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1 **NEW SPECIES OF THE GENUS *ARBACIA* (ECHINOIDEA, ARBACIIDAE)**
2 **FROM THE NEOGENE OF CHILE**
3 **NUEVAS ESPECIES DEL GÉNERO *ARBACIA* (ECHINOIDEA, ARBACIIDAE)**
4 **DEL NEÓGENO DE CHILE**

5
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19 Short Description: New fossil echinoids from the Neogene of Chile give more clues to
20 decipher the paleobiogeography of South America.

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22

23

24 **Abstract.** Recent fieldwork on Neogene deposits of northern Chile led to the discovery of
25 new material including three new species of the echinoid genus *Arbacia*: *Arbacia quyllur*
26 sp. nov. from the Miocene, *Arbacia terraeignotae* sp. nov. and *Arbacia larraini* sp. nov
27 from the Pliocene. In the Pleistocene, the new material includes the first fossil occurrence
28 of the extant species *Arbacia spatuligera* and new specimens of the extant species
29 *Tetrapygyus niger*. The specimens and new species here described reveal the significant
30 past diversity of the genus *Arbacia* and increase our knowledge of the overall diversity of
31 the genus in South America, showing an older origin (upper Miocene) and higher species
32 richness of the genus *Arbacia* along the Chilean coasts than previously thought.

33 **Keywords.** Paleobiogeography. Fossils. Echinoid. *Arbacia*. Chile.

34 **Resumen.** NUEVAS ESPECIES DEL GÉNERO *ARBACIA* (ECHINOIDEA,
35 *ARBACIIDAE*) DEL NEÓGENO DE CHILE. Recientes trabajos de campo en el Neógeno
36 del norte de Chile han permitido descubrir nuevos materiales, entre ellos tres nuevas
37 especies del género de equinoideo *Arbacia*: *Arbacia quyllur* (Mioceno), *Arbacia*
38 *terraeignotae* y *Arbacia larraini* (Plioceno), pero también la primera aparición de *Arbacia*
39 *spatuligera* y nuevo material de *Tetrapygyus niger* (Pleistoceno). Los especímenes y las
40 nuevas especies aquí descritas revelan la diversidad pasada del género *Arbacia*. Estos
41 descubrimientos muestran la existencia de una mayor riqueza de *Arbacia* a lo largo de las
42 costas chilenas y un origen más antiguo del género en la costa del Pacífico Sureste
43 (Mioceno superior).

44 **Palabras clave.** Paleobiogeografía. Fósiles. Equinoide. *Arbacia*. Chile.

45

46 THE PALEOBIOGEOGRAPHY OF SOUTH AND NORTH AMERICA drastically changed during the
47 Neogene as a consequence of the uplift of the Isthmus of Panama. This major
48 paleogeographic event considerably and irreversibly impacted the composition of
49 terrestrial and marine biota of both Americas (Leigh *et al.*, 2014; O’Dea *et al.*, 2016).
50 Numerous studies documented terrestrial faunal exchanges between North and South
51 America after the closure of the Isthmus of Panama, also known as the Great American
52 Biotic Interchange (Webb, 2006; Cody *et al.*, 2010; Stehli & Webb, 2013; Leigh *et al.*,
53 2014). In the Miocene, the progressive emergence of the Isthmus of Panama also impacted
54 global ocean circulation (Schneider & Schmittner, 2006), resulting in the intensification of
55 the Gulf Stream (Nie, 2018; Auderset *et al.*, 2019), of the California Current (Kamikuri &
56 Motoyama, 2020) and Humboldt Current (Amiot *et al.*, 2008; Bosio *et al.*, 2020). In turn,
57 this affected the composition of marine fauna as well as faunal connections between North
58 and South America (Cuitiño *et al.*, 2017; Trayler *et al.*, 2020; del Río, 2021). Mainly
59 documented in Atlantic marine fauna, comparatively few studies have investigated
60 paleobiogeographic changes occurring in the east Pacific at that time to understand the
61 origin of Pacific marine fauna of North and South America.

62 The order Arbacioida Gregory, 1900 is a small clade of regular echinoids (Kroh &
63 Smith, 2010; Kroh, 2020; Mongiardino-Koch & Thompson, 2021) counting eight extant
64 genera, which are mainly represented by poorly known, deep-sea forms in the Caribbean
65 Sea, Indo-Pacific, Hawaii, Indian Ocean and Malaysia (Kroh & Smith, 2010; Smith, 2011).
66 Only three extant genera are commonly encountered in shallow waters: *Arbacia* (Gray,
67 1835), *Tetrapygus* (Agassiz, 1841), and *Coelopleurus* (Agassiz, 1840). Arbacioid
68 echinoids are characterized by unique morphological characters within regular echinoids.
69 They have a single basicoronal interambulacral plate at the margin of the peristome, while
70 this plate is generally resorbed, reduced, or internalized in other regular echinoids (Smith,

71 2011). They also show a well-developed epistroma that is a morphological feature that
72 takes the form of complex relief patterns on the echinoid test surface (Oldfield, 1976), and
73 often a strong differentiation between oral and aboral tube-feet, those on the aboral side
74 being specialized for gaseous exchange, while oral ones are highly muscular and adhesive
75 tube feet specialized to cling to the seabed (Smith, 1978; Santos *et al.*, 2005). These unique
76 characters have long put the systematics and position of arbacioids within the phylogenetic
77 tree of the class Echinoidea into question (Smith *et al.*, 2006; Kroh & Smith, 2010;
78 Mongiardino-Koch & Thompson, 2021).

79 Within the arbacioids, the genus *Arbacia* is represented by five extant species with
80 contrasting distribution ranges. *Arbacia lixula* (Linné, 1758) has a wide distribution across
81 the Atlantic Ocean, including the Brazilian coast, the Gulf of Guinea, The Azores, East
82 Atlantic Islands as well as the Mediterranean Sea. In contrast, four species of *Arbacia* are
83 restricted to the coasts of South and North America: *Arbacia punctulata* (Lamarck, 1816)
84 along west Atlantic coasts, being known from Cape Cod (Massachusetts) to French Guiana
85 (Mortensen, 1935; Durand, 1959), *Arbacia stellata* (Blainville, 1825) from California to
86 Peru, *Arbacia spatuligera* (Valenciennes, 1846) from Ecuador to Puerto Montt in Chile
87 and *Arbacia dufresnii* (Blainville, 1825), from Puerto Montt to Bueno Aires, and also
88 extending to the Falkland Islands and Tristan da Cunha in the South Atlantic (Mortensen,
89 1935). The relative richness of *Arbacia* species in the east Pacific led to infer a potential
90 origin of the genus alternatively in North or South America (Linder *et al.*, 1988, Lessios *et*
91 *al.*, 2012).

92 Seven species of *Arbacia* have been reported in the fossil record (Cooke, 1959;
93 Kier, 1972; Linder *et al.*, 1988; Ciampaglio *et al.*, 2009). Four of them are known from the
94 Oligocene to the Pleistocene of North America. *Arbacia abiquaensis* Linder *et al.* (1988) is
95 the oldest one, it was reported from the late Late Oligocene of Oregon (Linder *et al.*,

1988). *Arbacia improcera* Conrad, 1843 is known from the late late Pliocene of Florida (Tamiami Formation and Intracoastal Formation), the middle/late late Pliocene of North and South Carolina, the late Pliocene of Virginia (Yorktown Formation) and the lower Pliocene of Curaçao (Cooke, 1959; Kier, 1972; de Buissonjé, 1974; Whitmore, 1987; Campbell & Campbell, 1995; Ciampaglio *et al.*, 2009; Ciampaglio & Osborn, 2011; Osborn *et al.*, 2020). *Arbacia waccamaw* Cooke, 1941 from the late Pliocene of South Carolina (Goose Creek Limestone; Cooke, 1959) and the lower Pleistocene of Florida (Waccamaw Formation; Cooke, 1959). *Arbacia rivuli* Cooke, 1941 was reported from the lower Pleistocene of Florida (Waccamaw Formation; Cooke, 1959). Two extant species are also represented in the fossil record of North America. *Arbacia stellata* is also known from the late Pliocene of Cedros Island (Baja California, Mexico) and Pacific Beach (California). *Arbacia punctulata* (Lamarck, 1816) was reported from the mid/late Pleistocene of Florida (Anastasia Formation; Herrera *et al.*, 2006) and the middle Pleistocene of North and South Carolina (Canepatch Formation; Cooke, 1959; Ciampaglio *et al.*, 2009). In contrast, the fossil record of the genus *Arbacia* is poor in South America. It is restricted to representatives of the extant species *A. stellata* from the Late Pliocene/Pleistocene of Ecuador (Canoan Formation, Di Celma *et al.*, 2002) and *A. punctulata* in the lower Pleistocene of Venezuela (San Gregorio Formation; Mihaljević *et al.*, 2010). This poor fossil record departs from the present diversity of the genus that comprises the four extant species *A. stellata* (Blainville, 1825), *A. punctulata* (Lamarck, 1816), *A. dufresnii* Blainville, 1825 and *A. spatuligera* (Valenciennes, 1846), without mentioning the closely related species *Tetrapygyus niger* (Molina, 1782). This could suggest either a recent diversification of the genus *Arbacia* in South America, or the absence of adequate marine deposits, or taphonomic biases.

Figure 2

144

145 Specimens of *Arbacia quyllur* sp. nov. were uncovered from the Bahía Inglesa
146 Formation, located south of the town of Caldera (Atacama region; Fig. 1), which is dated
147 from the middle Miocene to the lower Pliocene on the basis of foraminifer assemblages
148 (Rojo, 1985; Marquardt *et al.*, 2000). The lower part of the Formation is dated to 16 Ma
149 (Marquardt *et al.*, 2000). The Bahía Inglesa Formation is composed of clastic, fossiliferous
150 and semi-consolidated sandstones and marls ranging from rocky shoreline to upper
151 continental slope (Marquardt *et al.*, 2000; Le Roux *et al.*, 2016). The base of the formation
152 corresponds to a basal conglomerate deposited in erosive discordance on deposits of
153 Miocene gravels (Angostura Gravels) or directly on Jurassic intrusive units (Granodiorite
154 of Morro Copiapó). Throughout its exposure, the formation lies under the Estratos de
155 Caldera Formation separated by an erosive discordance. In Bahía Inglesa and nearby
156 localities, lithofacies of coquinas, sandstones, marls and fangolites predominate. Fangolites
157 include diatoms, phosphorites, marls, and to a lesser extent cluster and breccia (Godoy *et*
158 *al.*, 2003). The Bahía Inglesa Formation was formerly divided into three lithostratigraphic
159 members: the basal Morro Member, older than late Late Miocene according to the presence
160 of the seal *Acrophona* (Walsh & Naish, 2002) and Middle-late Late Miocene according to
161 shark fauna (Suárez *et al.*, 2004); the phosphoritic Bonebed Member, late Late Miocene
162 (Tortonian, Walsh & Suárez, 2005); and the Lechero Member whose dating remains poorly
163 defined: Upper Miocene to Pliocene (4.5-2.6Ma based on microfossils according to
164 Ibaraki, 1995; Suárez & Marquardt, 2003) but the lower part of the Member was dated at
165 7.6+-1.3Ma, Tortonian (Godoy *et al.*, 2003; Marquardt *et al.*, 2000). Recent studies have
166 divided the Formation in nine different members (Le Roux *et al.*, 2016). The material
167 reported here comes from the Mina Fosforita Member (Le Roux *et al.*, 2016), more

168 precisely the upper part of the unit 4 described by Carreño (2012) and is part of the
169 Bonebed Member, according to Walsh & Suárez (2005) (Fig 2).

170 Figure 3

171 Specimens of *Arbacia terraeignotae* sp. nov. and *Arbacia larraini* sp. nov. come
172 from the Estratos de Agua Amarga Formation. This formation is located east of Caldera
173 (Fig. 1) and is dated as late late Pliocene (Marquardt *et al.*, 2000). It corresponds to a
174 succession of decametric to metric levels of coquinas, gravels and sands corresponding to
175 coastal marine environments. They overlap the Gravels of Copiapó forming a heavily
176 eroded band interpreted as an irregular former coastline, now elevated between 200 and
177 350 meters above sea level. They are covered by the Estratos de Caldera Formation
178 (Pleistocene) and wind deposits. Specimens described herein comes from two consecutive
179 levels (Fig. 3), a first one of about 15cm and composed by poorly consolidated brown
180 sands, with a high concentration of shells, both broken and complete, and the level just
181 above (50cm) of really indurated sands with a high concentration of serpulids, balanids
182 and fragmented and complete shells like pectinids or gastropods.

183 Specimens of *Arbacia spatuligera* originate from the Mejillones Formation
184 (Antofagasta region), also called the Littoral Succession of Mejillones, which corresponds
185 to marine deposits dated to the Pleistocene (Ferraris & Di Biase 1978; Cortés, 2000; Cortés
186 *et al.*, 2007). It is a sedimentary succession of clastic deposits composed of coquinas,
187 boulders, gravels and sands, more or less cemented, and corresponding to marine coastal
188 platforms, which emerged as a consequence of the uplift of the coastal area.

189 Specimens of *Tetrapygyus niger* come from the Pleistocene of Iquique. These
190 sediments are considered as coastal deposits (Pleistocene-Holocene) with conglomerates,
191 calcareous sandstones and coquinas preserved in a succession of marine abrasion terraces
192 and littoral ridges. It also includes medium to coarse calcareous bioclastic sands of

193 littoral/coastal origin that accumulate on the present-day beaches. It was deposited in a
194 littoral environment, in which the conglomerates correspond to high-energy deposits,
195 accumulated in the wave breaker zone on the rocky substrate. This environment varies
196 from littoral to sublittoral zones of lower energy, represented by sandstone and coquina
197 layers (Marquardt *et al.*, 2000; Rivadeneira & Carmona, 2008). The remarkable
198 concentration of the fossil fauna and the mixture of disarticulated shells of infaunal and
199 epifaunal organisms would indicate little transport prior to deposition (Rubilar-Rogers *et*
200 *al.*, 2009). A large proportion of bivalves and some gastropods are burrowing species that
201 currently inhabit soft substrates in intertidal to subtidal environments (Rivadeneira &
202 Carmona, 2008; Rubilar-Rogers *et al.*, 2009).

203 **SYSTEMATIC PALEONTOLOGY**

204 Systematics and terminology for morphological description follow Kroh (2020). As for
205 extant species of *Arbacia*, morphological variations during growth are important making it
206 difficult to assign the smallest specimens (below 30mm in diameter) to one or the other
207 species. Species descriptions here are based on the examination of the largest specimens
208 (above 30mm in test diameter) for which morphological differences between species are
209 clearly marked.

210 Specimens are deposited in collections of the Mining and Geology National Survey of
211 Chile (SERNAGEOMIN) (*Arbacia quyllur*), Museo Paleontológico de Caldera (*Arbacia*
212 *terraeignotae* & *Arbacia larraini*), Universidad Católica del Norte, Coquimbo (*Arbacia*
213 *spatuligera*), and the Regional Museum of Iquique (*Tetrapygyus niger*).

214 Phylum ECHINODERMATA Klein, 1778

215 Class ECHINOIDEA Leske, 1778

216 Order ARBACIOIDA Gregory, 1900

217 Family ARBACIIDAE Gray, 1855

218

Genus *Arbacia* Gray, 1835

219

Type species. *Arbacia lixula* Linné, 1758. Extant species with a wide distribution across
220 the Atlantic Ocean, including Brazilian coasts, the Gulf of Guinea, the Azores, East
221 Atlantic Islands as well as the Mediterranean Sea. Also known from the Pleistocene of
222 Madera, the Azores and Italy (Stefanini, 1911; Madeira *et al.*, 2011).

223

Arbacia quyllur sp. nov.

224

Figure 4

225

Etymology. The species name “quyllur” means Southern Star in Quechua, the indigenous
226 language spoken by Quechua peoples inhabiting the area where the fossil was discovered.

227

Type material. The Holotype n°SNGM-2034(1) (Fig. 4) is housed in Mining and Geology
228 National Survey of Chile (SERNAGEOMIN).

229

Referred material. Five denuded and complete tests along with numerous isolated spines.
230 Specimens n°SNGM-2034(1-5).

231

Locus typicus. 14 km southwest of Caldera, Copiapó Province, northern Chile. Mina
232 Fosforita Member of Bahía Inglesa Formation, late Late Miocene of Caldera, Chile. (Figs.
233 1, 2)

234

Stratigraphy. The material published here comes from a well-sorted and non-consolidated
235 fine, bioclastic and quartzitic sand layer of 1 m thickness. Three specimens were found in
236 living position (Fig. 2). The only well-preserved fossils in this band is *Arbacia quyllur* sp.
237 nov. The other species are rare, poorly preserved and almost always fragmented. The
238 associated fauna comprises bioclasts of balanids, entire shells of oysters (*Crassostrea* sp.)
239 and of small gastropods (*Concholepas kieneri* and *Acanthina katzi*, JF Araya pers. comm.
240 The section lies approximately 2.50m under a bone bed, a phosphate conglomerate
241 correlated with the Mina Fosforita Member (*ca.* 7 Ma, Late Miocene; Peralta-Prat &
242 Solórzano, 2019). It corresponds to unit 4 of Carreño (2012).

243 **Taphonomy.** Specimens of *Arbacia quyllur* sp. nov. occur exclusively as complete but
244 denuded specimens with no preserved Aristotle's lanterns. They are preserved in life
245 position with size comprised between 15 and 50mm in test diameter. Observation using a
246 scanning electron microscope highlights evidence of soft abrasion but tests are not
247 encrusted nor bioeroded. The density of specimens is low within deposits (less than 1
248 individual/m²). As mentioned below, *A. quyllur* sp. nov. is the only echinoid species found
249 in the studied deposits.

250 **Diagnosis.** Interambulacral area entirely naked aborally but for one single adradial column
251 of small tubercles, with one tubercle per plate abutting the adoral suture; gonopores large
252 (>1 mm), occupying a large part of genital plates; ambulacral plates trigeminate aborally;
253 epistroma well-developed, forming large vertical crenulations.

254 **Measurements.**

255 TABLE 1

256 **Description.** Test low domed in profile (height to diameter ratio <0.4), flattened orally,
257 test outline circular in apical view (Fig. 4).

258 Apical disc large, more than one third the test diameter (ratio=37%), dicyclic (all
259 ocular plates exsert). Periproct almost circular, slightly elongated in direction 1-IV.
260 Gonopores large (>1mm) abutting the outer margin of genital plates.

261 Peristome only partially preserved but likely very large (more than 50% of test
262 diameter).

263 Ambulacra narrow, less than half the width of interambulacra. Each ambulacral
264 plate with one small imperforate and non-crenulate tubercle perradially but for the first
265 plates located directly above the ambitus, which may have two primary tubercles each.
266 Ambulacral tubercles the same size as interambulacral tubercles, much larger at the
267 ambitus and orally (Figs. 4, 2, 3). Presence of small granules in between tubercles

268 perradially (Fig. 4. 3). Ambulacral plates trigeminate throughout, of the arbaciid type
269 aborally, forming more complex compound plates and significantly widening adorally to
270 form wide, short phyllodes. Pores rounded and strongly conjugate aborally. On the oral
271 side, perradial pits for sphaeridia the latter of which are not preserved (Fig. 4. 2).

272 Interambulacral plates wide and narrow ($H/L = 0,19$) at the ambitus, with three
273 imperforate and non-crenulate primary tubercles, the tubercles decreasing in diameter
274 toward the interradius. Numerous plates narrow and large at the ambitus and above, height
275 of the plate almost not variable along the aboral surface (between 1.5 and 2mm). Above
276 the ambitus, one single adradial tubercle per plate abutting the adoral suture, all tubercles
277 forming an adradial column from the ambitus to the apex (Figs. 4. 1, 3). These tubercles
278 are surrounded by several, tiny granules. Areoles of tubercles poorly developed. Except for
279 the adradial column of tubercles, interambulacral areas otherwise naked from the ambitus
280 to the apex but for very fine and evenly distributed granules, forming more or less marked
281 vertical ridges (Figs. 4. 1, 3).

282 **Remarks.** Many isolated spines were found in the sediment and are herein described
283 separately as they were not in connection with echinoid tests. These spines are abundant,
284 almost always complete, small (never reaching above 20 mm in length) and of two types.
285 The first type consists in short and narrow spines similar in shape to aboral spines
286 commonly found in extant species of *Arbacia*. The second type consists in short, flat and,
287 wide spine covered with a well-developed cortex-layer tip (Figs. 4. 4, 5). These spines are
288 attributed to *Arbacia quyllur* on the basis of: the imperforate stabilum, the presence of a
289 developed ring at the base of the spine, fine striation and an enameled tip, which are all
290 characteristics of the genus *Arbacia*. Moreover, *Arbacia quyllur* is the only known
291 echinoid species of the outcrop.

292 The presence of a dicyclic apical system without tubercles and of a well-developed
293 epistroma support the attribution of this new species to the order Arbacioida. The presence
294 of a trigeminate plate compounding of the arbaciid type, of imperforate and non-crenulate
295 tubercles, with ambulacral and interambulacral tubercles similar in size at the ambitus, and
296 of a clear difference in tuberculation between oral and aboral sides (aboral tubercles highly
297 reduced or even absent) are diagnostic features of the family Arbaciidae. The presence of a
298 straight pore-zone, narrow above the ambitus, of the outer row of interambulacral tubercles
299 reaching the apical system, and of a large peristome, are typical of the genus *Arbacia*.

300 *Arbacia quyllur* sp. nov. differs from other species of *Arbacia* by the presence of an
301 extended naked interambulacral area aborally, which is not restricted to the interradius but
302 extends from the ambitus to the apex and from the interradius to the adradial column of
303 tubercles. The presence of a unique column of tubercles above the ambitus is unique within
304 the genus *Arbacia*. The important width of interambulacral plates ($H/L = 0,19$) in *A.*
305 *quyllur* reminds of the extant species *A. dufresnii* ($H/L = 0.24$) that is distributed along the
306 coasts of Patagonia. Interambulacral tubercles decrease in size toward the interradius, as in
307 other Chilean and Patagonian species *A. spatuligera* and *A. dufresnii*.

308 *A. quyllur* is the first species of *Arbacia* from the Miocene of South America to be
309 described. The occurrence of this species along the Chilean coast, in the late Miocene
310 considerably extends the known distribution range and fossil record of the genus *Arbacia*,
311 present in South America as soon as the Miocene.

312 *Arbacia larraini* sp. nov.

313 Figure 5

314 **Etymology.** In tribute to Senior Alberto Larrain (1949-), specialized in Zoology,
315 Ecotoxicology and Environmental Sciences at the University of Concepción (Chile) for his

316 seminal works on extant and fossil sea urchins from Chile (Larrain, 1975). He was the first
317 to report the occurrence of fossils of *Arbacia* and *Tetrapygyus* in Chile (Larrain, 1975;
318 1982).

319 **Type material.** The Holotype is CB-391 (Fig. 5), housed in the collections of the Museo
320 Paleontológico de Caldera.

321 **Referred material.** Eleven complete specimens (CB-387, CB-388, CB-391, CB-392, CB-
322 394, CB-395, CB-403, CB-405, CB-421, CB-422, CB-424), two fragments (CB-389, CB-
323 427). Specimens CB-390, CB-393 cf. *A. larraini* sp. nov.

324 **Locus typicus.** Specimens of *Arbacia larraini* sp. nov. were collected in the Agua Amarga
325 Formation, late late Pliocene of Caldera, Chile (Marquardt *et al.*, 2000; Mourgues & Pérez,
326 2014).

327 **Stratigraphy.** Specimens were collected from a grayish to whitish medium sand layer
328 composed of numerous shells and other bioclasts of up to 5cm long. The associated fauna
329 comprises both entire and broken shells of bivalves, gastropods, serpulids, and balanids
330 (*Austromegabalanus*) (Marquardt *et al.*, 2000). The section has also provided three
331 bonefish vertebrae and a shark tooth (*Isurus oxyrinchus*). Numerous trace fossils of
332 *Ophiomopha nodosa* are present (Marquardt *et al.*, 2000). The Aqua Amarga Formation is
333 dated to the late late Pliocene (Marquardt *et al.*, 2000). The Pliocene age of the section is
334 also confirmed by the association of the pectinid *Chlamys vidali* and of the two gastropods
335 *Chorus doliaris* and *Concholepas nodosa* (Guzmán *et al.*, 2000; Nielsen, 2013). Finally,
336 the section overlies with an erosional unconformity the uppermost part of the Bahía Inglesa
337 Formation (Rojo, 1985), which was attributed to the lower Pliocene based on foraminifer
338 assemblages (Marquardt *et al.*, 2000).

339 **Taphonomy.** Specimens of *Arbacia larraini* sp. nov. commonly occur in high density,
340 with up to 40 fragments/m². Entire specimens are far scarcer (less than 2 individuals/m²).

341 The size of complete specimens is comprised between 10 and 50mm in diameter. Both
342 complete and fragmented specimens were found, the material ranging from isolated
343 interambulacral plates to nearly complete specimens. Complete isolated apical systems are
344 also preserved. Only inter-plate fragmentation was observed. Isolated interambulacral
345 plates can be readily recognized thanks to the occurrence of small inner tubercles, the lack
346 of secondary tubercles, and plate narrowness. Fragments of ambulacral plates are also easy
347 to identify based on the present of quinquegeminate plates. Test remains are dispersed
348 within deposits with no specific orientation. Scanning electron microscope highlights the
349 lack of abrasion. The tests are not encrusted, nor bioeroded or distorted. Aristotle's lanterns
350 are always missing. *A. larraini* sp. nov. was found associated with specimens of *A.*
351 *terraeignotae* and very rare fragments attributed to *Loxechinus* sp.

352 **Diagnosis.** Ambulacral plates quinquegeminate throughout; well-developed neural canal;
353 periproct almost circular; wide naked interambulacral area down to the ambitus; all
354 interambulacral plates of the same size on the aboral surface.

355 **Measurements.**

356 TABLE 2

357 **Description.** Well-preserved specimens show a sub-conical, low test in profile ($H/D =$
358 0.48), flattened below, with a sub-circular to sub-pentagonal outline in aboral view
359 (Fig. 5).

360 Apical disc small ($AP/D = 20\%$) hemi to dicyclic. Ocular plate V is often insert and
361 ocular plate I is occasionally insert, all other oculars are exsert. The periproct is almost
362 circular, slightly elongated in direction 1-IV. Gonopores are large and located near the
363 outer margin of genital plates. The epistroma covers both genital and ocular plates forming
364 fine punctuations (Fig. 5), without organization.

365 The peristome is wide, about 50% of the test diameter sub-pentagonal in outline,
366 with very shallow buccal notches and a faint perradial notch (Fig. 5).

367 Ambulacra very narrow (one third the width of interambulacral), each plate with
368 one imperforate and non-crenulate primary tubercle of the same size as interambulacral
369 ones at the ambitus and decreasing in size above the ambitus (Fig. 5). The tubercles are
370 widely spaced and separated from each other by fine granules perradially (Fig. 5).
371 Adambulacral margin straight, with aligned pores. Ambulacral plates quiquegminate
372 (Fig. 5) forming more complex compound plates adorally, then expanding to form short
373 phyllodes. Aborally, in a pore pair, inner and outer pores rounded, pores of a pair deeply
374 conjugate and pore-pairs separated from each other by marked transversal ridges. Neural
375 canal well-developed. Orally, pore-pairs with well-developed partitions between pores,
376 with a broad circular attachment. On the oral side, close to the peristome, presence of one
377 single perradial pit for the sphaeridium in each ambulacrum (Fig. 5).

378 Interambulacra wide with three to four imperforate and non-crenulate primary
379 tubercles per plate at the ambitus, the smallest specimens (~25 mm) only bearing two
380 tubercles per plate. Plate height similar all along the aboral surface (between 1.5 and 2mm;
381 Tab. 2). Above the ambitus, one adradial column of large primary tubercles reaches the
382 apical system. These tubercles have large mamelons, narrow platforms and broad areoles
383 occupying all of the plate width at the ambitus (Fig. 5). Presence of three (adambitally) to
384 one (adapically) inner smaller tubercle per plate that leaves a well-developed naked area in
385 the interradius (Fig. 5). These tubercles, reducing in size near the interradius suture, abut
386 the adoral margin of plates. Adapically, the three last plates only bear one tubercle each.
387 Tuberculation leaves a wide naked interrarial area. Small granules sparse, distributed
388 around primary tubercles. Epistroma poorly developed, forming fine punctuation, without
389 orientation, similar to the epistroma of the apical system.

390 **Remarks.** This species differs from other species of the genus *Arbacia* by the combined
391 presence of quinquegeminat ambulacral plates, developed bare interambulacral area and
392 small inner interambulacral tubercles, up to three in each plate. The presence of a hemi- to
393 dicyclic apical system without tubercles and of a well-developed epistroma supports the
394 assignment of the new species to the order Arbacioida. The presence of compound,
395 arbaciid-like plates in ambulacra, of imperforate and non-crenulate tubercles, similar in
396 size in ambulacra and interambulacra at the ambitus, and of a clear difference in
397 tuberculation between the oral and aboral sides (aboral tubercles highly reduced in size or
398 even absent) is diagnostic of the family Arbaciidae. The presence of a straight pore-zone,
399 narrow above the ambitus, of ambulacral tubercles forming a regular series throughout, of
400 a large peristome (>30% of test diameter), of interambulacral with numerous primary
401 tubercles arranged in horizontal and vertical series are all characters shared by species of
402 *Arbacia*. The presence of quinquegeminat ambulacral plates is a character only known in
403 the extant species *Tetrapygyus niger*, a shallow-water species of Arbaciidae. *A. larraini* nov.
404 sp. differs from *T. niger* by the presence of a second row of poorly-developed ambulacral
405 tubercles, well-spaced ambulacral tubercles, vertical line of pore pairs and developed bare
406 interambulacral area. These characters are unknown in *T. niger* but common in species of
407 *Arbacia*, supporting the assignment of this new species to the genus *Arbacia*.

408 *Arbacia terraeignotae* sp. nov.

409 Figure 6

410 **Etymology.** The name “terraeignotae” is given after the consulting company Terra Ignota,
411 in recognition of its contribution to the improvement of our knowledge and conservation of
412 the fossil record of Chile and support to the present field work and project.

413 **Type material.** The Holotype is CB-400 (Fig. 6); housed in the collections of the Museo
414 Paleontológico de Caldera.

415 **Referred material.** Six complete tests (CB-400, CB-402, CB-403, CB-410, CB-428, CB-
416 429) and isolated spines. Specimens CB-404, CB-406: cf. *A. terraeignotae*.

417 **Locus typicus.** Specimens of *Arbacia terraeignotae* sp. nov were collected at Cerro
418 Ballena, next to the highway, 3 km northeast of Caldera.

419 **Stratigraphy.** Same as for *A. larraini* sp. nov (see p. 13–14).

420 **Taphonomy.** Specimens of *Arbacia terraeignotae* sp. nov. commonly occur in high
421 density, up to 40 fragments/m². Complete specimens are far scarcer. Both complete and
422 fragmented specimens were found, ranging from isolated interambulacral plates to nearly
423 complete specimens. Only inter-plate fragmentation is present. Isolated interambulacral
424 plates can be readily recognized thanks to the occurrence of small secondary tubercles and
425 high plates. Aristotle's lanterns were not preserved. Remains are dispersed within deposits
426 and show no specific orientation. Scanning electron microscope highlights the lack of
427 abrasion. The tests are not encrusted nor bioeroded. As mentioned below, *A. terraeignotae*
428 sp. nov. was found in association with *A. larraini* and very rare fragments attributed to
429 *Loxechinus* sp.

430 **Diagnosis.** Ambulacral plates quinquegminate; secondary tubercles present above the
431 ambitus; interambulacral primary tubercles not aligned along the adoral margin of plates;
432 height of interambulacral plates increasing adapically; genital pores large (>50%D genital
433 plate) abutting the outer margin of genital plates.

434 **Measurements.**

435 TABLE 3

436 **Description.** Well-preserved specimens show a sub-conical, high test in profile (H/D
437 =41%), flattened below, with a sub-circular outline in aboral view (Fig. 6).

438 Apical disc small (AP/D = 22%), hemi to dicyclic, without tubercles. Epistroma
439 well developed, forming punctuation on genital plates and fine crenulations at the margin
440 of genital and ocular plates. Ocular plate V is insert in most specimens, ocular plate I
441 occasionally insert, all other oculars are exsert. The periproct is oval in outline and well
442 extended in direction 1-IV as it is usually the case in species of the genus *Arbacia* (Fig. 5).
443 Gonopores very large, abutting the outer margin of genital plates and often occupying
444 more than 50% of the length of the genital plate (Fig. 6).

445 The peristome is wide, about 55-60% of the test diameter, sub-pentagonal in
446 outline, with very shallow buccal notches and a faint perradial notch (Fig. 6).

447 Ambulacra very narrow (one third the width of interambulacra), each plate with one
448 imperforate and non-crenulate primary tubercle of almost the same size as interambulacral
449 ones at the ambitus and progressively decreasing in size adapically (Fig. 6). Tubercles
450 sparse, separating from each other by fine granules perradially (Fig. 6). Only one row of
451 tubercle adapically, reaching the apical system. Ambulacral plates 5-geminate, of the
452 arbaciid type aborally, forming more complex compound plates adorally, then expanding
453 to form poorly developed phyllodes. Aborally, in a pair, inner pore rounded, outer pore
454 slightly elongate, pores of a pair deeply conjugate and pore-pairs separated from each other
455 by marked ridges. On the oral side, close to the peristome, presence of one single perradial
456 pit for the sphaeridium in each ambulacrum.

457 Interambulacra wide with three to four imperforate and non-crenulate primary
458 tubercles per plate at the ambitus. Smallest specimens (Fig. 6) with only two tubercles at
459 the ambitus. Height of plates increase along the aboral surface adapically (from 2 to more
460 than 4 mm height). Above the ambitus, one single, adradial column of large primary
461 tubercles reaches the apical system. Second row of interambulacral tubercles present up to
462 the second plates before the apical system. These tubercles with large mamelons, narrow

463 platforms and broad areoles occupying most of the plate width (Fig. 6). Presence of three
464 (adambitally) to one (adapically) inner smaller tubercle per plate and secondary tubercles
465 above. Primary tubercles not aligned along the adoral margin of the plate. Those tubercles,
466 occupying most of the plates, does not leave a naked medial interambulacral area.
467 Otherwise, the plates are coarsely granulated in between tubercles. Epistroma well
468 developed, covering all the plates and forming punctuation (Fig. 6).

469 **Remarks.** This species differs from all other species of the genus *Arbacia* by the combined
470 presence of quinquegeminat ambulacral plates aborally, sometimes quadrigeminates
471 adapically and the presence of secondary tubercles. The presence of a hemi to dicyclic
472 apical system without tubercles and of a well-developed epistroma support the assignment
473 of the new species to the order Arbacioida. The presence of compound, arbaciid-like plates
474 in ambulacra, of imperforate and non-crenulate tubercles, similar in size in ambulacra and
475 interambulacra at the ambitus, and of a clear difference in tuberculation between the oral
476 and aboral side (aboral tubercles highly reduced in size or even absent) is diagnostic of the
477 family Arbaciidae. The presence of a straight pore-zone, of ambulacral tubercles forming a
478 regular series throughout, of a large peristome (>30% of test diameter), of interambulacra
479 with numerous primary tubercles arranged in horizontal and vertical series are all
480 characters shared by species of *Arbacia*. This species differs from *A. larraini* by its larger
481 gonopores, more developed epistroma and the presence of secondary tubercles above the
482 ambitus. However, the presence of secondary tubercles and large gonopores abutting the
483 outer margin of genital plates are characters only known in the extant species *Tetrapygyus*
484 *niger*, a shallow-water member of the Arbaciidae. This also questions the very taxonomic
485 status of the genus *Tetrapygyus* and of *Tetrapygyus niger*, which would deserve to be
486 revised.

487 **Isolated Spines found in the Agua Amarga Formation.**

488

Figure 7

489 All spines are straight, finely striated and the size sometimes exceed 5cm. The distal end of
490 spines is rarely preserved but for at least seven spines of variable length. Short spines with
491 tips not larger than the base. The enameled tips are long and well-developed (Fig. 7). The
492 base of the spine is marked by a developed oblique bulge, as in other species of the genus
493 *Arbacia* and *Tetrapygyus*. The upper part of the spines is not wider than the base. These
494 spines are similar in shape to the spines of the extant *Arbacia* species with no species
495 diagnostic features to be identified so that it is so far impossible to attribute those spines to
496 either *A. terraeignotae* or *A. larraini*.

497

Arbacia spatuligera (Valenciennes, 1846)

498

Figure 8

499 *Echinus spatuliger* Valenciennes, 1846. pl. 5, fig 2.

500 *Echinus (Agarites) spatuligera* Agassiz & Desor, 1846. p. 353.

501 *Arbacia spatuligera* Agassiz, 1872. p. 93; p. 403, pl. 35, fig 7.

502 **Referred material.** Nine test fragments (coding CM-170, CM-171, CM-172, CM-173,
503 CM-175, CM-176, CM-177, CM-178, CM-179; Fig. 7) housed at the Universidad Católica
504 del Norte, Coquimbo, Chili. Tests of all specimens are broken, but fragments are well
505 preserved with ambulacra and interambulacra articulated, along with two broken spines.
506 The peristome and the apical disc are missing.

507 **Locality.** Mejillones (North of Antofagasta), Chile.

508 **Age.** Middle/late Pleistocene, 96 000-118 000 years BP (Rivadeneira & Carmona, 2008).

509 **Stratigraphy.** The examined specimens of *Arbacia spatuligera* (Fig. 8) were collected
510 from coastal deposits associated to a marine terrace composed of an alternation of fine
511 sands and levels of fine gravels with a high content in bioclasts, located about 55 to 60

512 meters above the present sea level. The associated fauna is composed of balanids, bones of
513 sea birds and marine mammals, cetaceans and otariids (Anchelergues & De Los Arcos,
514 2016). Isotopic analyses performed on mollusk shells located 10m below the studied
515 section gave an age of no more than 321ka (Regard *et al.*, 2010), that is, the Middle or Late
516 Pleistocene.

517 **Emended diagnosis.** Ambulacral tubercles not reaching the apical system; four
518 subtriangular supra-anal present plates forming a pyramid; tip of supra-anal plates with a
519 small and narrow extension; interambulacral area covered by numerous inner smaller
520 tubercles, up to 6 per plate just above the ambitus; interambulacral bare area vestigial in
521 the largest specimens ($D > 65\text{mm}$); color brown to light green with slightly lighter spines.

522 **Measurements.**

523 TABLE 4

524 **Description.** Apical disc hemicyclic, with no tubercles. Ocular plates I, IV and V insert.
525 The periproct is oval with maximum diameter in direction 1-IV as it is usually the case in
526 species of the genus *Arbacia* (Fig. 8). Gonopores are large and abut the adoral margin of
527 genital plates.

528 Ambulacra narrow (half of interambulacra), each plate with one imperforate and
529 non-crenulate primary tubercle of the same size as interambulacral ones at the ambitus and
530 progressively decreasing in size adapically. Tubercles not reaching the apical system
531 (Fig. 8). The tubercles are separated by fine granules at the perradial suture (Fig. 8).
532 Ambulacral plates trigeminate from the ambitus to the apical system, of the arbaciid type
533 aborally. Aborally, pores of a pair deeply conjugate and pore-pairs separated between each
534 other by marked ridges. Neural canal poorly developed. Phyllodes and oral part of the test
535 not preserved.

536 Interambulacra wide with five imperforate and non-crenulate primary tubercles per
537 plate at the ambitus, all similar in size. Tubercles decrease in size above the ambitus and
538 are up to seven per plate, with three large tubercles, and four smaller. The number of
539 tubercles decrease adapically with five tubercles per plate at mid distance from the apex.
540 The adradial column of large primary tubercles reaches the apical system. A second
541 column of tubercles almost reaches the apical system. Tubercles have large mamelons,
542 narrow platforms and broad areoles occupying most of the plate width at the ambitus (Fig.
543 8). Except for the naked, interradial area, the plates are coarsely granulated in between
544 tubercles.

545 Spines long, finely striated and showing a developed biased bulge close to the
546 bottom part. Tips of the spines are not preserved (Fig. 8).

547 **Remarks.** An emended diagnosis is suggested here, based on Larrain's work (Larrain,
548 1975) to highlight specific characters. The studied specimens are morphologically identical
549 to the extant species *Arbacia spatuligera* and differ from all other species of the genus
550 *Arbacia* by the presence of numerous small tubercles (between 3 and 6) above the ambitus.
551 This is the first occurrence of *Arbacia spatuligera* in the fossil record so far.

552 Genus *Tetrapygyus* (Agassiz, 1841)

553 **Type species.** *Tetrapygyus niger* (Molina, 1782)

554 Figure 9

555 *Echinus nigra* Molina, 1782, Chili, p. 175.

556 *Tetrapygyus niger* Mortensen, 1935. p. 582-584.

557 **Referred material.** One complete specimen DA-327 and another almost complete
558 specimen DA-328 housed in the collection of the project "Expansion and Improvement of
559 Diego Aracena Airport" of Iquique. Regional Museum of Iquique.

560 **Locality.** Iquique, Chile; close to the airport.

561 **Age.** In the latter sector, Vásquez *et al.* (2012) worked on the morphostratigraphy of the
562 marine terraces and located terrace III between 35 to 49 masl and terrace VI between 77 to
563 85 masl, which were dated by Ratusny and Radtke (1988) in 302.000- and 685.000-years
564 BP in fossil fragments from terraces III and VI, respectively. According to these
565 antecedents, our materials would come from the Middle Pleistocene (Chibanian), but the
566 lack of precise data on the geology of these Pleistocene terraces does not allow us to date
567 these specimens more precisely.

568 **Stratigraphy.** The examined specimens of *Tetrapygyus niger* (Fig. 9) were collected from
569 coastal deposits associated to a marine terrace composed of an alternation of fine sands and
570 levels of fine gravels with a high content in bioclasts, located about approximately 50
571 meters above sea level. Some authors pointed out that on the coast south of Iquique the
572 littoral marine deposits are preserved in five terrace levels at Playa Blanca to six levels at
573 Punta Patache (Ratusny & Radtke, 1988; Vásquez *et al.*, 2012).

574 **Emended diagnosis.** Ocular plate V invariably insert; aboral interambulacral plates with
575 one to several secondary tubercles, increasing in number progressively from the apex
576 towards the ambitus and arranged in horizontal series above and below primary tubercles;
577 arbacioid-type ambulacral plate quadrigeminate, compressed, with isopores not aligned in
578 a single, regular column; primary spines with poorly developed enameled tips; color deep
579 violet to black.

580 **Measurements.**

581 TABLE 5

582 **Description.** Apical disc hemicyclic, with neither tubercles nor epistroma. Ocular plates I,
583 IV and V insert. The periproct is oval, almost circular, with maximum diameter in
584 direction 1-IV as it is usually the case in species of the genus *Arbacia* (Fig. 9). Gonopores

585 are large and abut the adoral margin of genital plates, often occupying half of the part of
586 the genital plate.

587 Ambulacra narrow (half of interambulacra), each plate with one imperforate and
588 non-crenulate primary tubercle of same size as interambulacral ones at the ambitus and
589 slowly decreasing in size adapically (Fig. 9). The tubercles are separated by fine granules
590 at the perradial suture (Fig. 9). Ambulacral plates sometimes quinquegminate at the
591 ambitus and always quadrigeminate above. Ambulacral plate compressed with isopores not
592 aligned in a single, regular column as in species of *Arbacia*. Aborally, conjugate isopores
593 large and elongate, both pores large and circular (outer pore often slightly elongate).
594 Interporal area broad with a developed interporal furrow. Neural canal in perradial pore
595 well developed. Pores more spaced than in *Arbacia* species. These conjugate isopores
596 correspond to the Smith's C1-type classification (Smith, 1978). Orally, P4 isopores
597 numerous, forming wide but poorly extended phyllodes, forming a slightly circular margin
598 at the peristome.

599 Interambulacra wide with five imperforate and non-crenulate primary tubercles per
600 plate at the ambitus, all similar in size. Tubercles decreasing in size adapically above the
601 ambitus. Presence of secondary tubercles forming a second row of small tubercles just
602 above primary tubercles. The adradial column of large primary tubercles reaches the apical
603 system. A second column of tubercles is developed close to the apical system, up to the
604 second adapically plate. Tubercles with large mamelons, narrow platforms and broad
605 areoles occupying most of the plate width at the ambitus (Fig. 9). The high number of
606 primary and secondary tubercles does not leave space to a naked interradian area. The
607 plates are coarsely granulated in between tubercles. Height of plates increase along the
608 aboral surface adapically (from 3 to more than 6 mm height).

609 **Remarks.** An emended diagnosis is suggested here, based on Larrain's work (Larrain,
610 1975) to highlight specific characters. The studied specimens are morphologically identical
611 to specimens of the extant species *Tetrapygyus niger*. Those are the first complete
612 specimens of *Tetrapygyus niger* to be reported in the fossil record of Iquique. *T. niger* has
613 already been reported in Pleistocene deposits of Caldera (Roa *et al.*, 2016).

614 The summary table (Tab. 6) includes important diagnostics features used to identify
615 species.

616 TABLE 6

617 **DISCUSSION**

618 **Functional morphology and paleoecology**

619 In *Arbacia quyllur*, primary spines are restricted to the adradial margin of
620 interambulacral and to ambulacra aborally. In echinoids and more precisely, in arbacioids,
621 the loss of interambulacral spines is believed to result from two phenomena (Baumeister &
622 Leinfelder, 1998). In high-energy waters, this makes the test flatter and smoother and
623 hence less prone to overturning by currents or waves. It may be also an adaptation to high
624 sedimentation rates, for aboral spines could act as bafflers of unwanted sediment particles.
625 A denuded test can be more easily cleaned off unwanted sediment particles, either
626 passively by water motion (wave and current action), or actively, by means of
627 pedicellariae.

628  Figure 10

629 The studied Pliocene species are very well-preserved and thus allow for the precise
630 study of pore morphology, which is correlated to the biological function of the tube feet
631 (Smith, 1978). A detailed description of isopores, based on SEM images (Fig. 10) along
632 with the comparison of extant species' ecology, *A. dufresnii*, *A. spatuligera* and *T. niger*,
633 allow for paleoecological inferences for the fossil species.

634 The morphology of oral pores is similar in *Tetrapygyus niger* and the investigated
635 species of *Arbacia* with partitioned isopores correspond to Smith's P4-type (Smith, 1978).
636 The pores are characterized by a large circular interporal partition and a very broad circular
637 attachment area. Tube feet that end in large adhesive discs with thick connective tissues are
638 associated with large periporal areas and small pores used for strong fixation to hard
639 substrates. Sharp and Gray (1962) and Märkel and Titschack (1965) showed that even if P4
640 isopores are associated to thick and strong tube feet with large adhesive discs, the number
641 of oral tube feet plays a major role in the ability to cling to the substrate. Species with P4
642 oral isopores are found in echinoids inhabiting rocky bottoms in exposed, high-energy
643 environments. According to Smith (1978), these echinoids may live in the intertidal or
644 subtidal zones on the exposed surface of rocks, though they may inhabit crevices
645 intertidally. This is the case of all species of *Arbacia* and of *Tetrapygyus niger*, with only
646 the number of isopores differing between species.

647 The aboral ambulacral plating, pore size and pattern, however, differ between
648 *Tetrapygyus niger* and species of *Arbacia*. While P4 oral isopores are used for clinging to
649 the sea bottom, aboral tube feet are used for gaseous exchanges with the sea water and
650 breathing. The presence of two equal-sized pores allows for a one-way current flow of
651 coelomic fluids through the tube feet favoring efficient gaseous exchanges (Fenner, 1973;
652 Smith, 1978). The occurrence of polyporous ambulacral plating also allows the presence of
653 numerous tube feet and thus facilitates the rate of gaseous exchanges in echinoids (Smith,
654 1978). This is central for shallow-water species of echinoids due to the lower availability
655 of dissolved oxygen to marine species in shallow waters (Smith, 1978). The high number
656 of aboral ambulacral pores in *T. niger* (quadrigeminate plates) and in *A. terraeignotae* and
657 *A. larraini* (quinquegeminate plates) suggests an adaptation of these species to living in
658 shallow-water, high-energy environments. While *T. niger* is only reported from rocky

659 bottoms and shallow waters, between 0 and 40 m depth, *A. dufresnii* and *A. spatuligera* are
660 known at greater depth, down to 250 meters, from soft bottoms. *A. quyllur* from the
661 Miocene has trigeminate ambulacral plates and narrow phyllodes, similar in shape to *A.*
662 *dufresnii* and *A. spatuligera*. These data are congruent with sedimentological data and
663 associated faunas that suggest very shallow nearshore environments. In addition to the
664 morphology of spines, this could suggest the presence of the species in shallow waters, in
665 sandy areas with high sedimentation rates.

666 **The fossil record of the genus *Arbacia***

667 The first fossils of the genus *Arbacia* ever reported from Chile are described herein,
668 including three new fossil species —*A. quyllur* from the Late Miocene, *A. terraeignotae*
669 and *A. larraini* from the late Pliocene—, the first occurrence of specimens of the extant
670 species *A. spatuligera* in the fossil record and new fossil records for *T. niger*. Except for a
671 specimen of *Arbacia stellata* from Ecuador (Di Celma *et al.*, 2002) and a specimen of
672 *Arbacia punctulata* from Venezuela (Mihaljević *et al.*, 2010), the genus *Arbacia* has been
673 mainly reported as fossil from North America so far, in addition to few specimens from the
674 West Indies (Curaçao, Cuba; de Buissonjé, 1974). Therefore, the new material here
675 described fills in an important gap in the fossil record of the genus and improves our
676 knowledge of its paleobiogeography. It shows that the genus was present in South America
677 long before the final closure of the Isthmus of Panama, about 3 Ma (Saito, 1976; O’Dea *et*
678 *al.*, 2016), and as soon as the Late Miocene. Further field surveys along the coasts of South
679 America should prove useful and may lead to new discoveries in the future.

680 The specimens of newly described species reveal the past diversity of the genus
681 *Arbacia* and increase our knowledge of the overall diversity of the genus in South
682 America, which includes four extant species, *A. stellata*, *A. punctulata*, *A. spatuligera*, and
683 *A. dufresnii*, and four fossil taxa, *A. quyllur*, *A. terraeignotae*, *A. larraini* and *A.*

684 *spatuligera*. The diversity of the family Arbaciidae also includes the occurrence of
685 *Tetrapygyus niger* in shallow waters of Chile, and *Dialithocidaris gemmifera* from deep
686 waters of the Pacific coast of Panama (Maluf, 1988). Altogether, this emphasizes the
687 diversity of the genus *Arbacia* and family Arbaciidae along and off the coasts of South
688 America, back to the end of the Miocene through to the present day. After *A. abiquaensis*,
689 a species from the late Late Oligocene of Oregon (Linder *et al.*, 1988), *A. quyllur* is the
690 second oldest species of the genus *Arbacia* ever reported worldwide. The relative high
691 richness and age of the genus in South America fits well with a potential origin and/or
692 diversification of the genus in the South Pacific as suggested by Lessios *et al.* (2012).

693 **CONCLUSIONS**

694 The description of three new species of the genus *Arbacia* considerably increases
695 our knowledge of the fossil record of the genus and gives us new clues to decipher the
696 paleobiogeographic history of the genus along Chilean coasts. The description of *A.*
697 *terraeignotae*, *A. larraini* and *A. quyllur* highlights the occurrence of morphological
698 characters shared by either species of *Arbacia* (narrow and straight pore-zone above the
699 ambitus, trigeminate ambulacral plates adapically, presence of granules and of a naked
700 interradial area, interambulacral tubercles arranged in regular series) or *Tetrapygyus*
701 (presence of quinquegeminate ambulacral plates, large gonopores abutting the outer
702 margin of genital plates and of secondary tubercles). The occurrence in *A. terraeignotae*, of
703 morphological features otherwise present in two distinct arbaciid genera calls for further
704 investigations to check the taxonomic significance of the monospecific genus *Tetrapygyus*.
705 The newly described material also indicate an older origin (late Late Miocene) and higher
706 species richness of the genus *Arbacia* along the Chilean coasts than previously thought.

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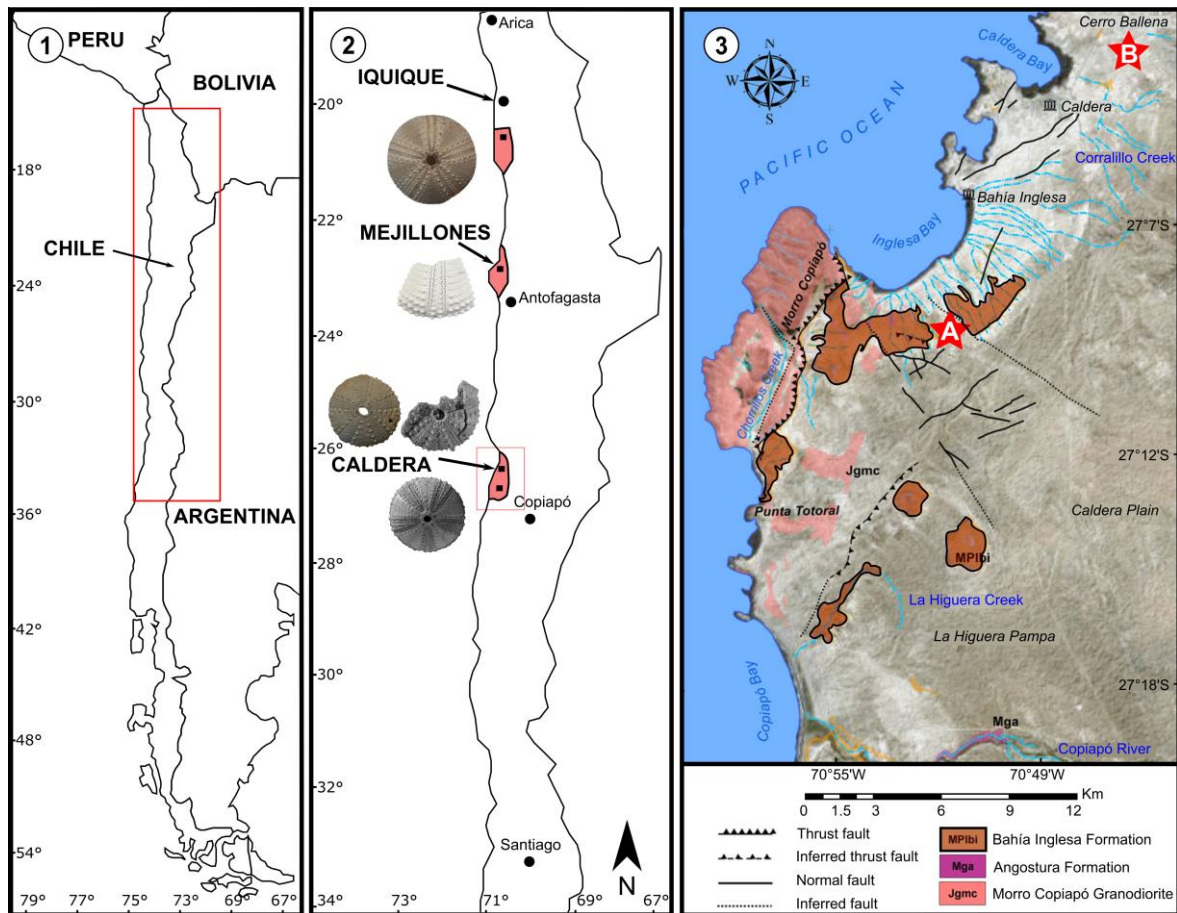
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962 **Figure captions**

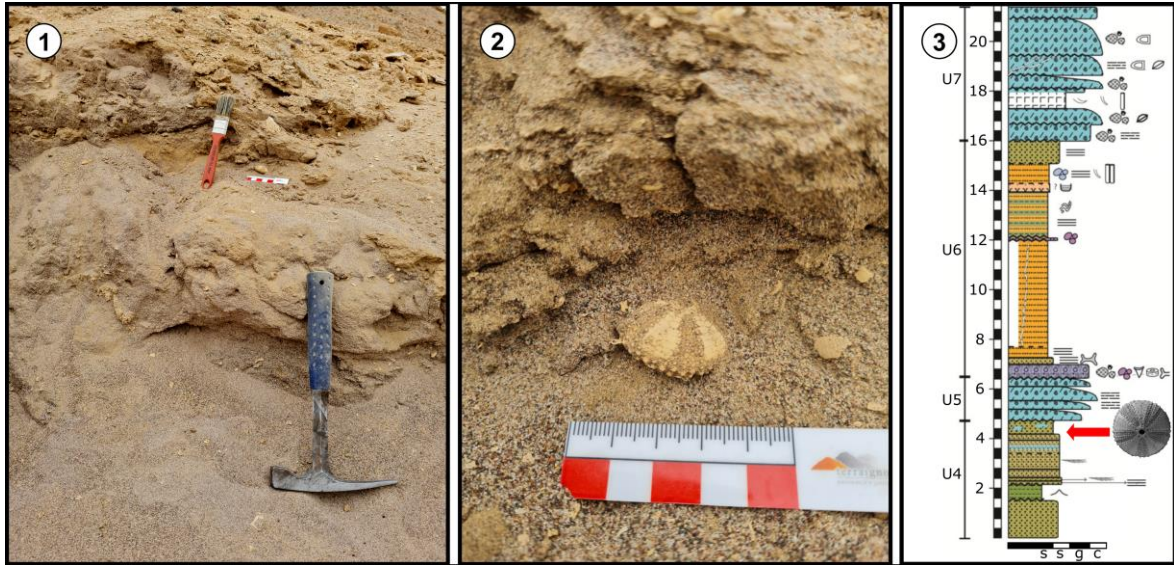
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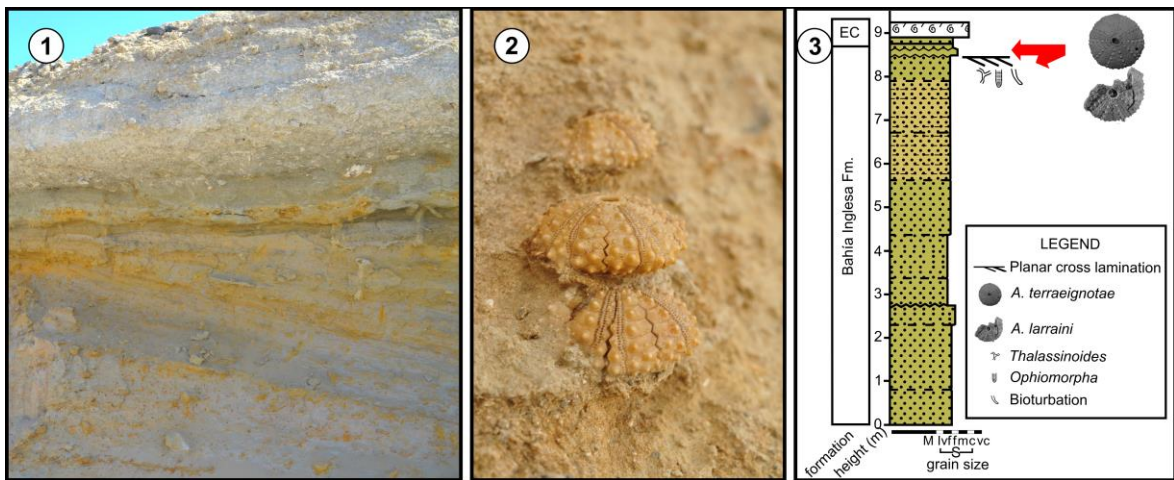
965 **Figure 1.** 1, Map of Chile; 2, location of fossil outcrops where species of *Arbacia*
 966 *quyllur*, *Arbacia terraeignotae*, and *Arbacia larraini* (Caldera), *Arbacia spatuligera* (Mejillones) and
 967 *Tetrapygus niger* (Iquique); 3, view of the Caldera area (modified from Le Roux *et al.*, 2016) (A), location of
 968 *Arbacia quyllur* and (B) location of *Arbacia terraeignotae* sp. nov. and *A. larraini* sp. nov.

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970

971 **Figure 2.** Field view of the Mina Fosforita Member of the Bahía Inglesa Formation near Caldera. **1**, outcrop;
 972 **2**, *in situ* specimen of *Arbacia quyllur* sp. nov., **3**, log of the Mina Fosforita Member (U4, 5, 6; Le Roux *et*
 973 *al.*, 2016) modified from Carreño, 2012 with location of type material of *Arbacia quyllur*.



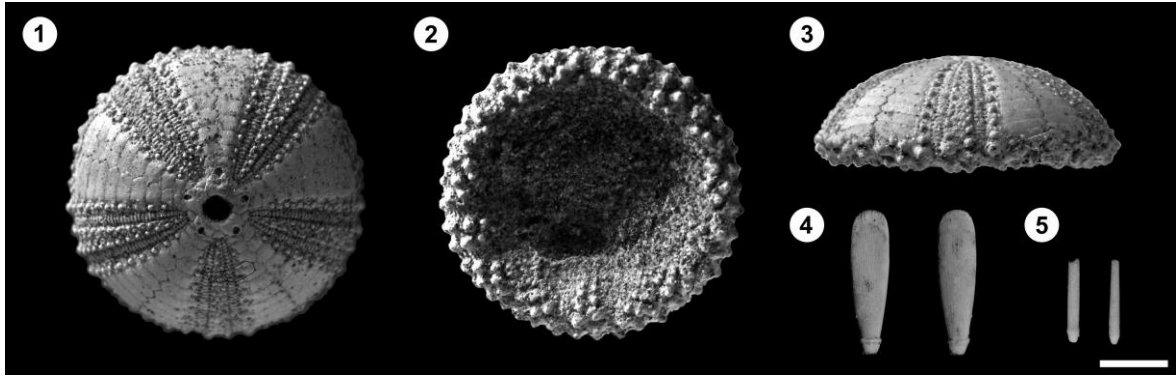
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975 **Figure 3.** Field view of the Cerro Ballena of the upper Bahía Inglesa Formation and Estratos de Agua
 976 Amarga Formation near Caldera. **1**, outcrop; **2**, *in situ* specimen of *Arbacia terraeignotae* sp. nov.; **3**, log of
 977 the Cerro Ballena Member modified from Pyenson *et al.*, 2014 with location of type material of *Arbacia*
 978 *terraeignotae* and *Arbacia larraini*.

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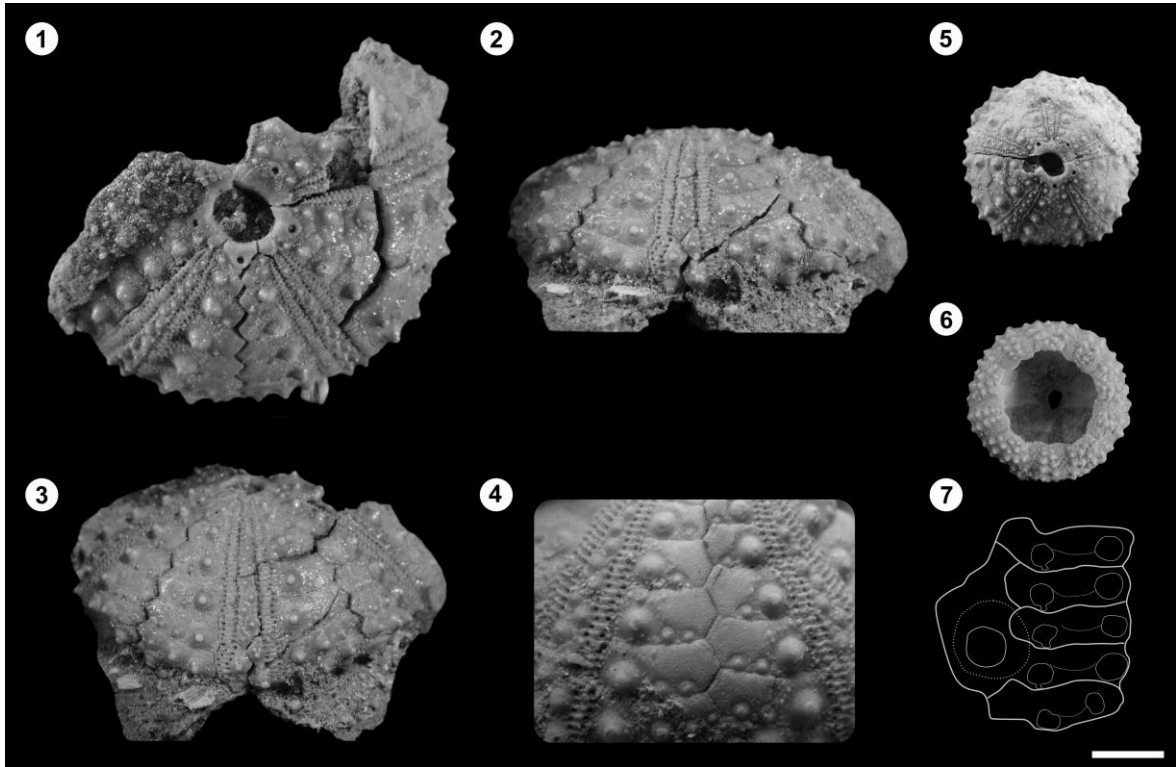
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983 **Figure 4.** 1–5, *Arbacia quyllur* sp. nov., SNGM-2034(1) from Late Miocene deposits of Chile; 1, aboral
 984 view; 2, oral view; 3, lateral view; 4, oral spines; 5, aboral spines. Scale bare equals 10 mm. Photos by A.
 985 Mourgues.

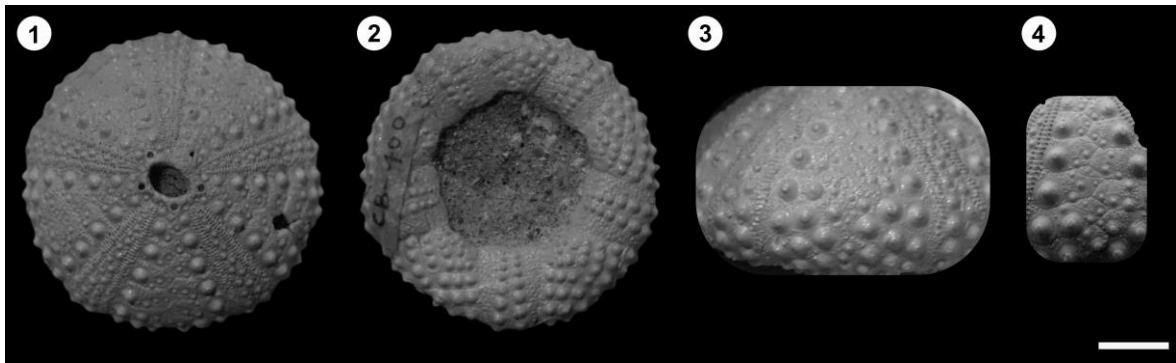


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987 **Figure 5.** *Arbacia larraini* sp. nov. from the late Pliocene of Chile. 1–3, CB-391; 1, aboral view; 2, lateral
 988 view; 3, latero-aboral view; 4, CB-392 in lateral view; 5–7, CB-403; 5, aboral view; 6, oral view; 7,
 989 ambulacral plate. Scale bare equals 10 mm. Photos by A. Mourgues.

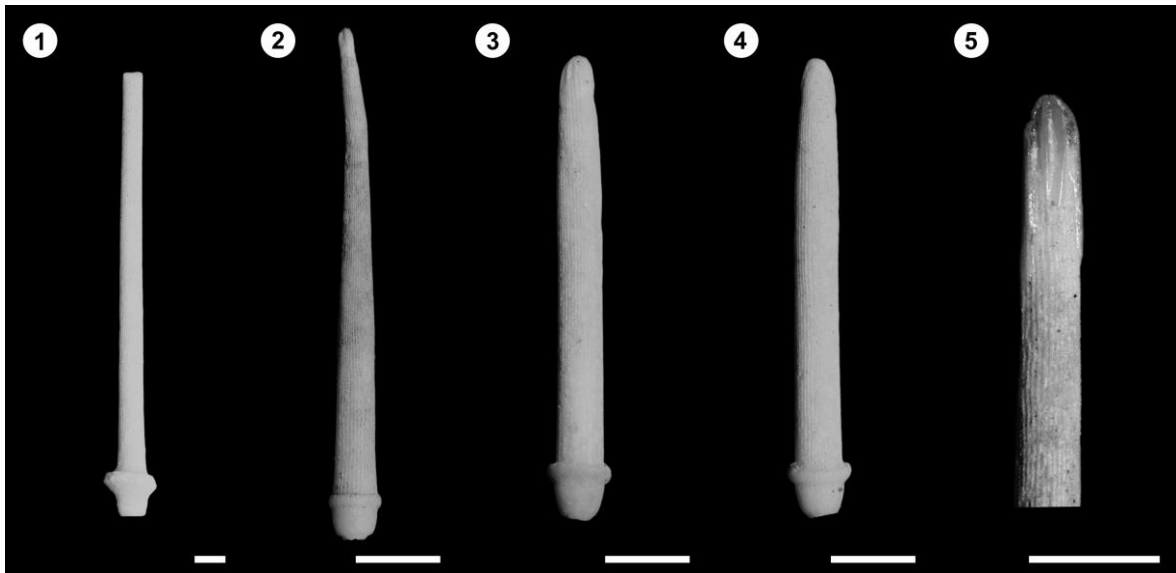
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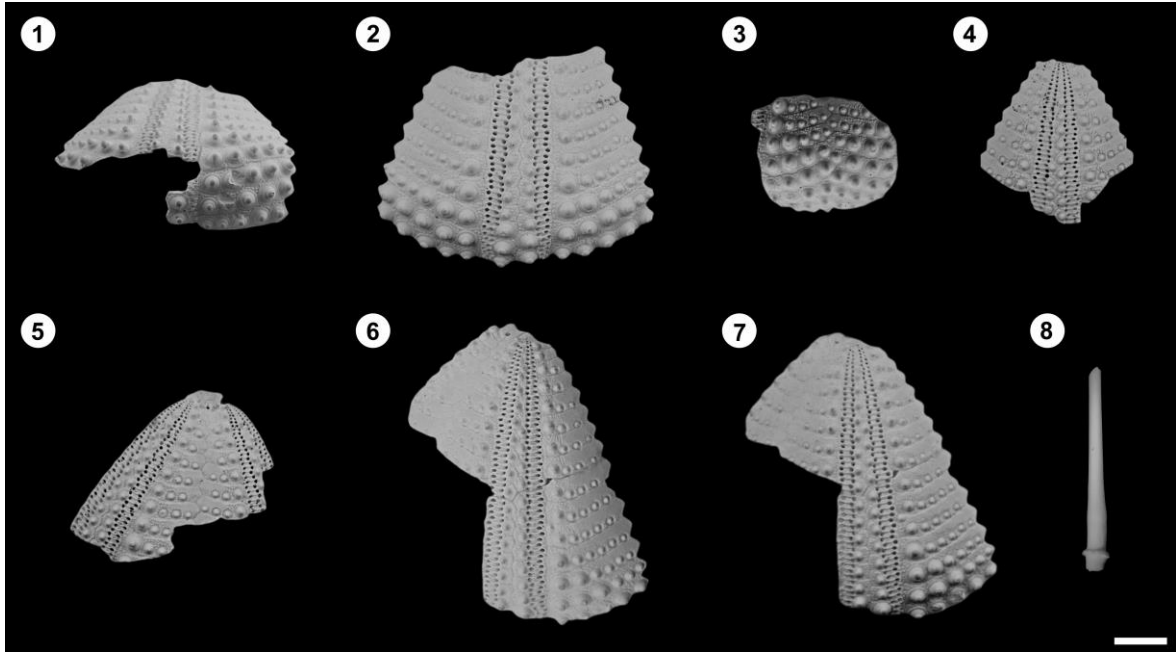
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993 **Figure 6.** 1–4, *Arbacia terraeignotae* sp. nov., CB-400 from the late Pliocene of Chile; 1, aboral view; 2,
 994 oral view; 3, latero-aboral view; 4, CB-429 in lateral view. Scale bare equals 10 mm. Photos by A.
 995 Mourgues.



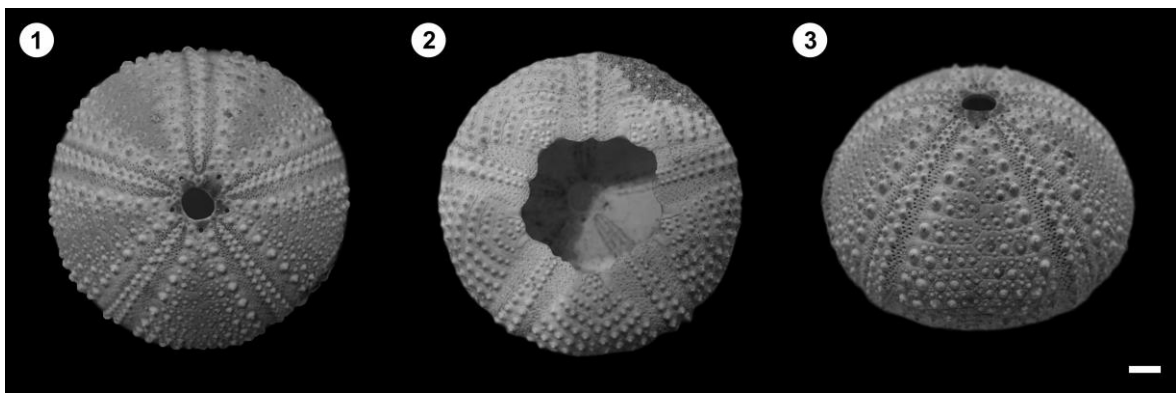
996

997 **Figure 7.** 1–5, Spines found with *A. terraeignotae* and *A. larraini* from the late Pliocene; 1, longest spine
 998 found; 2–4, complete spines; 5, zoom on the tips with large cortex-layer. Scale bare equals 2 mm.



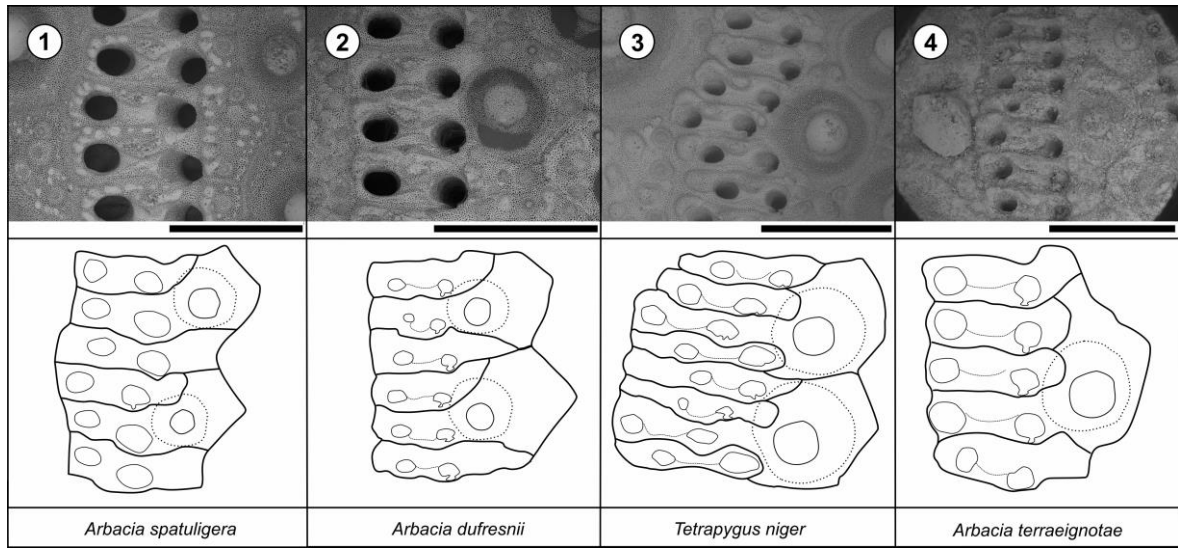
999

1000 **Figure 8.** 1–7, *Arbacia spatuligera* from the late Pleistocene of Mejillones (Chile); 1–6, best preserved
 1001 fragment; 7, spines CM-174. Scale bare equals 10 mm. Photos by A. Mourgues.



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1003 **Figure 9.** 1–3, *Tetrpygus niger*, DA-327 from the late Pleistocene of Iquique (Chile); 1, aboral view; 2, oral
 1004 view; 3, lateral view. Scale bare equals 10 mm. Photos by A. Mourgues.



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Figure 10. Ambulacral plate pattern in Chilean species of *Arbacia* and *Tetrypygus*, SEM photos and

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drawings. **1,** *Arbacia spatuligera*; **2,** *Arbacia dufresnii*; **3,** *Tetrypygus niger*; **4,** *Arbacia terraeignotae*.

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1027 **TABLE 1. Test dimensions in *Arbacia quyllur* sp. nov, SNGM-2034(1).**

Test horizontal diameter	40.0 mm
Test height	8.6 mm
Apex max. diameter	14.8 mm
Estimated peristome diameter	21.0 mm
Ambulacra max. width	7.0 mm
Interambulacra max. width	16.1 mm
Height of interambulacral plates at ambitus	1.4 mm
Width of interambulacral plates at ambitus	8.2 mm
Height of interambulacral plates at plate 12	1.9 mm
Width of interambulacral plates at plate 12	6.1 mm

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1029 **TABLE 2. Test dimensions in *Arbacia larraini* sp. nov, CB-391.**

Test horizontal diameter	41.6 mm
Test height	20 mm
Apex max. diameter	6.5 mm
Ambulacra max. width	6.2 mm
Interambulacra max. width	17.2 mm
Height of interambulacral plates at ambitus	1.5 mm
Width of interambulacral plates at ambitus	8.2 mm
Height of interambulacral plates at plate 12	1.8 mm
Width of interambulacral plates at plate 12	6.9 mm

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1034 **TABLE 3. Test dimensions in *Arbacia terraeignotae* sp. nov, CB-400.**

Test horizontal diameter	46.5 mm
Test height	21.4 mm
Apex max. diameter	10.1 mm
Peristome diameter	23.1 mm
Ambulacra max. width	7.6 mm
Interambulacra max. width	19.2 mm
Height of interambulacral plates at ambitus	2.8 mm
Width of interambulacral plates at ambitus	10.3 mm
Height of interambulacral plates at ambitus	4.1 mm
Width of interambulacral plates at ambitus	6.5 mm

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1037 **TABLE 4. Test dimensions in *Arbacia spatuligera*, CM-170 to CM-179.**

Test horizontal diameter	61.0 mm
Test height	33.0 mm
Apex max. diameter	10.0 mm
Ambulacra max. width	17.0 mm
Interambulacra max. width	24.0 mm
Height of interambulacral plates at ambitus	3.7 mm
Width of interambulacral plates at ambitus	20.0 mm

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1040 **TABLE 5. Test dimensions in *Tetrapygyus niger*, DA-327.**

Test horizontal diameter	61.0 mm
Test height	33.0 mm
Apex max. diameter	10.0 mm
Ambulacra max. width	17.0 mm
Interambulacra max. width	24.0 mm
Height of interambulacral plates at ambitus	3.7 mm
Width of interambulacral plates at ambitus	20.0 mm

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1045 **TABLE 6. Synthesis of morphological features.**

	<i>Arbacia spatuligera</i>	<i>Arbacia dufresnii</i>	<i>Tetrapygyus niger</i>	<i>Arbacia quyllur</i> sp. nov.	<i>Arbacia terraesignotae</i> sp. nov.	<i>Arbacia larraini</i> sp. nov.
Ambulacral plates	3-geminate	3-geminate	4-geminate	3-geminate	5-geminate	5-geminate
Gonopores	small	small	large, abuts outer margin	large, abuts outer margin	large, abuts outer margin	small
Secondary tubercles	absent	absent	present	absent	present	absent
Adoral spines	long and flat	short and flat	short and flat	short, flat and wide	short and flat	short and flat
Smaller 1st tubercles	up to 5	often 3	absent	present at the ambitus	1-2	often 3
Position of smaller 1st tub	adoral margin of plates	adoral margin of plates	NA	adoral margin of plates	middle of the plate	adoral margin of plates

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