

New Species of the Genus Arbacia (Echinoidea, Arbaciidae) from the Neogene of Chile.

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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						

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 richness of the genus Arbacia along the Chilean coasts than previously thought. 32

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

GÉNERO 34 NUEVAS ESPECIES DEL Resumen. ARBACIA (ECHINOIDEA, ARBACIIDAE) DEL NEÓGENO DE CHILE. Recientes trabajos de campo en el Neógeno 35 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.

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 Biotic Interchange (Webb, 2006; Cody et al., 2010; Stehli & Webb, 2013; Leigh et al., 52 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).

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

96 1988). Arbacia improcera Conrad, 1843 is known from the late late Pliocene of Florida 97 (Tamiami Formation and Intracoastal Formation), the middle/late late Pliocene of North 98 and South Carolina, the late Pliocene of Virginia (Yorktown Formation) and the lower 99 Pliocene of Curaçao (Cooke, 1959; Kier, 1972; de Buisonjé, 1974; Whitmore, 1987; Campbell & Campbell, 1995; Ciampaglio et al., 2009; Ciampaglio & Osborn, 2011; 100 101 Osborn et al., 2020). Arbacia waccamaw Cooke, 1941 from the late Pliocene of South 102 Carolina (Goose Creek Limestone; Cooke, 1959) and the lower Pleistocene of Florida 103 (Waccamaw Formation; Cooke, 1959). Arbacia rivuli Cooke, 1941 was reported from the 104 lower Pleistocene of Florida (Waccamaw Formation; Cooke, 1959). Two extant species are 105 also represented in the fossil record of North America. Arbacia stellata is also known from 106 the late Pliocene of Cedros Island (Baja California, Mexico) and Pacific Beach 107 (California). Arbacia punctulata (Lamarck, 1816) was reported from the mid/late 108 Pleistocene of Florida (Anastasia Formation; Herrera et al., 2006) and the middle 109 Pleistocene of North and South Carolina (Canepatch Formation; Cooke, 1959; Ciampaglio 110 et al., 2009). In contrast, the fossil record of the genus Arbacia is poor in South America. It 111 is restricted to representatives of the extant species A. stellata from the Late 112 Pliocene/Pleistocene of Ecuador (Canoan Formation, Di Celma et al., 2002) and A. 113 punctulata in the lower Pleistocene of Venezuela (San Gregorio Formation; Mihaljević et 114 al., 2010). This poor fossil record departs from the present diversity of the genus that 115 comprises the four extant species A. stellata (Blainville, 1825), A. punctulata (Lamarck, 116 1816), A. dufresnii Blainville, 1825 and A. spatuligera (Valenciennes, 1846), without 117 mentioning the closely related species Tetrapygus niger (Molina, 1782). This could 118 suggest either a recent diversification of the genus Arbacia in South America, or the 119 absence of adequate marine deposits, or taphonomic biases.

Recent field works carried out in the Atacama, Antofagasta and Tarpacá regions, in the north of Chile, led to the discovery of original fossil material that sheds new light on the ancient origin and diversity of the genus *Arbacia* in South America, and documents the evolution of paleobiogeographic connections between North and South America since the Miocene.

Institutional abbreviations. CB, Museo Paleontológico de Caldera, Caldera, Chili; CM;
Universidad Católica del Norte, Coquimbo, Chile; DA, Collection "Expansion and
Improvement of Diego Aracena Airport" of Iquique, Regional Museum of Iquique, Chile;
SNGM, Mining and Geology National Survey of Chile, Chile.

- 129 GEOLOGICAL SETTINGS
- 130

Figure 1

131 The studied material comes from the north of Chile, with two sites located in the 132 Atacama region (west of Copiapo), one site in the Antofagasta region and one site in the 133 Tarpacá region (Fig. 1). The Miocene material was collected as part of the design and 134 implementation of the cultural heritage management plan in the "Isla Grande de Atacama 135 Multipurpose Protected Coastal Marine Area" (2016). The Pliocene material of Caldera 136 was collected during the project "Geological Study, Paleontological Baseline and Zoning 137 of the Cerro Ballena Protected National Asset, Municipality of Caldera, Atacama" (2013), 138 while the Pleistocene material from Iquique is part of the collection rescued during the 139 paleontological supervision of excavations performed for public works of the project 140 "Expansion and Improvement of the Diego Aracena Airport", Iquique. The Pleistocene 141 material from Mejillones was collected during the paleontological monitoring of the 142 project "Tratamiento Corporativo de Concentrado de Molibdeno" (CODELCO) in 143 Mejillones, Antofagasta region.

Figure 2

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 Bahia 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

precisely the upper part of the unit 4 described by Carreño (2012) and is part of the
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 andfragmented and complete shells like pectinids or gastropods.

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

189 Specimens of *Tetrapygus 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 from littoral to sublittoral zones of lower energy, represented by sandstone and coquina 196 197 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

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

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

214	Phylum ECHINODERMATA Klein, 1778
215	Class ECHINOIDEA Leske, 1778
216	Order ARBACIOIDA Gregory, 1900
217	Family ARBACIIDAE Gray, 1855

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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).

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

Diagnosis. Interambulacral area entirely naked aborally but for one single adradial column
of small tubercles, with one tubercle per plate abutting the adoral suture; gonopores large
(>1 mm), occupying a large part of genital plates; ambulacral plates trigeminate aborally;
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).

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

261 Peristome only partially preserved but likely very large (more than 50% of test262 diameter).

Ambulacra narrow, less than half the width of interambulacra. Each ambulacral plate with one small imperforate and non-crenulate tubercle perradially but for the first plates located directly above the ambitus, which may have two primary tubercles each. Ambulacral tubercles the same size as interambulacral tubercles, much larger at the ambitus and orally (Figs. 4. 2, 3). Presence of small granules in between tubercles perradially (Fig. 4. 3). Ambulacral plates trigeminate throughout, of the arbaciid type aborally, forming more complex compound plates and significantly widening adorally to form wide, short phyllodes. Pores rounded and strongly conjugate aborally. On the oral side, perradial pits for sphaeridiae 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

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

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

Formation, late late Pliocene of Caldera, Chile (Marquardt *et al.*, 2000; Mourgues & Pérez,
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 oxyrhinchus). 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 uppermostpart of the Bahía Inglesa 337 Formation (Rojo, 1985), which was attributed to the lower Pliocene based on foraminifer 338 assemblages (Marquardt et al., 2000).

Taphonomy. Specimens of *Arbacia larraini* sp. nov. commonly occur in high density,
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.

Diagnosis. Ambulacral plates quinquegeminate throughout; well-developed neural canal; periproct almost circular; wide naked interambulacral area down to the ambitus; all 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).

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

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

366

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 quiquegeminate 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 interradial 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 quinquegeminate 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 quinquegeminate ambulacral plates is a character only known in 403 the extant species *Tetrapygus 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 tubercles, well-spaced ambulacral tubercles, vertical line of pore pairs and developed bare 405 406 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 quinquegeminate; 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).

Apical disc small (AP/D = 22%), hemi to dicyclic, without tubercles. Epistroma well developed, forming punctuation on genital plates and fine crenulations at the margin of genital and ocular plates. Ocular plate V is insert in most specimens, ocular plate I occasionally insert, all other oculars are exsert. The periproct is oval in outline and well extended in direction 1-IV as it is usually the case in species of the genus *Arbacia* (Fig. 5). Gonopores very large, abutting the outer margin of genital plates and often occupying 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 in446 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.

Interambulacra wide with three to four imperforate and non-crenulate primary tubercles per plate at the ambitus. Smallest specimens (Fig. 6) with only two tubercles at the ambitus. Height of plates increase along the aboral surface adapically (from 2 to more than 4 mm height). Above the ambitus, one single, adradial column of large primary tubercles reaches the apical system. Second row of interambulacral tubercles present up to the second plates before the apical system. These tubercles with large mamelons, narrow platforms and broad areoles occupying most of the plate width (Fig. 6). Presence of three
(adambitally) to one (adapically) inner smaller tubercle per plate and secondary tubercles
above. Primary tubercles not aligned along the adoral margin of the plate. Those tubercles,
occupying most of the plates, does not leave a naked medial interambulacral area.
Otherwise, the plates are coarsely granulated in between tubercles. Epistroma well
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 quinquegeminate 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 *Tetrapygus* 484 niger, a shallow-water member of the Arbaciidae. This also questions the very taxonomic 485 status of the genus Tetrapygus and of Tetrapygus 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 Tetrapygus. 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>65mm); 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, 1975) to highlight specific characters. The studied specimens are morphologically identical to the extant species *Arbacia spatuligera* and differ from all other species of the genus *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 *Tetrapygus* (Agassiz, 1841)

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

554

Figure 9

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

556 Tetrapygus 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.

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

568 **Stratigraphy**. The examined specimens of *Tetrapygus 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).

Emended diagnosis. Ocular plate V invariably insert; aboral interambulacral plates with one to several secondary tubercles, increasing in number progressively from the apex towards the ambitus and arranged in horizontal series above and below primary tubercles; arbacioid-type ambulacral plate quadrigeminate, compressed, with isopores not aligned in a single, regular column; primary spines with poorly developed enameled tips; color deep 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 are large and abut the adoral margin of genital plates, often occupying half of the part ofthe 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 quinquegeminate 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 interradial 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).

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

614 The summary table (Tab. 6) includes important diagnostics features used to identify615 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

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

634 The morphology of oral pores is similar in *Tetrapygus 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 intertidally. This is the case of all species of Arbacia and of Tetrapygus niger, with only 645 646 the number of isopores differing between species.

647 The aboral ambulacral plating, pore size and pattern, however, differ between 648 Tetrapygus 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 A. larraini (quinquegeminate plates) suggests an adaptation of these species to living in 657 658 shallow-water, high-energy environments. While T. niger is only reported from rocky

bottoms and shallow waters, between 0 and 40 m depth, *A. dufresnii* and *A. spatuligera* are known at greater depth, down to 250 meters, from soft bottoms. *A. quyllur* from the Miocene has trigeminate ambulacral plates and narrow phyllodes, similar in shape to *A. dufresnii* and *A. spatuligera*. These data are congruent with sedimentological data and associated faunas that suggest very shallow nearshore environments. In addition to the morphology of spines, this could suggest the presence of the species in shallow waters, in 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, including three new fossil species —A. quyllur from the Late Miocene, A. terraeignotae 668 669 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 Buisonjé, 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.

The specimens of newly described species reveal the past diversity of the genus *Arbacia* and increase our knowledge of the overall diversity of the genus in South America, which includes four extant species, *A. stellata, A. punctulata, A. spatuligera,* and *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 Tetrapygus 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 Tetrapygus 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 *Tetrapygus*. 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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 960 292(5515), 274–278.
- 961
- 962 **Figure captions**



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



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

al., 2016) modified from Carreño, 2012 with location of type material of *Arbacia quyllur*.



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



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

985 Mourgues.





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

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





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997 Figure 7. 1–5, Spines found with *A. terraeignotae* and *A. larraini* from the late Pliocene; 1, longest spine







1000 Figure 8. 1–7, Arbacia spatuligera from the late Pleistocene of Mejillones (Chile); 1–6, best preserved





1003 Figure 9. 1–3, *Tetrapygus 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.



1006 Figure 10. Ambulacral plate pattern in Chilean species of Arbacia and Tetrapygus, SEM photos and

1007 drawings. 1, Arbacia spatuligera; 2, Arbacia dufresnii; 3, Tetrapygus niger; 4, Arbacia terraeignotae.

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

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

TABLE 3. Test dimensions in Arbacia terraeignotae sp. nov, CH	3-400.
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

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

1040	TABLE 5. Test dimensions in Tetrapygus 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		



1042 1043

	Arbacia spatuligera	Arbacia dufresnii	Tetrapygus niger	Arbacia quyllur sp. nov.	Arbacia terraeignotae sp. nov.	Arbacia larraini 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