs familles, leurs*
420 *genres, et le citation des principales espèces qui s’y rapportent; précédée d’une Introduction*
421 *offrant la Détermination des caractères essentiels de l’animal, sa distinction du végétal et*
422 *des autres corps naturels, enfin, l’Exposition des Principes fondamentaux de la Zoologie.*
423 *Verdière, Paris.*
- 424 **Larraín A** (1975) Los equinoideos regulares fósiles y recientes de Chile. *Gayana Zoología*
425 **35**, 5-189.
- 426 **Lebrato M, Iglesias-Rodríguez D, Feely RA, Greeley D, Jones DO, Suarez-Bosche N, ...**
427 **and Alker B** (2010) Global contribution of echinoderms to the marine carbon cycle: CaCO₃
428 budget and benthic compartments. *Ecological Monographs* **80**, 441-467.
- 429 **Lessios HA, Lockhart S, Collin R, Sotil G, Sanchez-Jerez P, Zigler KS, ... and Kessing**
430 **BD** (2012) Phylogeography and bindin evolution in *Arbacia*, a sea urchin genus with an
431 unusual distribution. *Molecular Ecology* **21**, 130-144.
- 432 **Linné CV** (1758) *Systema naturae. Tomus I, Regnum animale. Holmiae: Laurentii Salvii.*
- 433 **Lovén S** (1874) Études sur les Échinoïdées. *Kongliga Svenska Vetenskaps-Akademiens*
434 *Handlingar* **11**, 1–91.
- 435 **Lovén S** (1887) *On the species of Echinoidea described by Linnaeus in his work Museum*
436 *Ludovicae Ulricaе, Vol. 13. Kongl. boktryckeriet.*

- 437 **Luparello C, Ragona D, Asaro DML, Lazzara V, Affranchi F, Arizza V and Vazzana**
438 **M** (2020) Cell-free coelomic fluid extracts of the sea urchin *Arbacia lixula* impair
439 mitochondrial potential and cell cycle distribution and stimulate reactive oxygen species
440 production and autophagic activity in triple-negative MDA-MB231 breast cancer cells.
441 *Journal of Marine Science and Engineering* **8**, 261.
- 442 **Micael J, Alves MJ, Costa AC and Jones MB (2016)** Exploitation and conservation of
443 echinoderms. In *Oceanography and Marine Biology* pp. 203-220. CRC Press.
- 444 **Millán C, Díaz A, Poulin E, Merino-Yunnissi C and Martínez A (2019)** Genetic diversity
445 and demographic history of the endemic Southeastern Pacific sea urchin *Arbacia spatuligera*
446 (Valenciennes 1846). *Gayana*, **83**, 81-92.
- 447 **Molina GI (1810)** *Saggio sulla storia naturale del Chili*. Masi.
- 448 **Mortensen T (1910)** *Echinoidea of the Swedish South Polar Expedition*, Nordenskjöld O.
449 Stockholm: Lithographisches Institut.
- 450 **Mortensen T (1935)** A monograph of the Echinoidea. v II. Bothriocidaroida,
451 Melonechinoida, Lepidocentroida and Stirodonta. C.A. Reitzel, Copenhagen.
- 452 **Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz O J, Pyle RL and**
453 **Bongaerts P (2018)** Mesophotic coral ecosystems are threatened and ecologically distinct
454 from shallow water reefs. *Science* **361**, 281-284.
- 455 **Roma J, Schertenleib K, Ramalhosa P, Gestoso I, Canning-Clode J and Lenz M (2021).**
456 Moderately elevated temperatures increase macroalgal food consumption in two sea urchin
457 species from coastal waters of Madeira. *Journal of Experimental Marine Biology and*
458 *Ecology* **542**, 151603.
- 459 **Schumacher CF (1817)** *Essai d'un nouveau système des habitations des vers testacés : avec*
460 *XXII planches*, pp. 1–348. À Copenhague: De l'Imprimerie de Mr. le directeur Schultz.
- 461 **Shreeves K and Richardson D (2006)** Mixed-Gas Closed-Circuit Rebreathers: An
462 Overview of Use in Sport Diving and Application to Deep Scientific Diving.

463 **Smith AB** (1980) The structure and arrangement of echinoid tubercles. *Philosophical*
 464 *Transactions of the Royal Society of London. B, Biological Sciences* **289**, 1–54.

465 **Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS,**
 466 **Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA**
 467 **and Robertson J** (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal
 468 and Shelf Areas. *BioScience* **57**, 573–583.

469 **Valenciennes AM** (1846) *Voyage autour du monde sur la fregate La Venus pendant les*
 470 *annees 1836-39. Atlas 4: Zoophytes.*

471 **World Echinoidea Database** <https://www.marinespecies.org/echinoidea> Accessed online
 472 10 October 2022.

473 Figures

474 **Fig. 1.** Map of distribution and records of the sea urchin *Arbacia spatuligera* in shallow (<30
 475 m depth) and mesophotic reefs (36–63 m depth) in the Southeastern Pacific Ocean: The black
 476 asterisk represents all previous records in the literature and OBIS.org; (2) the green points
 477 represents two locations of the shallow rocky reefs with *Macrocystis pyrifera*; (3) the orange
 478 point is a single location of a mesophotic rocky reef covered by turf algae; (4) the yellow
 479 point represents a mesophotic sandy slope; and finally (5) the black-flagged points represent
 480 two shipwrecks within the mesophotic reef ecosystem.

481 **Fig. 2.** Photographic records of *Arbacia spatuligera* and their habitats in three of four
 482 mesophotic temperate reefs off Central Coast of Chile: (A–C) individuals recorded on deck
 483 and hull of a shipwreck between 36–46 m deep with the presence of filamentous algae and
 484 the striped anemone *Anthothoe chilensis*; (D–H) individuals recorded on a sandy slope with
 485 plastic debris, abandoned fishing gear, and a car wheel between 40–56 m deep with the
 486 presence of filamentous algae and the lobed anemone *Antholoba achates*; (G) aggregation of
 487 10 individuals; (I–O) individuals from the rocky reef between 40–58 m deep with filamentous
 488 algae, sponges, crustose algae (order Corallinales), and channels with sand.

489 **Fig. 3.** Morphology of *A. spatuligera* from Chile: (A–C), *Arbacia spatuligera* from
 490 Pichidangui; (A), aboral view; (B), oral view; (C), lateral view; (D–F), *Arbacia spatuligera*
 491 from Las Cruces; (D), aboral view; (E), oral view; (F), lateral view. Scale bar equals 10 mm.

492 **Fig. 4.** *Arbacia spatuligera*, details of test plating. A–B, apical system: A, small specimen
 493 (TD = 30 mm); B, larger specimen (TD = 45 mm); C, aboral plate of ambulacrum; D–E,
 494 aboral plates of interambulacrum: D, small specimen (TD = 30 mm); E, larger specimen (TD
 495 = 70 mm). Scale bars equal 10 mm.

496 **Fig. 5.** A–D, SEM photographs of valves of pedicellariae of *Arbacia spatuligera*; A, valve of
 497 apical ophicephalous pedicellaria; B, valve of oral ophicephalous pedicellaria; C, valve of

498 apical tridentate pedicellaria; D, valve of apical tridentate pedicellaria. Scale bars equal 300
499 μm .

500 **Fig. 6.** *Arbacia spatuligera* new morphotype recorded off Algarrobo, Chile at 60 m deep.
501 Photo credit: Millenium Nucleus for Ecology and Conservation of Temperate Mesophotic
502 Reef Ecosystem (NUTME) 2023.

503 **Fig. 7.** Shallow records of *Arbacia spatuligera* in two rocky reefs in the Biobio Region,
504 Chile: (A-B) Laraquete; (C-D) Penco.

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For Review Only

Table I. Localities surveyed with the sampling year, geographical coordinates, country, reef type, habitat (**RRWM**: Rocky reef with *Macrocystis pyrifera*; **SWCK**: Shipwreck; **RRWCA**: Rocky reef with calcareous algae; **SSWD**: Sandy slope with debris), depth range, number of organisms, survey technique (**VC**: Visual census; **C**: Collected) diving system, and references.

Year	Location	Longitude	Latitude	Country	Reef type	Habitat	Depth range (m)	# organisms	Survey technique	Diving System	Reference
1999	Islas Lobos de Afuera	-80,7083	-6,925	Peru	Shallow	N/A	20	>50	VC	Hookah (air)	Hooker et al., 2005
2018	Lima	-77,2464	-11,9883	Peru	Shallow	N/A	10-30	17	C	Open circuit (air)	Millán et al., 2019
2018	Arica	-70,3217	-18,4531	Chile	Shallow	N/A	10-30	18	C	Open circuit (air)	Millán et al., 2019
2016	Taltal	-70,5158	-25,3897	Chile	Shallow	N/A	10-30	29	C	Open circuit (air)	Millán et al., 2019
2016	Coquimbo	-71,3531	-29,9639	Chile	Shallow	N/A	10-30	46	C	Open circuit (air)	Millán et al., 2019
2022	Pichidangui	-71,541	-32,1325	Chile	Mesophotic	RRWCA	40-58	80	VC	CCR (trimix)	This work
2022	Valparaíso	-71,6288	-33,0217	Chile	Mesophotic	SSWD	40-56	23	VC	CCR (trimix)	This work
2019	Valparaíso	-71,6188	-33,0337	Chile	Mesophotic	SWCK	58-63	10	VC	CCR (trimix)	This work
2022	Valparaíso	-71,6092	-33,0359	Chile	Mesophotic	SWCK	36-46	15	VC	CCR (air)	This work
N/A	Faro Cabo Carranza	-72,7	-35,5667	Chile	Shallow	N/A	NA	N/A	C	N/A	David et al., 2005
N/A	Los Morros	-73	-36,5333	Chile	Shallow	N/A	NA	N/A	C	N/A	David et al., 2005
N/A	Costa Larga	-73,1	-36,6667	Chile	Shallow	N/A	NA	N/A	C	N/A	David et al., 2005
2021	Penco	-72,9963	-36,7292	Chile	Shallow	RRWM	5,1	220	VC	Open Circuit (air)	This work
2016	Concepción	-73,1703	-36,7603	Chile	Shallow	N/A	10-30	30	C	Open circuit (air)	Millán et al., 2019
2021	Laraquete	-73,1735	-37,1411	Chile	Shallow	RRWM	7,4	188	VC	Open Circuit (air)	This work

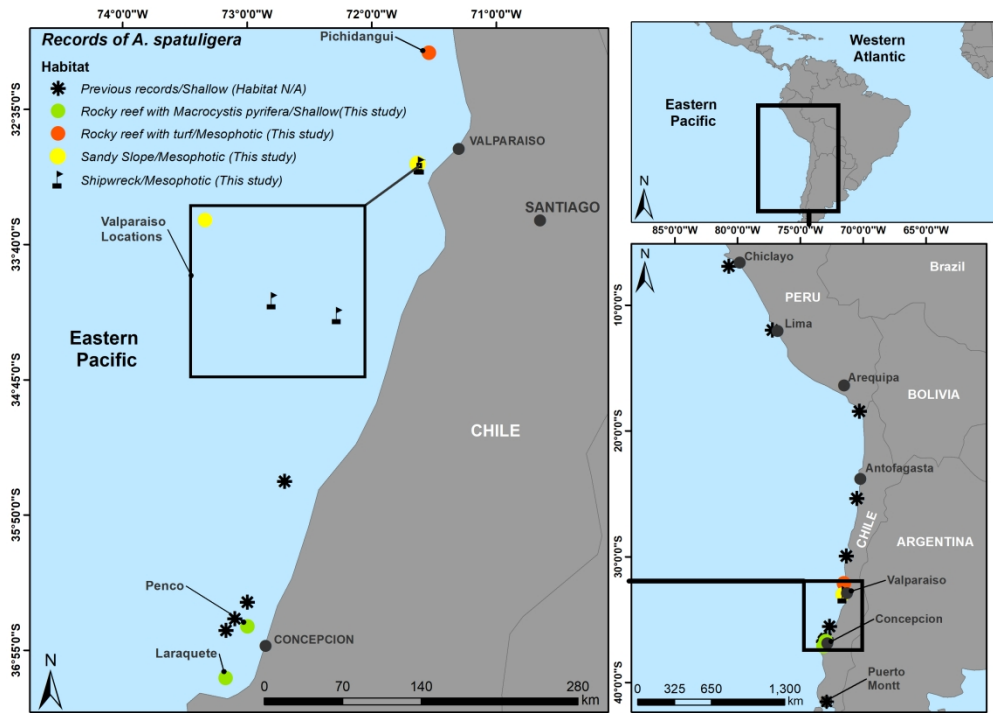


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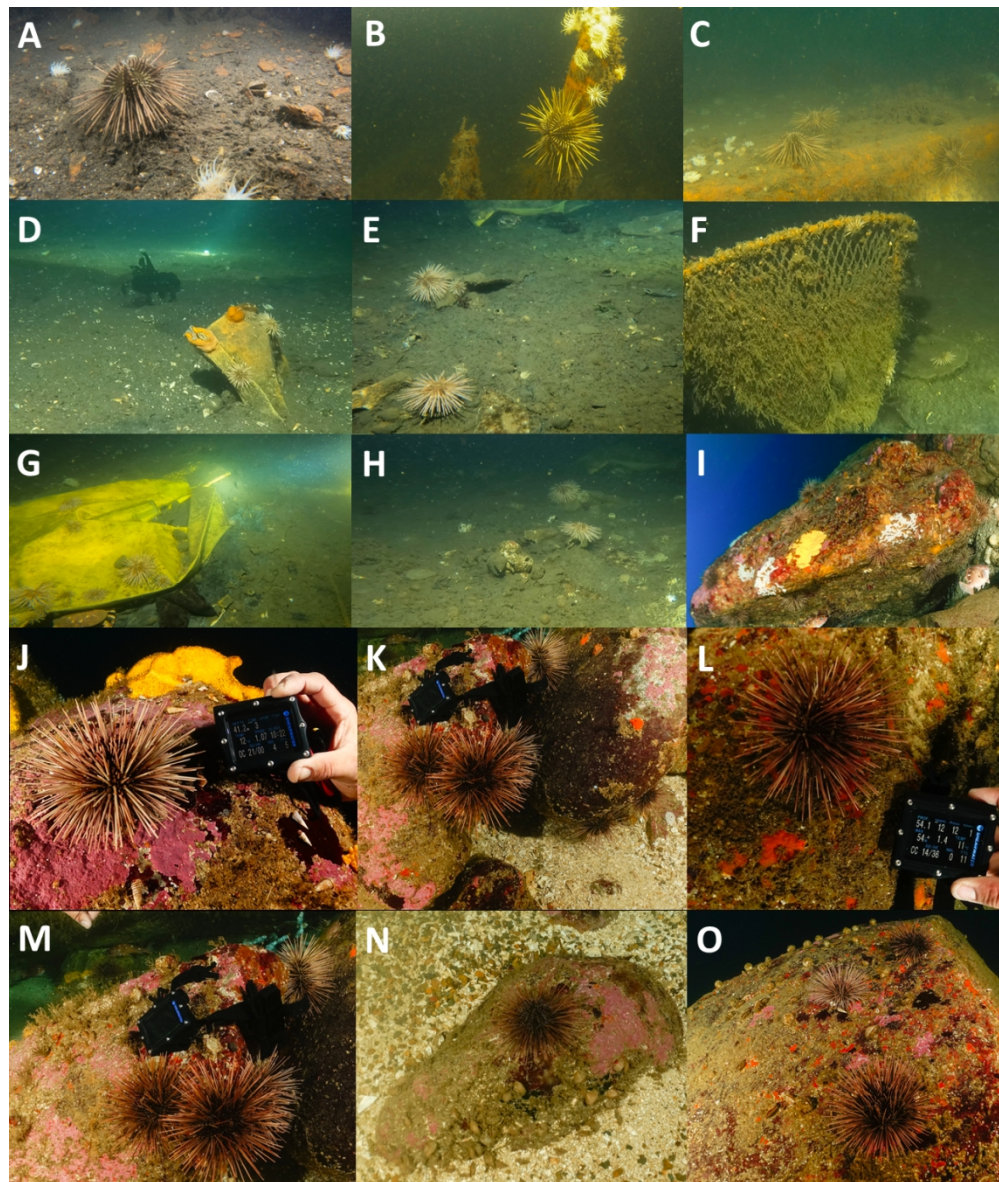


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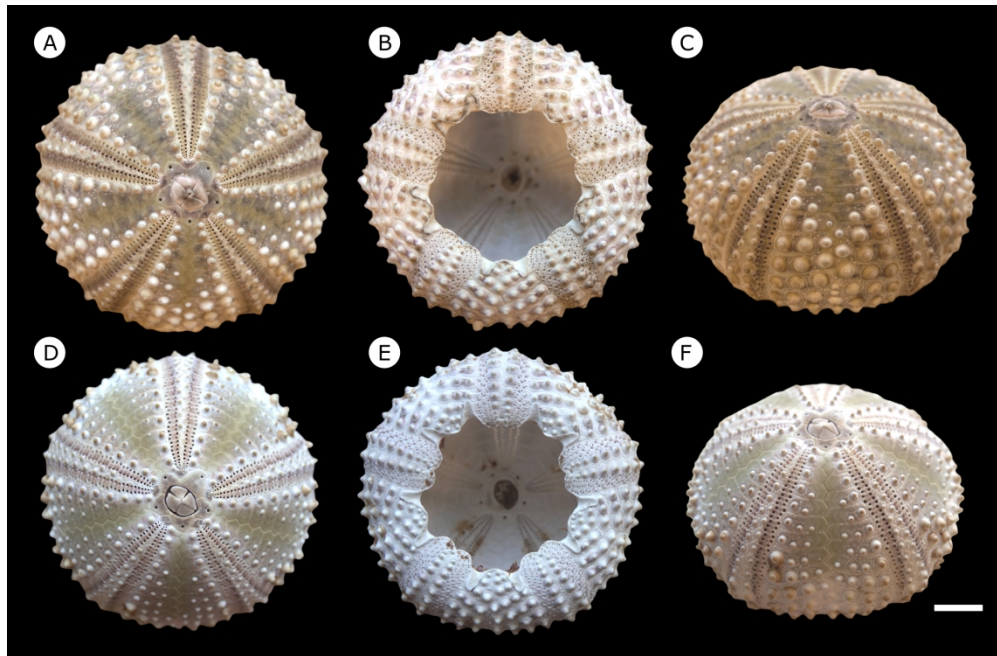


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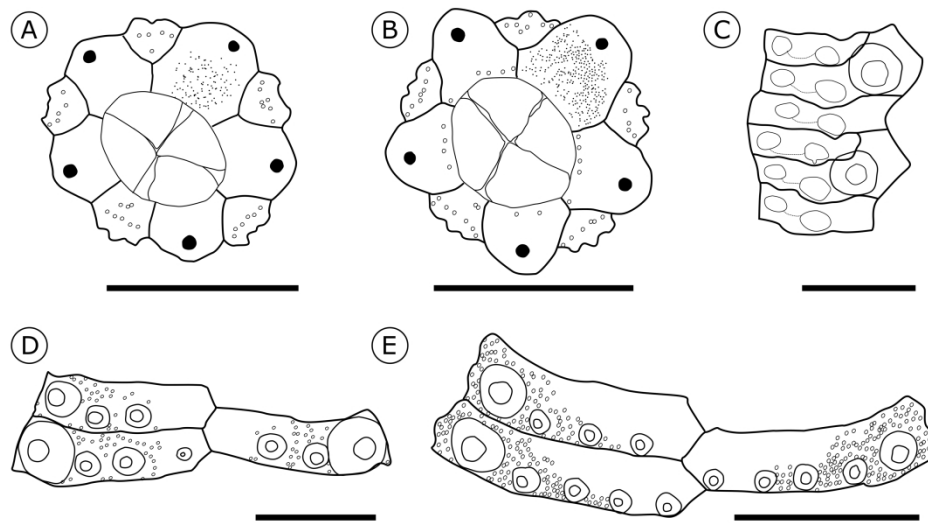


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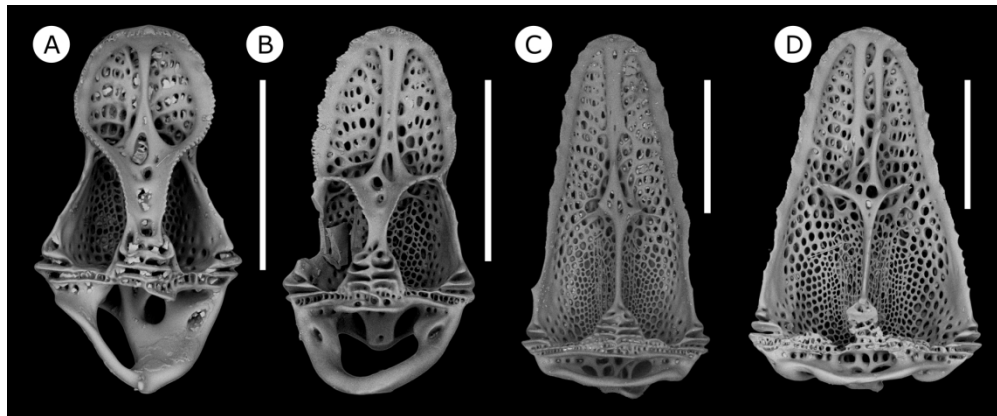


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170x70mm (300 x 300 DPI)

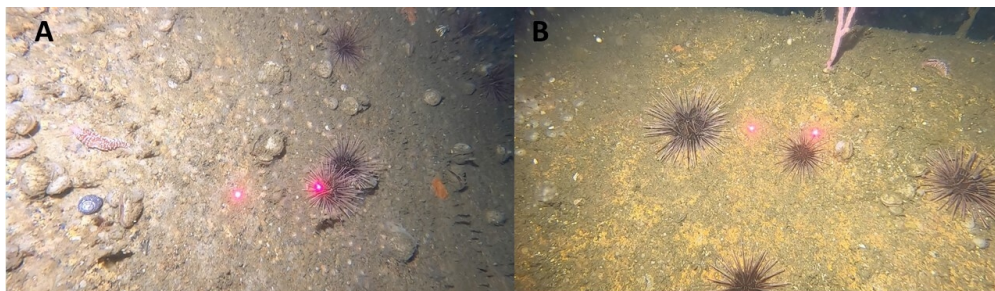


Fig. 6. *Arbacia spatuligera* new morphotype recorded off Algarrobo, Chile at 60 m deep. Photo credit: Millenium Nucleus for Ecology and Conservation of Temperate Mesophotic Reef Ecosystem (NUTME) 2023.

108x31mm (300 x 300 DPI)

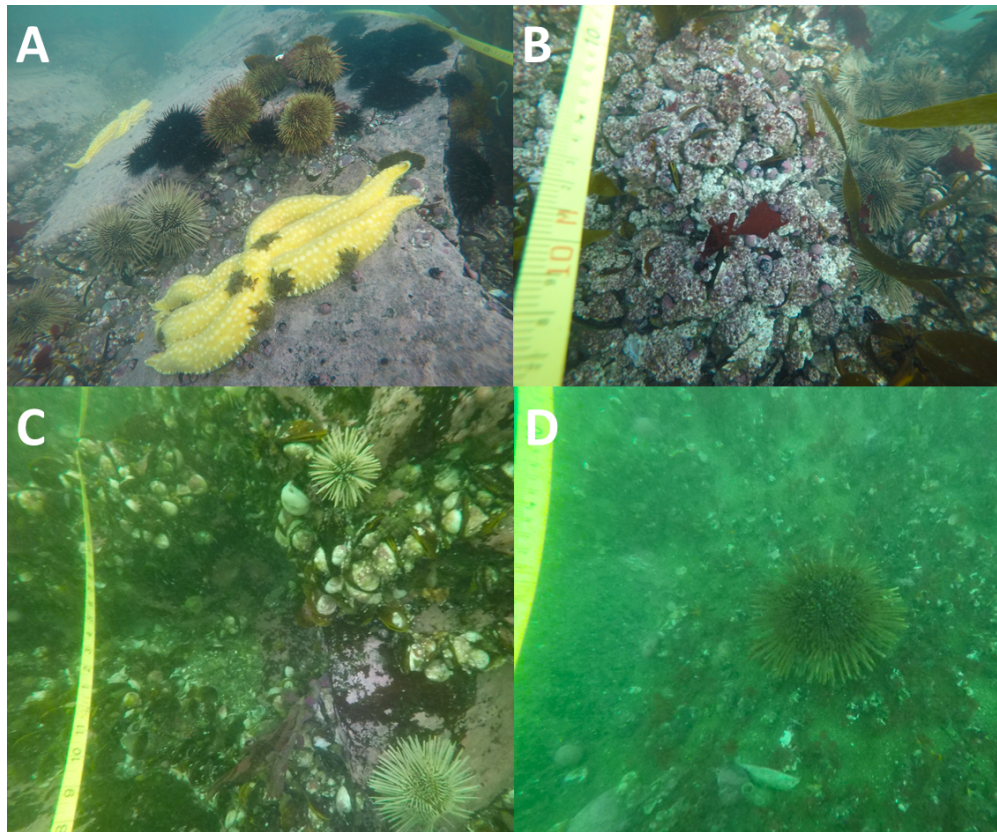


Fig. 7. Shallow records of *Arbacia spatuligera* in two rocky reefs in the Biobio Region, Chile: (A-B) Laraquete; (C-D) Penco.

96x79mm (300 x 300 DPI)