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***Arbacia ballenensis* sp. nov. (Echinoidea, Arbacioida): A new species reveals diversification of the genus in Central America.**

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Abstract

A new species of *Arbacia* (Echinoidea, Arbacioida), *A. ballenensis* **sp. nov.**, from the Late Pliocene – Early Pleistocene of Baja California Norte, México, is described from a series of 62 specimens ranging in size from 6 to 20 mm test diameter. It differs from all extant species in the genus by its high number of interambulacral plates, numerous small interambulacral tubercles, and the size of the interambulacral tags at the peristomial edge. This new species yields new evidence concerning the diversification of the genus along the Pacific coast of North America where previously, only one extinct species was described, *Arbacia abiquaensis* from the Oligocene of Oregon. *A. ballenensis* **sp. nov.** is closely related to the recently described *Arbacia quyllur* from the late Miocene of Chile. Study of the new species in the context of events such as the mid-Pleistocene Transition helps shed light on patterns of extinction and speciation within the genus.

Keywords: Echinoidea, Arbaciidae, *Arbacia*, Pliocene – Pleistocene, new species, Baja California fauna.

Introduction

The order Arbacioida Gregory, 1900 is a small clade of Echinoidea that includes 26 known extant species in eight presently recognized genera belonging to a single family, the Arbaciidae Gray, 1855. The two largest genera, *Arbacia* Gray, 1835 and *Coelopleurus* L. Agassiz, 1840 contain the majority of these species (five and 11 respectively), with an additional species in each of *Tetrapygyus* L. Agassiz, 1841, and *Sexypyga* Shigei, 1975 (Kroh 2020; Kroh & Smith 2010; Mortensen 1935). Although *Arbaciella* Mortensen, 1910 is presently listed as a valid genus in the World Echinoidea Database (Kroh & Mooi 2023), we follow the first hypothesis indicated in Kroh *et al.* (2012), namely that this genus represents the juveniles of other species of Atlantic *Arbacia*. The remainder of the extant arbaciid species are placed in relatively poorly-known, deep-sea genera: *Dialithocidaris* A. Agassiz, 1898 from the Caribbean Sea and the Indo-Pacific region, *Habrocidaris* A. Agassiz & H.L. Clark, 1907 from the Caribbean Sea, *Podocidaris* A. Agassiz, 1869 from the Caribbean Sea and the Indo-Pacific region, and *Pygmaeocidaris* Döderlein, 1905 from the Indian Ocean (Mortensen, 1935).

The genus *Arbacia* alone exhibits a wide distribution, including the West and East coasts of the USA, the West coast of Africa, and the Mediterranean Sea. Several extant and fossil species have been described along the Atlantic coast of North and South America. The extant species, *Arbacia punctulata* (Lamarck, 1816), is found along the west Atlantic coasts, from Cape Cod (Massachusetts, USA) to French Guiana (Durand 1959; Mortensen 1935). An additional extant Atlantic species, *Arbacia lixula* (Linné, 1758), has a wide distribution there, including off Brazil, in the Gulf of Guinea, the Azores, and the eastern Atlantic into the Mediterranean Sea (Durand 1959, Mortensen 1935). There are at least three fossil species from the Late Pliocene and Early Pleistocene of Florida, North and South Carolina, and Virginia: *Arbacia improcera* Conrad, 1843, *Arbacia waccamaw* Cooke, 1941, and *Arbacia rivuli* Cooke, 1941.

Along the eastern Pacific coasts, the genus includes *Arbacia stellata* (Blainville, 1825), which ranges from California (USA) to Peru, *Arbacia spatuligera* (Valenciennes, 1846), from northern Peru to Puerto Montt (Chile), and *Arbacia dufresnii* (Blainville, 1825), from Puerto Montt to Buenos Aires (Argentina), the Falkland Islands and Tristan da Cunha in the South Atlantic Ocean (Mortensen 1935). Recent work (Courville *et al.* 2023) led to the description of three new fossil species from the northern coast of Chile, including *Arbacia quyllur* from the uppermost Miocene, plus *Arbacia terraeignotae* and *Arbacia larraini* from the uppermost Pliocene. These findings demonstrated that the genus also diversified during the Pliocene along southeastern Pacific coasts.

Compared with Atlantic and southeast Pacific regions, the fossil record of the genus along Pacific shores of Central and North America is surprisingly poor. One might expect more fossil *Arbacia* taxa considering that the oldest species, *Arbacia abiquaensis* Linder, Durham & Orr, 1988 is already known from the Late Oligocene of Oregon (Linder *et al.* 1988). Therefore, the genus was presumably present along Pacific North American coasts at least since that time. The only other specimens known from fossil deposits from the west coast of North America and northern South America have been attributed to the extant species *A. stellata* (an attribution that is in doubt based on personal, as yet unpublished observations by two of the authors (EC, RM)). This species also being recorded from the Pliocene of California, Cedros Island (Baja California, México, see Linder *et al.* 1988) and Ecuador (Di Celma *et al.* 2002).

In the present work, we describe a new species of *Arbacia* from the uppermost Pliocene – Early Pleistocene deposits of Baja California, México. Based on a wide size range of specimens, the morphology of the new taxon is compared with other *Arbacia* species including what we suggest is the closely related species, *Arbacia quyllur* Courville, Gonzales, Mourgues, Poulin, Saucède, 2023 from the uppermost Miocene of Chile. We discuss possible causes for the extinction of at least three species of *Arbacia* during the middle Pleistocene transition.

Material and methods

The materials examined in this study are housed in the Geology collections at the California Academy of Sciences, San Francisco, USA (CASG). The holotype is catalogued under CASG 103360. The main collection consists of 50 specimens, both complete and incomplete, catalogued under CASG 91189. Additional specimens were also discovered within the Academy's collection, including three single-specimen lots identified as CASG 58896-4, CASG 58887-01, and CASG 91171, two two-specimen lots labeled CASG 58890 and CASG 58892.04, one three-specimen lot identified as CASG 61050.02, and one four-specimen lot designated as CASG 91697. In total, the material examined in this study comprises 62 complete tests ranging in diameter from 6 to 20 mm (lacking articulated spines), along with fragments of tests and several isolated spines found within the loosely consolidated sandy sediments. Additional informal numbers are assigned to individual specimens within the CASG 91189 lot to establish a direct connection between specimen numbers, the holotype, paratypes, and figured specimens.

FIGURE 1

Geological setting. The type locality (Figs. 1A, B) is at the east end of Bahía San Rafael, upper Golfo de California, 85 km southeast of the village of Bahía de Los Angeles, Baja California (México). It is a remote area accessible only by gravel and dirt roads. The region is characterized by widespread exposures of igneous rocks, mainly Cretaceous granites and tonolites, Miocene and Pliocene andesites and Pliocene basalts (Gastil *et al.* 1971; Johnson *et al.* 2017). Sedimentary deposits from the upper Neogene also occur along coastal embayments near Punta Ballena (Johnson *et al.* 2017). They make up part of the San Francisquito Basin

(Johnson 2014; Johnson & Ledesma-Vázquez 2009), which is composed of Pliocene sandstones and conglomerates unconformably overlying the Cretaceous substrate. The Pliocene shoreline crops out as high as 140 m above the current sea-level due to a local tectonic coastal uplift and accompanying drop in sea-level (Johnson 2014).

Pliocene sediments were deposited in a deltaic system described as the Punta Ballena fan (Johnson *et al.* 2017). They contain a unique echinoid-rich bed characterized by high densities of the dendrasterid sand dollar *D. vizcainoensis* ("sand dollars" in Fig. 1C) with no equivalent in Baja California. This species of dendrasterid was listed by Johnson *et al.* (2017) and Johnson (2021) as "*D. granti*" which, however, had already been formally synonymized by Mooi (1997) with *D. vizcainoensis* Grant & Hertlein, 1938. The unpublished material described in the present work was collected by D.S. Baumbach with numerous specimens of *D. vizcainoensis* in several localities nearby (Fig. 1B) at Bahía San Rafael from coastal terraces. The associated fauna (*D. vizcainoensis*, as "*D. granti*", and bivalves) indicates the material was sampled from the echinoid-rich bed (Markes E. Johnson, and Jorge Ledesma-Vasquez, personal communications).

Biostratigraphy and age. The Punta Ballena fan deposits' central region has a layer up to 2.3 m thick containing high densities of the echinoid *D. vizcainoensis*, suggesting a maximum age range from 3 to 2 million years. Besides echinoids, this fossil-rich bed in Baja California has also yielded numerous bivalve remains consisting of *Patinopecten* sp. indeterminate (as *Patinopecten* sp.), *Argopecten abietis* s.s. (Jordan and Hertlein), (as *Aequipecten abitis*), *Leopecten vogdesi* (Arnold) (as *Pecten rogedesi*), and *Ostrea megodon* Hanley (as *O. megado*) (Johnson 2021; Johnson *et al.* 2017). In the adjacent San Francisquito basin, *Nodipecten arthriticus* (unaccepted name, *N. subnodosus*), *Pecten vogdesi* (unaccepted name, *Leopecten vogdesi*), and another echinoid species identified as *Clypeaster revellei* Durham, 1950 were collected. The latter species is considered diagnostic of the middle Pliocene, as defined by

Durham (1950), but is better recognized today as Late Pliocene. Other Pliocene deposits located north of Punta Ballena, such as Isla Ángel de la Guarda, Isla Monserrat, and Santa Rosaliita on Peninsula de Concepción, provide index fossils indicating similar stratigraphic levels (Johnson & Ledesma-Vázquez 2009). All of these were deposited in transgressive tracts dated at around 3 Mya, during the Placenzian Stage (Johnson *et al.* 2017).

Pliocene basins further north, such as El Mangle and San Nicolas, are characterized by a different set of index fossils and assigned to a lower position in the Pliocene (Johnson *et al.* 2017). These basins include interbedded volcanic deposits, which were dated at around 3.3 (\pm 0.5 Ma) (Johnson *et al.* 2003) or early Late Pliocene, giving a younger age for the Punta Ballena fan deposits. These additional data concerning the regional biostratigraphy of concurrent range zones, supplemented by absolute age dates from inter-bedded volcanics in other places, suggest an origin for the delta complex of not more than 3 Mya. The dendrosterid sand dollar bed, located in the middle part of the delta fan complex, would suggest an even younger age corresponding at least to the Late Pliocene (middle Placenzian) but could also include a large part of the Early Pleistocene (Gelasian, see Johnson *et al.* 2017; <https://stratigraphy.org/ICSchart/ChronostratChart2023-06.pdf>).

Taxonomy. The description of the new species, *A. ballenensis* **sp. nov.** is based on a concurrent study of the fossil species of *Arbacia* that suggests assignment using the proposed diagnostic features of the genus supported by previous taxonomic studies (Kroh & Smith 2010; Smith *et al.* 2006). Systematic nomenclature and terminology for morphological description largely follow Kroh (2020). As for extant species of *Arbacia*, important ontogenetic changes make it difficult to assign the smallest specimens to a given species. The present species description is based on examination of the largest specimens (above 20 mm in test diameter), for which

morphological differences between species are most strongly developed. Additional information on ontogenetic variation is given when appropriate.

Abbreviations:

CAS California Academy of Sciences

CASG California Academy of Sciences (Geology)

TD Test Diameter

PD Peristome Diameter

Systematic part

Phylum Echinodermata Klein, 1778

Class Echinoidea Schumacher, 1817

Order Arbacioida Gregory, 1900

Family Arbaiidae Gray, 1855

Genus *Arbacia* Gray, 1835

***Arbacia ballenensis* n. sp.**

Figures 2–4, table 1.

Diagnosis. *Arbacia* with low, numerous interambulacral plates (N = 19 at TD = 20 mm); up to five subequal tubercles in interambulacral plates at the ambitus (TD = 20 mm); inner interambulacral tubercles close to the adoral plate margin; naked interambulacral areas elevated above adjacent ambulacra.

Type material. Holotype specimen CASG 103360, housed in the Geology collections at the CAS, San Francisco, California, USA (Figs. 2A–D). The remaining specimens in lot CASG 91189, which includes 49 complete or partial tests, are designated as paratypes.

Referred material. Sixty-two complete tests lacking articulated spines ranging from 6 to 20 mm TD, plus seven test fragments. In addition, there are several isolated spines in the poorly consolidated sandy sediments, some of which are also preserved within the peristome.

Etymology. The name is derived from the type locality on Punta Ballena, as this species is so far known only from the Pliocene – Pleistocene of this point along Bahía San Rafael, close to San Francisquito (Baja California Norte, México).

Stratigraphy. Late Pliocene to Early Pleistocene. Unnamed beds, middle part of the Punta Ballena fan (Johnson *et al.* 2017).

Taphonomy. Specimens with complete tests (except for seven fragments), locally abundant in one specific layer, sometimes with attached balanomorph barnacles. It would appear from this, and the excellent condition of the surface details on the specimens that they were dead when buried, with little or no post-mortem transport (see below).

FIGURE 2

FIGURE 3

Description. Test small, largest specimen barely reaching 20 mm TD (Fig. 2), test relatively low (height to diameter ratio <0.5 ; Fig. 2C), flattened orally, test outline circular in apical view (Figs. 2A, 3A, C).

Apical system—Approximately one third test diameter (Figs. 2A, 3A, C, D), ratio of apical system diameter to TD decreasing with size from 35% TD (TD = 6 mm) to 29% TD (TD = 20 mm), apical system dicyclic, all ocular plates always exsert (Figs. 2A, 3A, C, D, F). Periproct elongated in direction 1-IV. Gonopores usually large, slightly elongated, positioned close to adoral edge of genital plates (Figs. 2A, 3A, D, F). Gonopores already developed in specimens between 8 and 10 mm TD (Figs. 3A–D). Ocular plates with large granule (possibly a small tubercle) close to adoral margin. Genital plates free of tubercles.

Peristome—Usually less than 50% of test diameter (mean ratio PD/TD = 46%; Figs. 2B, 3B). Buccal notches shallow. Tags short (length $<$ width, spanning <1 tubercle). Perignathic girdle thin, auricles separate, not in contact over interior of perradial suture (Fig. 3G). Epistroma well-developed, forming homogeneous granulation on ocular and genital plates (Fig. 3A).

Ambulacra—Wider than half width of interambulacra. At ambitus, each ambulacral plate with one small, imperforate, non-crenulate tubercle positioned adradially (Figs. 2A, 3F). Ambulacral plates small and numerous. Ambulacral tubercles same size as interambulacral tubercles at ambitus, slightly decreasing in size adapically (i.e. above ambitus). Tubercles small and well-developed aborally, forming two rows of tubercles on aboral surface, almost reaching apical system (Figs. 2A, 3A, D). Presence of well-developed granules in between tubercles perradially. Ambulacral plates trigeminate, of arbaciid type (Fig. 2D), forming more complex compound plates adorally, slightly widening to form short, narrow phyllodes. Pores rounded, spaced, strongly conjugate aborally with large, prominent ridge between pores (Fig. 2D). On oral side, one perradial sphaeroidal pit (usually well preserved) near peristomial edge (Figs. 2B, 3B, E).

Interambulacra—Plates wider than their height at ambitus (height/width ratio < 0.2), with up to five (TD = 20 mm), small, imperforate, non-crenulate primary tubercles (Fig. 2C), slightly decreasing in diameter toward interradius, on adoral margin of plates. Maximum number of interambulacral tubercles at ambitus decreases to four (TD = 17 mm), three (TD = 15 – 8 mm) and commonly only two in smallest specimens (TD = 10 – 8 mm). Number of interambulacral plates usually between 17 and 18 (TD > 17 mm), decreasing in number slightly in small specimens to 12 or 13 plates in each interambulacrum (TD = 8 mm). Plates lowest above ambitus, height of plate constant on aboral surface (< 1 mm, TD = 20 mm; Fig. 2A). Tubercles in outer row slightly reduced in size above ambitus (Fig. 2A). Number of interambulacral tubercles reduced abruptly from five at ambitus to two or three plates above ambitus (TD = 20 mm). Inner tubercles slightly smaller than outer ones (Fig. 2C), abutting adoral margin of plates, close to outer row of primary tubercles. Second inner tubercle well developed along aboral surface, usually forming columns adapically to middle part of aboral surface (Figs. 2A, 3A, D). Outer row of tubercles same size from ambitus to apical system (Fig. 2A). Additional column

of interambulacral tubercles between first column and pore area developed in largest specimen (TD = 20 mm; Fig. 2A) but restricted to ambitus and lowermost part of aboral surface (Fig. 2D). Large tubercles surrounded by several tiny granules. Areoles of tubercles poorly developed above ambitus, barely larger than mamelon. Interambulacral naked area wide, extended adorally to ambitus (Figs. 2A, 3A, C–D). Epistroma consisting of conspicuous, randomly distributed punctation (Fig. 3A). On aboral side, members of second perradial column of tubercles progressively reduced, conjoined adapically to form continuous ridge between adradial column of tubercles and perradial naked area of ambulacrum (Fig. 3A).

Remarks

Taxonomic attribution—The presence of a well-developed epistroma, sphaeridia positioned in pits at the perradius, and imperforate, non-crenulate tubercles support the assignment of the new species to the order Arbacioida. The compound, arbaciid-like plates in the ambulacra, imperforate and non-crenulate tubercles that are similar in size in both ambulacra and interambulacra at the ambitus, and a pronounced difference in tuberculation between the oral and aboral side (aboral tubercles highly reduced in size and number), are diagnostic of the family Arbaciidae. Taken together, the presence of a straight pore-zone with pores not arranged in arcs, ambulacral tubercles forming a regular series throughout, a large peristome (> 30% TD), interambulacra with numerous primary tubercles arranged in horizontal and vertical series, and a single sphaeridial pit near the peristomial edge in each interambulacrum are features by which to recognize members of the genus *Arbacia*. The placement of the new species in this genus is also circumstantially supported by the occurrence of straight and finely striated spines with an enameled tip that we feel were shed by the echinoids at some point during taphonomy.

Comparison with other species—*Arbacia ballenensis* **sp. nov.** differs from all other species of *Arbacia* by the high number of interambulacral plates and numerous small tubercles on

interambulacral plates at the ambitus. However, it shares characters with and has an overall similarity to *Arbacia quyllur* from the uppermost Miocene of Chile (Courville *et al.* 2023), which is also characterized by a high number of interambulacral plates (N = 17, TD = 40 mm). An important difference is that in smaller *Arbacia quyllur*, similar in size to large *A. ballenensis* **sp. nov.**, there are only seven plates aborally (TD = 10 mm) versus twelve to thirteen in *A. ballenensis* **sp. nov.** The interambulacral tubercles are small and similar in size throughout the aboral surface in both *A. quyllur* and *A. ballenensis* **sp. nov.** Inner tubercles (that is, interambulacral tubercles that are situated medially in the interambulacrum relative to the most adradial tubercles) are reduced in size towards the interradius but are more numerous and more developed aborally in *A. ballenensis* **sp. nov.** The pore area is relatively wide for the genus in both species, with pores circular and widely separated. They are conjugated by a deep furrow connecting the pores, and each pore pair is separated from the next in the series by a prominent ridge. The gonopores are large in both species but are already open in smaller specimens of *A. ballenensis* **sp. nov.** In *A. quyllur*, they are open only in specimens 10 mm TD or larger (Courville *et al.* 2023). The peristome is also larger in *A. quyllur* (mean PD/TD = 50%). Despite these differences, *A. quyllur* and *A. ballenensis* **sp. nov.** are more similar to each other than either is to any other species of *Arbacia*, fossil or extant.

Variation during growth—Interestingly, as indicated by the data in the description above, morphology of the corona of *A. ballenensis* **sp. nov.** appears to be relatively unaffected by allometric changes during ontogeny. Unlike extant *Arbacia* species, changes in size do not strongly impact plate structure or tubercle position. Instead, size increase occurs primarily in the form of a constant addition of interambulacral plates and an increase in the number of interambulacral tubercles, without significant alterations in peristome or apical system size relative to test diameter (Table 1). The only other *Arbacia* in which this is seen is the extinct *A. quyllur*, in which small individuals (TD approximately 10 mm) are nearly identical in

proportion, tubercle configuration, and plate counts seen in larger ones (TD approximately 40 mm). This lack of pronounced allometric change, contrary to what is observed in other *Arbacia* species, may be attributable to the reduced maximum size of both *A. ballenensis* **sp. nov.** and *A. quyllur*, most notably *A. ballenensis* **sp. nov.** Even at small sizes (6 to 7 mm), specimens of *A. ballenensis* **sp. nov.** possess open gonopores, indicating that connectivity with the internal gonads has already been established at considerably smaller sizes than in other *Arbacia*. Given the reduced size at time of gonopore appearance relative to nearly all other taxa in the genus, this could be an instance of paedomorphosis resulting from progenesis. A full phylogenetic analysis will be necessary to make that determination. Based on current knowledge, *A. ballenensis* **sp. nov.** does not exceed 20 mm in test diameter. It has yet to be determined whether this small size represents potential paedomorphosis in this species, or if it is a plesiomorphic feature for the genus, or both. Based on the known sizes of other contemporaneous or even older species in the genus, such as *A. quyllur*, the very small size (TD < 20 mm) of *A. ballenensis* **sp. nov.** appears to be unique, which would argue more in favour of it being a derived condition seen in a single, younger fossil taxon. Phylogenetic analysis will be necessary to support this suggestion.

TABLE 1

FIGURE 4

Spines—Numerous isolated spines were also collected from deposits in which tests were found, some of them even occurring inside the corona of a few specimens. No spines were found articulated with tubercles on the echinoids. Therefore, spines found in close proximity to the echinoids are here described separately. Spines recovered from the unconsolidated matrix are long but shorter than the test diameter and circular in cross-section, with a large oblique

bulge at the base. In some specimens, a flat “enameled” tip was preserved. The shaft of all examples was finely striated, as is typical for species of *Arbacia* (Fig. 4).

Discussion

The material described herein represents the first extinct fossil *Arbacia* from Baja California, suggesting the occurrence of the genus during the Pliocene and Pleistocene as well as a broader distribution of the genus during warm Late Pliocene times than has been suggested to date. Previously, only material attributed to the extant *Arbacia stellata* had been recorded from the Pacific coast, specifically in the Pliocene deposits of Cedros Island (Baja California) and further north in southern California (USA). However, the knowledge of this material is limited, and a revision is much needed in order to ascertain if these specimens are in fact *A. stellata*.

The discovery of *A. ballenensis* **sp. nov.** increases our understanding of the past diversity of the genus during Pliocene – Pleistocene time on the Pacific side of the Isthmus of Panama. This finding is not surprising, given the recent identification of three new species from upper Neogene deposits in Chile (Courville *et al.* 2023), which further underscores the importance of studies in the region in order to understand the evolution of the genus. *A. ballenensis* **sp. nov.** was found in a single, thin layer that has not been found elsewhere in Baja California or, in fact, any other area (Johnson *et al.* 2017). The surprisingly rare description of such a deposit suggests that the limited distribution of this layer and its invertebrate community may be more due to lack of studies in the region containing similar localities or a general lack of focus on echinoid communities, rather than rarity of the deposit itself. On the other hand, as summarized in Mancosu & Nebelsick (2020) such rarity may also lie in the nature of shallow water, Plio-Pleistocene deposits. These are often only fortuitously preserved in tectonically active regions in which relatively young sediments have only recently been uplifted.

Pliocene and Pleistocene deposits of Baja California have been studied extensively for several decades, including invertebrate communities and echinoids (Durham 1950; Johnson

2021; Johnson *et al.* 2003; Johnson *et al.* 2017). Nevertheless, the discovery of an unexpected species of *Arbacia* in such a specific, geographically restricted layer is not without precedent. Other fossil species of the genus *Arbacia* are also known to be locally abundant, but in unique localities with highly specific layers that are restricted in time and geography. For example, *Arbacia rivuli* is found only within a thin layer between the uppermost beds of the Goose Creek Limestone and the Waccamaw Formation that occur at the Pliocene – Pleistocene boundary in North Carolina. Similarly, *Arbacia abiquaensis* has been found only at its type locality in Oregon (however, even there it is evidently a rare fossil). It is possible that these deposits represent highly specific environments that are not often preserved (Nebelsick & Mancosu 2021).

Extant species of *Dendraster* live partially buried in dense populations on sandy bottoms, characteristically between 6 and 12 m depth, but exceptionally down to 55 m (Johnson 2021). However, extant species in the genus *Arbacia* are associated with very different habitats, including rocky shores and shallow kelp forest environments (Mortensen 1935; Schultz 2005). They are usually abundant between 1 and 10 m with a maximum depth record for the genus of 350 m (Mortensen 1935). It is unusual to find a co-occurrence of dendrasterids and arbaciids in such close proximity in a deltaic deposit of the kind seen at Punta Ballena. As discussed in Johnson *et al.* (2017) and Johnson (2021), the echinoid-rich bed seems to result from outwash from heavy rainfall ashore that caused massive transfer of siliciclastic sand onto the delta during recurrent episodes. These events are considered to have been sudden, with the result that sand dollars and associated fauna living at shallower depths higher on the delta front became entrained into discrete death assemblages during the down-slope transfer of sediment. We speculate that the burial of *A. ballenensis* **sp. nov.** in these shallow deposits could be due to proximal storm activity, as lack of hummocky cross-stratification in sandstone layers of the delta does not preclude transport during mass flow events that might bring the *Arbacia* into

close proximity with deposits of dendroasterids. The existence of well-preserved, complete tests of *Arbacia* that can include attached barnacles (Johnson *et al.* 2017) suggests that the *Arbacia* were not subject to transport or significant weathering immediately after death. However, at least some of the individuals almost undoubtedly rested for some time on the sediment surface in relatively low energy hydrodynamic environments to allow settlement of barnacles on their surfaces before burial.

It seems that the high diversity of the genus *Arbacia* during the Late Pliocene and Early Pleistocene was strongly affected by geologically recent events, including turnover during the middle Pleistocene with the extinction of *Arbacia waccamaw*, *Arbacia rivuli*, and *Arbacia ballenensis* **sp. nov.** This could be due to factors related to the Mid-Pleistocene Transition event (MPT). The MPT occurred approximately 800 kyr ago and is associated with changes in period and amplitude of glacioeustatic sea-level cycles. According to Faichney *et al.* (2011), eustatic sea levels in the Pliocene and Pleistocene oscillated at different periods and amplitudes than today. The Gulfo de California was not directly affected by cycles of expansion and retreat of continental ice sheets over North America but was influenced by global sea-level variation (Durham & Allison 1980). This sea-level variation was recorded in numerous coastal terraces along the Gulfo de California (Johnson 2021). From about 2.5 to 0.8 Mya, the oscillation of sea levels was dominated by a 41 kyr period (Lisiecki & Raymo 2005) with sea-level fluctuations of 60 – 70 m (Dwyer *et al.* 1995). Since 0.8 Mya, eustatic sea-level fluctuations have been dominated by a period of 100 kyr and an amplitude of up to 120 m, with the period of change in cycles being cited as characteristic of the MPT (Dwyer *et al.* 1995). The MPT event is also responsible for surface salinity variation (at least in the Caribbean Sea, see Sepulcre *et al.* 2011) that might have strongly affected echinoid communities. Glacial periods, associated with strong sea-level regression inside the Gulfo de California, strongly modified available environments and could have led to the extinction of species that were living inside the Gulf.

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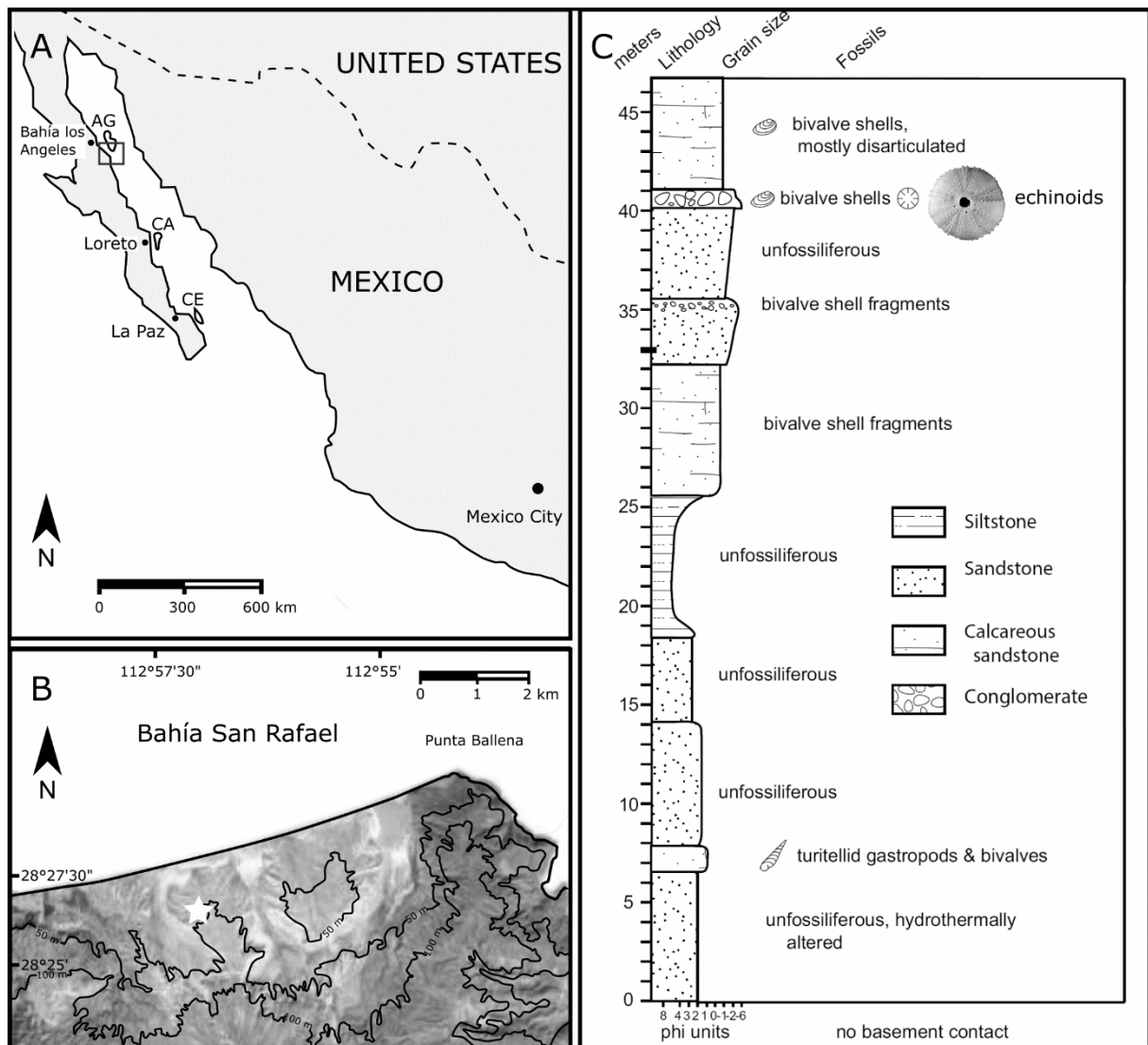


FIGURE 1. Type locality, area and stratigraphy of *Arbacia ballenensis* **sp. nov.** **A**, Locations of fossiliferous exposures Angel de la Guarda (AG), Carmen (CA), Cerralvo (CE). **B**, fossiliferous localities along Bahía San Rafael with location (star) of type locality for *Arbacia ballenensis* **sp. nov.** **C**, stratigraphic column representing seaward-dipping beds of upper Pliocene – lower Pleistocene Punta Ballena fan deposits (modified from Johnson *et al.* 2017) with position of *Arbacia ballenensis* **sp. nov.** indicated by image of holotype.

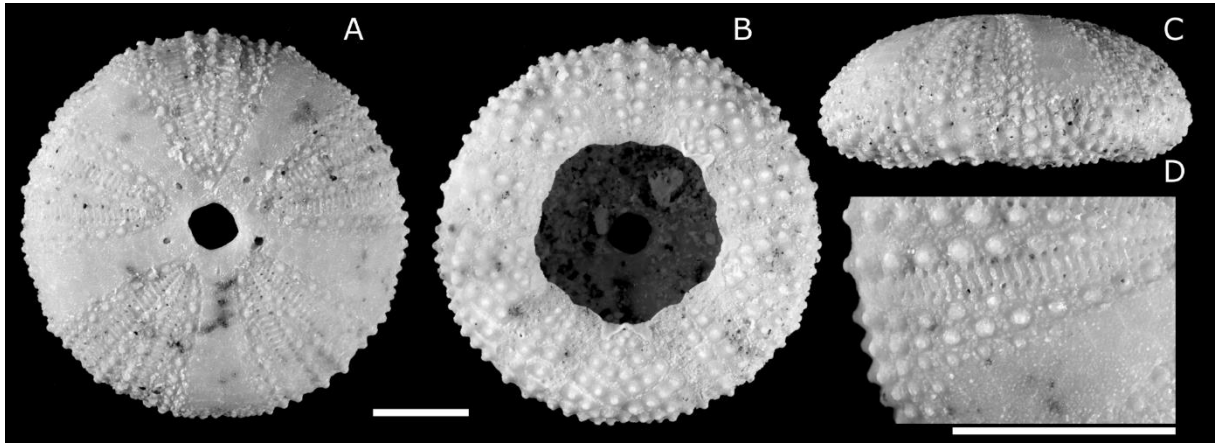


FIGURE 2. *A. ballenensis* sp. nov. **A-D**, holotype CASG 103360; **A**, aboral view; **B**, oral view; **C**, lateral view; **D**, details (magnified) of ambulacrum and interambulacrum on the aboral side. Scale bar equals 10 mm.

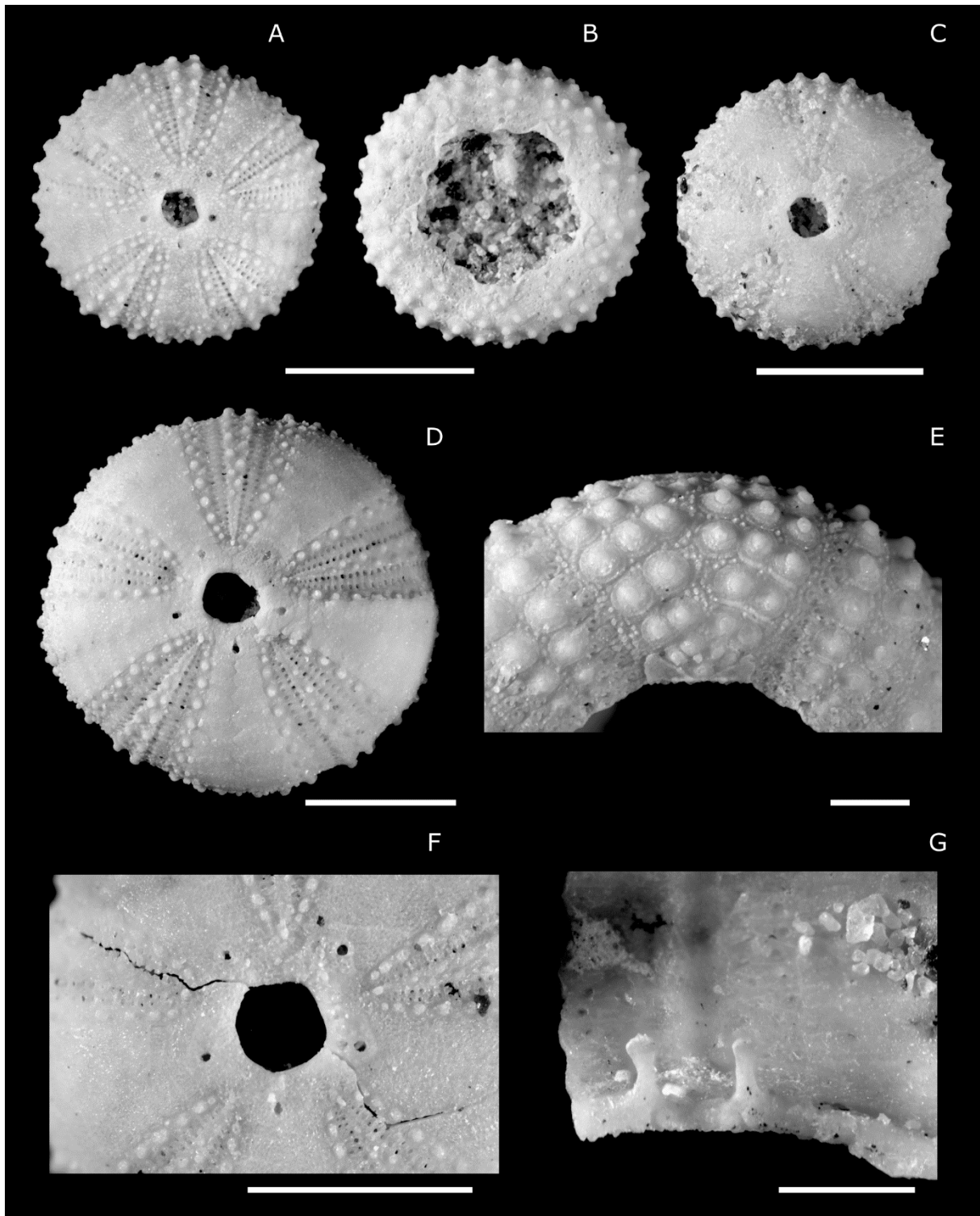


FIGURE 3. *A. ballenensis* sp. nov. **A-B**, paratypes in CASG 91189, specimen 21; **A**, aboral view; **B**, oral view; **C**, CASG 91189, specimen 20 in aboral view; **D**, paratype CASG 91189, specimen 24 in aboral view; **E-F**, CASG 91189, specimen 04; **E**, oral view; **F**, apical system; **G**, CASG 91189, specimen 03, perignathic girdle showing auricles. Scale bars equal 10 mm.

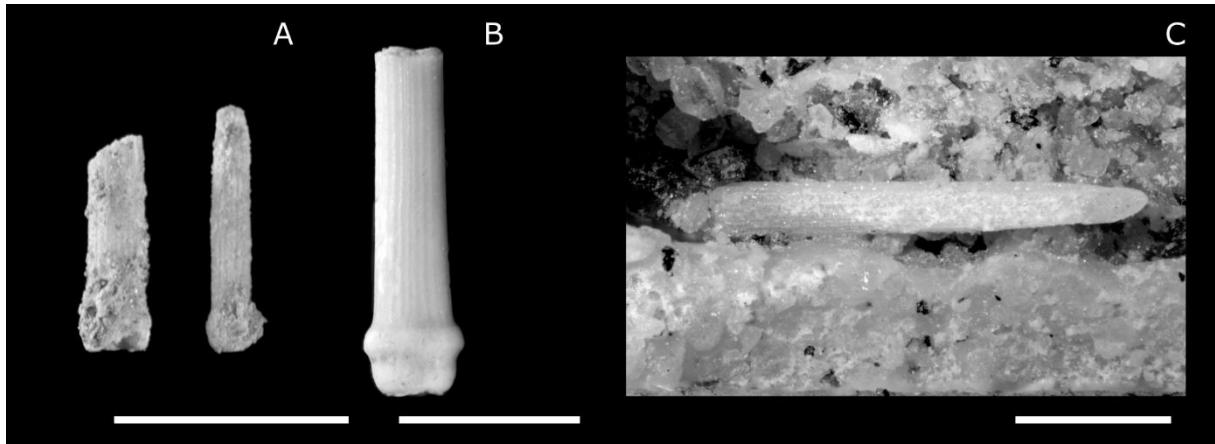


FIGURE 4. Spines attributed to *A. ballenensis* sp. nov. **A-B**, CASG 59779; **C**, spine found inside the peristome of CASG 91189, specimen 08. **A-B**, scale bars equal 2 mm. **C**, scale bar equals 1 cm.

TABLE 1. Test dimensions and morphological variations during growth in *A. ballenensis* sp. nov.

	TD = 8 to 10 mm	TD = 11 to 15 mm	TD = 16 to 20 mm
Peristome diameter	3.5 to 4.5 mm	4.5 to 6 mm	6 to 9 mm
Test height	3 to 5 mm	4.5 to 5 mm	6 to 9 mm
Iamb plate #	12-14	14-15	14-18
#Iamb ambital tubercles	2-3	3	4-5