# *Amusium cristatum* shell beds in the lower Pliocene deposits of Almería-Níjar Basin (SE Spain)

*Julio AGUIRRE*

Dpto. Estratigrafía y Paleontología, Facultad de Ciencias, Campus de Fuentenueva s.n. Universidad de Granada, 18002 Granada (Spain); jaguirre@ugr.es

## ABSTRACT

Densely packed monospecific-paucispecific *Amusium cristatum*-dominated shell beds are significant features in the lower Pliocene deposits of the Almería-Níjar Basin (SE Spain), embedded in distal prodelta fine-grained sand and silt. The shells in these concentrations are exceptionally well preserved: articulation is relatively high, fragmentation is low, abrasion is almost lacking, and many shells preserve the original colour pattern. These taphonomic signatures suggest *in situ* deposition forming autochthonous fossil assemblages, i.e. biological concentrations. Benthic foraminiferal assemblages found in the prodelta deposits indicate that they formed in mesotrophic mid-shelf settings.

The *A. cristatum* accumulations show similarities with recent concentrations of *A. balloti* from the Shark Bay (NW Australia). The latter species form dense populations in restricted positions of the bay from 10 to 75 m depth. The lowermost depth range of *A. balloti* is similar to the palaeobathymetry inferred for the *A. cristatum* beds. Furthermore, the shell beds studied occur in the centre of a relatively enclosed palaeobay. Apart from these coincidences, the proximate ecological causes accounting for the recent concentrations of *A. balloti* are still obscure. Thus, no straightforward actualistic comparison explains the biological origin of the *A. cristatum* shell beds. Based on benthic foraminiferal assemblages in the prodelta deposits, *A. cristatum* concentrations are most likely related to intermittent nutrient and food-particle supply from several deltas feeding

## RESUMEN

En los depósitos del Plioceno inferior de la Cuenca de Almería-Níjar (SE de España) se encuentran niveles de densas acumulaciones monoespecíficas-pauciespecíficas dominadas por *Amusium cristatum*. Dichos niveles están intercalados en arenas muy finas y limos depositados en zonas distales de prodelta. Los bivalvos muestran una excelente preservación: articulación relativamente alta, baja fragmentación, abrasion prácticamente nula, y algunos de los pectínidos preservan los patrones de coloración original. Estas propiedades tafonómicas indican una preservación *in situ* generando asociaciones autóctonas o concentraciones biológicas. Las asociaciones de foraminíferos bentónicos encontradas en los limos de prodelta indican que los niveles de pectínidos se formaron en un ambiente mesotrófico de plataforma media. Las acumulaciones de *A. cristatum* muestran similitudes con las concentraciones actuales de *A. balloti* de Shark Bay (NO de Australia). Esta especie forma densas poblaciones en zonas protegidas de la bahía entre 10 y 75 m de profundidad. El límite batimétrico inferior de *A. balloti* es similar a la profundidad estimada para las concentraciones de *A. cristatum*. Asimismo, los niveles estudiados se encuentran en el centro de una paleobahía semicerrada. A parte de estas coincidencias, las causas ecológicas últimas que explican las concentraciones actuales de *A. balloti* no son del todo conocidas. Por tanto, no se pueden usar aproximaciones actualistas para interpretar los niveles de *A. cristatum*. Las asociaciones de foraminíferos bentónicos de los limos de

the palaeobay. The advance of the deltas to the centre of the basin guaranteed rapid burial and the excellent preservation of the shells.

**Keywords:** Taphonomy, biological concentrations, *Amusium balloti*, *Amusium pleuronectes*, Abrioja delta.

prodelta indican que los niveles de *A. cristatum* se formaron probablemente en relación con aportes de nutrientes y partículas alimenticias del continente. El avance de los sistemas deltaicos garantizó el rápido enterramiento y la preservación excepcional de los pectínidos.

**Palabras clave:** Tafonomía, concentraciones biológicas, *Amusium balloti*, *Amusium pleuronectes*, delta Abrioja.

## 1. INTRODUCTION

*Amusium* (Bivalvia; Pectinidae) is a tropical, Indo-Pacific scallop with about 20 extant species. Some of these species, such as the Asian moon scallop *A. pleuronectes* and the saucer scallop *A. balloti*, are extensively gathered for human consumption. The life histories and biology of these two species are the best known among representatives of the genus due to their commercial harvesting (Morton, 1980; Dredge, 1985a, 1985b; Belda & Del Norte, 1988; Joll, 1989; Cropp, 1993; Joll & Caputi, 1995a, 1995b; Kangas *et al*., 2006; Mueller *et al*., 2012; Tremblay *et al*., 2015).

As in other scallops, larvae of *A. pleuronectes* and *A. balloti* secrete a byssus, which is lost during ontogeny (Hayami, 1991; Rose *et al*., 1998; Wang *et al*., 2001; Kangas *et al*., 2006), thus remaining as free-living organisms with highly active swimming ability (Yonge, 1936; Gould, 1971; Hayami, 1991; Morton, 1980; Joll, 1989; Tremblay *et al*., 2015). In this respect, *A. balloti* is the best swimmer among scallops, reaching longest distances (up to 30 m in two swims), and fastest velocities (up to 160 cm s$^{-1}$) (Joll, 1989). This swimming behaviour has been considered an adaptation primarily to escape from predators (Himmelman *et al*., 2009).

The spatial distribution of *A. pleuronectes* and *A. balloti* is controlled by different environmental factors, such as depth, temperature, substrate, currents, food, turbidity, oxygen content, and salinity (e.g. Brand, 2006; Mueller *et al*., 2012). Both species live on sandy bottoms swept by water currents, although the former species can tolerate a certain content of silt and mud in calmer waters (Young & Martin, 1989; Brand, 2006). They occupy a wide range of water depths, from a few meters to more than 100 m down (Brand, 2006). Within this broad bathymetric range, *A. balloti* is found mostly at 25-55 m deep in western Australia, while *A. pleuronectes* is preferentially distributed in slightly shallower waters, at 12-24 m deep in northern Australia or at 18-40 m in the Philippines (Kangas *et al*., 2006; Brand, 2006). In these depth ranges, both species form dense concentrations of individuals giving way to extensive, kilometre-scale beds (Kangas *et al*., 2006; Brand, 2006).

In the past geological record, *Amusium* species showed extratropical and wider geographic distributions. Among them, *Amusium cristatum* was a common inhabitant in the Mediterranean realm during the Neogene, at least up to the Pliocene (Raffi *et al*., 1985; Aguirre *et al*., 1996; Mandic, 2004; Jiménez *et al*., 2009; Dominici *et al*., 2009; Danise *et al*., 2010; Belaústegui *et al*., 2012). There are also Neogene records of this species in the Atlantic (Andrés & de Porta, 1987; Demarq, 1990; Aguirre, 1995).

In the lower Pliocene deposits of the Almería-Níjar Basin (SE Spain) (Fig. 1), *A. cristatum* was a very common pectinid. It occurs as isolated individuals dispersed in fine-grained sediments as well as in shell beds (Aguirre *et al*., 1996; Aguirre, 1998; Jiménez *et al*., 2009). In some of these shell beds, *A. cristatum* is a subsidiary component of multispecific assemblages accompanied, in order of abundance, by other bivalves (venerids, pectinids, and *Neopycnodonte*), and echinoids (regular cidaroids and infaunal spatangoids). The gastropod *Scalaria*, solitary corals (i.e. *Flabellum* and *Caryophyllia*), delicate and robust erect bryozoan colonies, and vertebrate remains (marine mammal bones, shark teeth, and complete and very well-preserved skate tail spines) can also be conspicuous components in some beds. The relative abundance of the accompanying organisms ranges from 30% to more than 50% of the total assemblage. Nonetheless, *Amusium cristatum* also occurs, forming monospecific-paucispecific concentrations (Aguirre, 1995, 1998, 2009; Aguirre *et al*., 1996; Jiménez *et al*., 2009).

Taphonomic analyses and sedimentological observations indicate that multispecific shell beds in the Almería-Níjar Basin were formed due to high-energy events, most likely storm events: 1) erosive bases, 2) fining-upward trends, 3) high taphonomic destruction of skeletal remains (high disarticulation, fragmentation, and abrasion), 4) imbrication of shells, and 5) concave-up stacked shells (Aguirre, 1995; Aguirre *et al*., 1996; Aguirre & Yesares-García, 2003; Yesares-García & Aguirre, 2004). However, the interpretation of the monospecific-paucispecific *A. cristatum* beds remains unclear. Aguirre (2009) suggested that they were the result of biological concentrations, but no detailed account of these beds were shown. In the present paper, a detailed sedimentological and taphonomical study
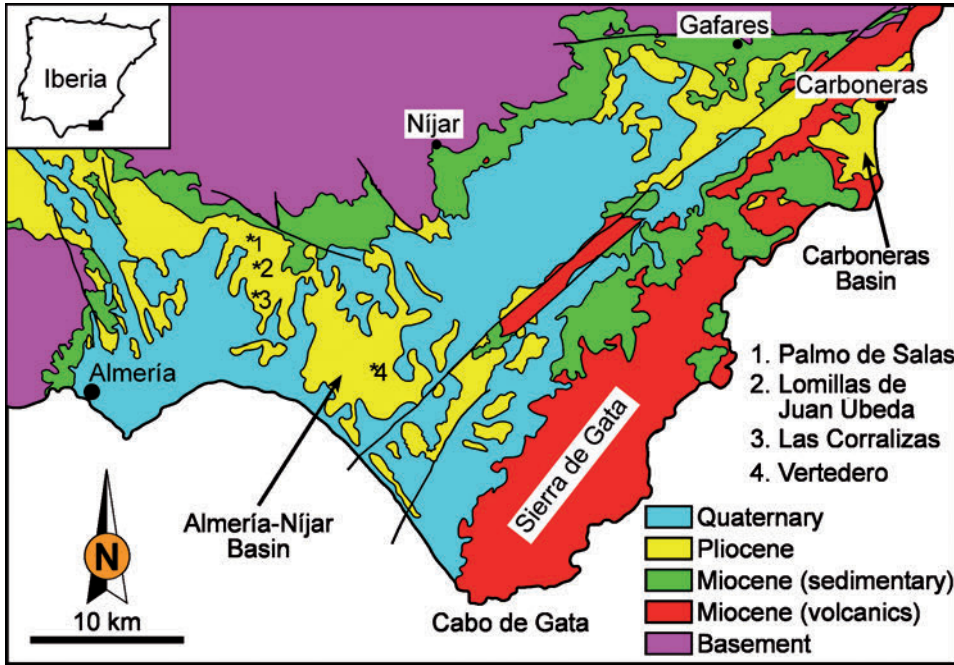
**Figure 1.** Geological map of the Almería-Níjar Basin and geographical location of the study sections.

of these *Amusium cristatum*-dominated shell concentrations from the lower Pliocene deposits of the Almería-Níjar Basin (SE Spain) is presented in order to: a) characterize the shell beds based on taphonomic signatures, b) infer the processes involved in their formation, and c) deduce the palaeoenvironmental contexts in which these shell beds formed.

## 2. MATERIAL AND METHODS

As mentioned above, *Amusium cristatum* is present in numerous shell beds found throughout the Almería-Níjar Basin. Nonetheless, for the purposes of this work, the taphonomic study has been made in 15 monospecific-paucispecific shell beds dominated by *A. cristatum* (Fig. 2). Previous works in the area (Aguirre, 1995; Aguirre *et al*., 1996; Aguirre & Yesares-García, 2003; Yesares-García & Aguirre, 2004; Jiménez *et al*., 2009) have facilitated the selection of those shell beds that fit this requirement. The shell beds studied are distributed in four sections located following a proximal to distal position in the basin: Palmo de Salas, Lomillas de Juan Úbeda, Las Corralizas and Vertedero (Figs 1, 3). All these shell beds are intercalated in silts and fine-grained sands of prodelta facies of the Abrioja delta (see description below).

Sampling and quantitative analysis followed the methodological procedure extensively described by Aguirre & Yesares-García (2003) and Yesares-García & Aguirre (2004). The taphonomic attributes measured were: size sorting, articulation, fragmentation, angle with respect
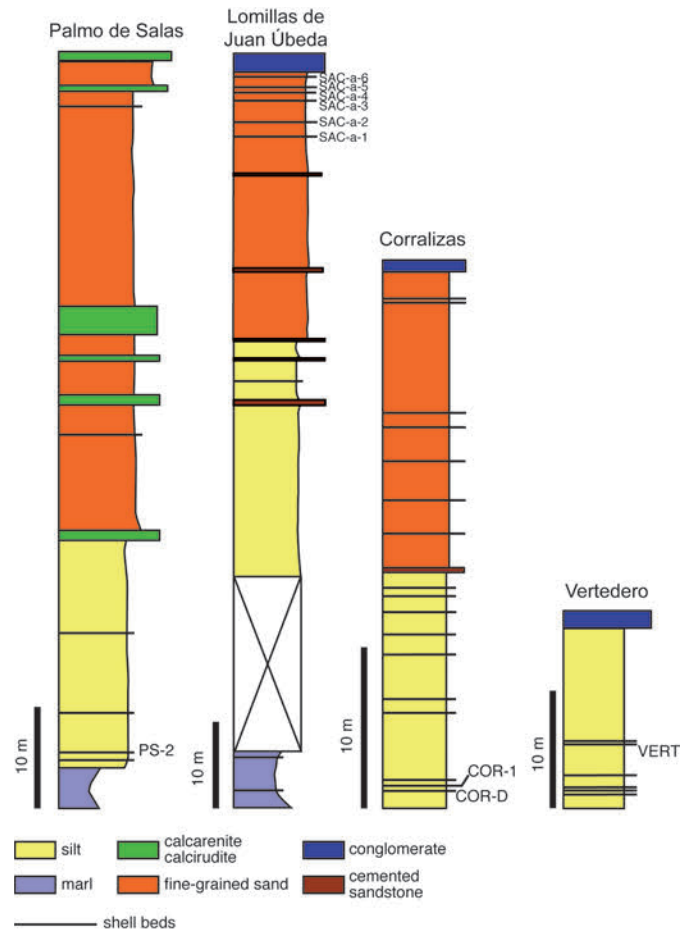


**Figure 2.** Stratigraphic logs indicating the position of the 15 shell beds studied. Abbreviations of the samples as in Table 1. Samples from SAC-II-1 to SAC-II-6 in Table 1 were collected about 500 m south of the laterally equivalent shell beds SAC-a-1 to SAC-a-6.

to stratification (horizontal, oblique, perpendicular), life orientation, concavity orientation (up and down), skeletal preservation, edge rounding, and biotic interactions (borings and encrustations). Measurements of these taphonomic attributes were carried out in 10 quadrats (20x20 cm), randomly distributed in each of the selected shell beds. Quadrats were oriented perpendicular to stratification. All fossils larger than 5 mm in cross-section found within the quadrats were quantified.

## 3. GEOLOGICAL CONTEXT AND PALAEOGEOGRAPHY

The Almería-Níjar Basin is an intermontane peri-Mediterranean basin with a sedimentary infilling ranging from middle Miocene to Quaternary (Serrano, 1990; Montenat *et al*., 1990; Aguirre, 1998; Aguirre & Sánchez-Almazo, 2004). The basin was isolated after tectonic uplifting of the Betic basements (Sierra de Gádor, Sierra Alhamilla and Sierra Cabrera) and the volcanic province of Cabo de Gata during the late Miocene and Miocene-Pliocene transition (Braga *et al*., 2003a; Martín *et al*., 2003). This uplifting led to the compartmentalization of several basins and subbasins in the south-eastern part of the Iberian Peninsula (Montenat *et al*., 1990; Boorsma, 1992; Martín & Braga, 1996; Aguirre, 1998; Braga *et al*., 2003a; Martín *et al*., 2003).

During the early Pliocene, the Almería-Níjar Basin was a large, open embayment in the north-west of the Alborán Basin, in the western Mediterranean. The basin was bordered by the Sierra de Gádor to the west, Sierra Alhamilla and Sierra Cabrera to the north, and the volcanic complex of the Sierra de Gata to the east (Fig. 3). The basin

was connected to the Mediterranean by the south and by a narrow strait located in the north-eastern edge of the basin (Dabrio *et al*., 1986-87). At the end of the early Pliocene, the Almería-Níjar and the Carboneras basins, separated during most of the early Pliocene by a volcanic threshold at their closest point, coalesced and were connected due to the opening of some straits (Braga *et al*., 2003a, 2003b; Martín *et al*., 2003, 2004; Aguirre *et al*., 2008) (Fig. 3).

During the late Pliocene, the combined effect of the tectonic uplifting of the basement and a sea-level drop led to a major palaeogeographic change (Aguirre, 1998). Most of the basin was exposed and marine deposition took place in a restricted area located to the central part of the Almería-Níjar Basin (Aguirre & Jiménez, 1997, 1998; Aguirre, 1998; Pérez-Asensio & Aguirre, 2010). Extensive coral banks, made up by the scleractinian coral *Cladocora caespitosa*, characterized these deposits (Aguirre & Jiménez, 1998).

The monospecific-paucispecific *A. cristatum* shell beds studied are in the lower Pliocene deposits of the Almería-Níjar Basin. A detailed description and interpretation of these sediments are provided elsewhere (Aguirre, 1998). Here, the general lithological facies description and the depositional contexts in which the shell beds are found is given below.

## 4. THE LOWER PLIOCENE DEPOSITS OF THE ALMERÍA-NÍJAR BASIN

The lower Pliocene deposits of the Almería-Níjar Basin onlap the Betic basement and an irregular palaeotopographic surface excavated on upper Miocene sediments (Montenat *et al*., 1990; Aguirre, 1998; Braga *et al*., 2003a, 2003b,
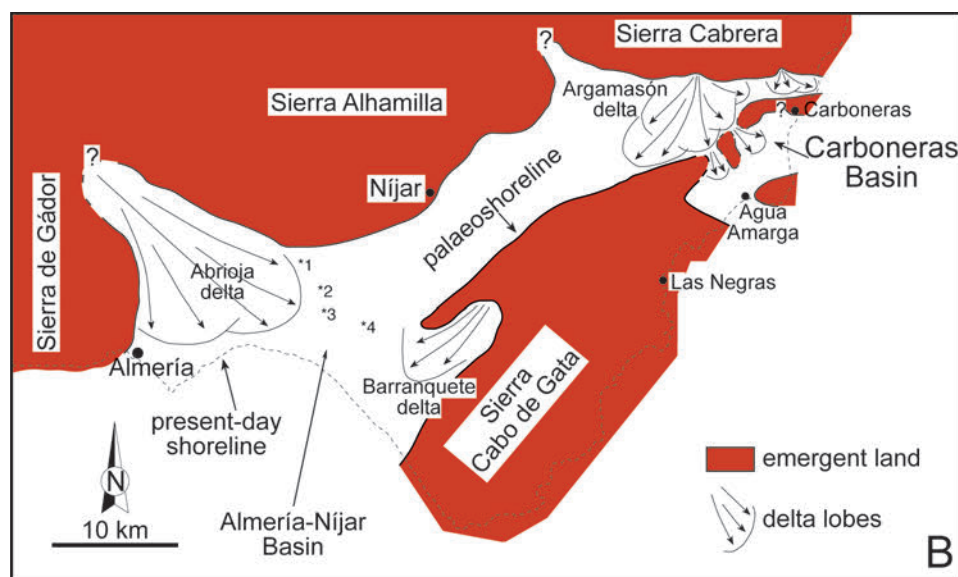


**Figure 3.** Palaeogeographic reconstruction of the Almería-Níjar Basin during the upper part of the early Pliocene, when this basin was connected with the Carboneras Basin. Numbers (as in Fig. 1) indicate the approximate position of the study sections. Modified from Braga *et al*. (2003b).

Martín *et al*., 2003, 2004). These show a variety of lithologies and facies, represented mainly by terrigenous sediments and by carbonate-siliciclastic mixed deposits. Locally, in the Carboneras Basin, carbonate deposition prevailed during most of the early Pliocene (Aguirre, 1998; Braga *et al*., 2003b; Martín *et al*., 2003, 2004; Aguirre *et al*., 2008, 2012).

Siliciclastics derived from three major delta systems, the Abrioja delta in the north-western corner of the basin (Postma, 1979, 1983), the El Barranquete Gilbert-type delta associated with La Serrata area in the eastern of the basin (Boorsma, 1992), and the El Argamasón delta in the north-eastern edge (Aguirre, 1998) (Fig. 3). Other sources of siliciclastics were localized fan deltas fed by the Betic basements surrounding the basin (Aguirre, 1998).

Terrigenous particles are mostly metamorphic rocks (quartz, schist, and micaschist) from the Betic basement. In the eastern margin of the basin, the surrounding volcanic substrate of the Sierra de Gata was another source of siliciclastics, though limited to the base of the lower Pliocene sequence. Then, volcanic clasts disappeared and metamorphic clasts fed the basin. This change of the major clast components of the conglomerates points to an important tectonic uplifting of the Betic metamorphic basement to the north, Sierra Cabrera.

In a more distal position of the fan deltas and delta front, grain size decreases and the sediments change to coarse-grained and medium-grained sand. In the prodelta, fine-grained sand to silt were deposited (Postma, 1979, 1983). Finally, to the centre of the basin, blue-grey marl formed. The marls crop out only locally, the silt and the very fine-grained sand being the most extensive sediments outcropping in the distal positions of the basin. *Amusium cristatum*-dominated shell beds occur in these distal prodelta facies (Aguirre *et al*., 1996; Aguirre, 1998, 2009; Jiménez *et al*., 2009) (Fig. 2).

Carbonates crop out in the northern (Palmo de Salas, Gafares-El Argamasón areas) and western margins (N of the city of Almería) of the Almería-Níjar Basin (Fig. 1). They are represented by bioclastic calcarenites and calcirudites deposited in areas of the platform starved by terrigenous inputs (Aguirre, 1998). Laterally, the carbonates change into siliciclastics of delta-front facies. Major components of the carbonates are bivalves, bryozoans, solitary corals, echinoids, brachiopods, barnacles, coralline red algae, and benthic foraminifers, all corresponding to heterozoan carbonate lithofacies (James, 1997). In the adjacent Carboneras Basin, heterozoan carbonate deposition prevailed during most of the early Pliocene (Aguirre, 1998; Braga *et al*., 2003b; Martín *et al*., 2004; Aguirre *et al*., 2012). Then, siliciclastic delta deposits prograded into the Carboneras Basin, thus suffocating the carbonate production that was limited to bivalves and barnacle concentrations (Aguirre *et al*., 2008, 2012).

## 5. DESCRIPTION OF THE *AMUSIUM CRISTATUM* SHELL-BEDS

The *Amusium*-dominated beds are among the most prominent and conspicuous features of fossil concentrations in the mid-to-distal prodelta silty facies of the Almería-Níjar Basin (Figs 4a-4c). Very rarely, they also interbed in sand and channelized conglomerates of the delta-front facies. They form single sheet-like concentrations that can be laterally followed in continuity for several tens to hundreds of meters (Fig. 4a). The *Amusium* beds vary in thickness from 5 cm to 15 cm, and their base and the top are sharp and planar.

Shell abundance varies from 30% to 50% of the rock volume and the shells are loosely to densely packed. In terms of taxonomic composition, the shell beds are monospecific-paucispecific since they are almost exclusively dominated by *Amusium cristatum* that can represent more than 90% of the faunal composition.

Regarding the taphonomic attributes, fragmentation is relatively high on average (77.9%), but most of the fragments show sharp edges (85.1%; Table 1) and preserve the original ornamentation in the inner part of the shells as well as the lustre of the outer surface and even the colour pattern (Figs 5a-5c). Disarticulated shells arrange mostly horizontally, showing a similar proportion of concave-up and -down orientation (Table 1; Fig. 5d). Articulation is relatively low except in the shell beds of Vertedero section, where 25.5% of *Amusium* are articulated (Table 1; Fig. 4b). Although disarticulated, a large portion of the shells is complete, averaging 22% (Table 1). In some beds, *Amusium* shows a distinct sequence of disarticulation from none to totally separated valves (Fig. 5d): 1) no disarticulation of valves, 2) valves slightly separated, i.e. the orientation of valves can be slightly ajar, 3) valves separated from one another, but still lying parallel to one another and somewhat overlap, 4) valves totally disarticulated, i.e. matching valves cannot be recognized in the sediment. There is a great dispersion of the size classes. Most of the fossils preserved the original shell mineralogy. The originally aragonitic organisms remain preserved as casts or moulds. When moulds are present, they are mostly articulated (Figs 4c, 5d) and show very delicate external shell ornamentation (such as growth lines, ridges, ribs, spines, etc.) or internal anatomical traits (such as muscle imprints, pallial line in the case of the bivalves, or septa in the case of the solitary corals). Epifaunal organisms, such as barnacles, are occasionally found on *Chlamys* shells. However, the most abundant taxon, *Amusium*, shows neither encrusting organisms nor borings.
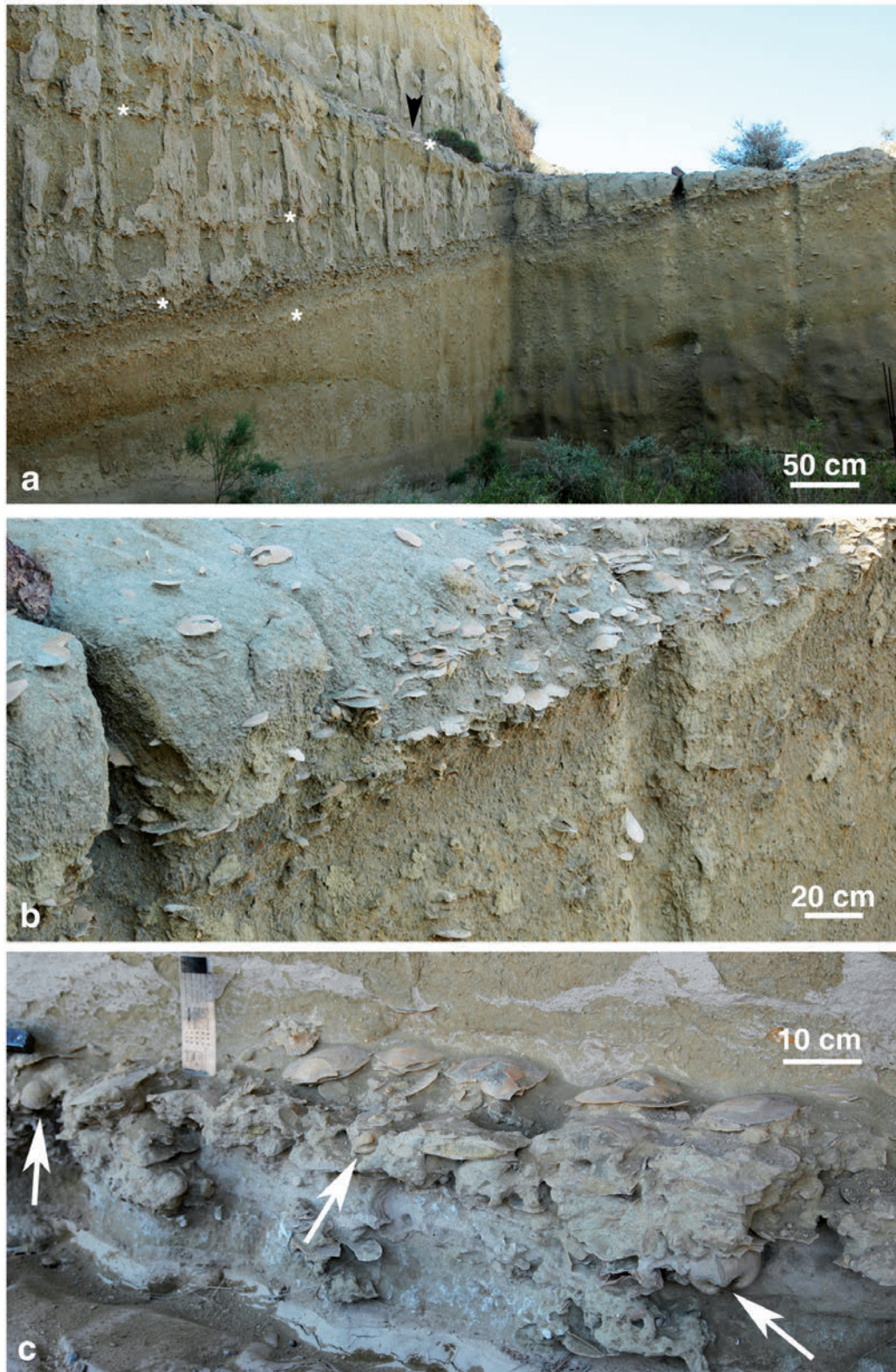
**Figure 4.** Examples of the *Amusium cristatum* beds from Vertedero **(a, b)** and Las Corralizas **(c)** sections. **a)** Several beds (asterisks) of *A. cristatum* from Vertedero section. Note the high concentration of shells and the lateral continuity of the beds. **b)** Detail of the uppermost shell bed of the previous picture (arrowhead in **a**). The high percentage of articulation and complete shells that can be seen are remarkable. The greenish colour of the sediment covering the *A. cristatum* bed is due to high concentration of glaucony. **c)** *A. cristatum* bed in the lowermost part of the Las Corralizas section (COR-D in Fig. 2). Together with the pectinid shells, several internal casts of different articulated bivalves are observed (arrows).

**Table 1.** Average values of taphonomic attributes measured in the study sections. Values represent the average percentages calculated from the 10 quadrats distributed in each sampling site. The percentages were calculated with respect to the total number of fossils in each sampling site (column n). frag. = fragmented; comp. = complete; art. = articulated; up = concave up; down = concave down; round. = rounded edges; indet. = indeterminate; encr. = encrusted shells. SAC = Lomillas de Juan Úbeda section; PS = Palmo de Salas section; COR = Corralizas section; VERT = Vertedero section.

| | n | frag. | comp. | life | art. | up | down | vertical | platy | indet. | 0-30º | 30-60º | 60-90º | original | moulds | sharp | round. | indet. | boring | encr. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SAC-a-1 | 529 | 82,4 | 17,6 | 0 | 1,1 | 29,7 | 21,2 | 6,2 | 30,7 | 10,2 | 45,1 | 23,6 | 31,3 | 100 | 0 | 93,6 | 0 | 6,4 | 0 | 0 |
| SAC-a-2 | 288 | 67,7 | 32,3 | 0 | 1 | 27,1 | 26 | 7,3 | 32,3 | 7,3 | 59,4 | 20,8 | 19,8 | 100 | 0 | 96,9 | 3,1 | 0 | 0 | 0 |
| SAC-a-3 | 495 | 82,4 | 17,6 | 0,6 | 0,7 | 11,8 | 13,2 | 5,9 | 17,6 | 51,5 | 62,5 | 22,1 | 15,4 | 100 | 0 | 98,2 | 0,9 | 0,9 | 0,6 | 0 |
| SAC-a-4 | 345 | 93,6 | 6,4 | 0 | 0 | 29 | 24,1 | 0,9 | 41,4 | 4,6 | 73,9 | 11,7 | 10,4 | 100 | 0 | 93,6 | 0 | 6,4 | 0 | 0 |
| SAC-a-5 | 516 | 90,1 | 8,9 | 0 | 0,6 | 24,4 | 20,9 | 7,6 | 44,8 | 2,3 | 33,1 | 40,1 | 26,8 | 100 | 0 | 89,5 | 1,1 | 9,3 | 0 | 0 |
| SAC-a-6 | 300 | 80 | 20 | 0 | 2 | 30,3 | 34,7 | 0 | 33 | 2 | 45,5 | 42,6 | 11,9 | 100 | 0 | 76,7 | 0 | 23,3 | 0 | 0 |
| SAC-II-1 | 368 | 80,7 | 19,3 | 0 | 2,2 | 29,3 | 19,3 | 8,7 | 40,8 | 1,9 | 43,7 | 16,7 | 39,4 | 100 | 0 | 80,7 | 0 | 19,3 | 0 | 0 |
| SAC-II-2 | 225 | 78,4 | 21,6 | 0 | 1,4 | 23 | 23 | 9,6 | 40,5 | 1,3 | 45,9 | 23 | 31,1 | 100 | 0 | 78,4 | 0 | 21,6 | 0 | 0 |
| SAC-II-4 | 582 | 76,4 | 23,6 | 0 | 0 | 35,1 | 28,8 | 3,7 | 32,5 | 0 | 53,4 | 29,9 | 26,7 | 100 | 0 | 76,4 | 0 | 23,6 | 0,5 | 0 |
| SAC-II-5 | 381 | 81 | 19 | 0 | 1,6 | 32,5 | 26,2 | 0 | 38,1 | 3,2 | 46,1 | 39,7 | 14,2 | 100 | 0 | 80,6 | 0 | 19,4 | 0 | 0 |
| SAC-II-6 | 465 | 83,9 | 16,1 | 0 | 1,2 | 25,8 | 19,4 | 8,6 | 45,1 | 1,1 | 36,4 | 38,2 | 25,4 | 100 | 0 | 83,9 | 0 | 16,1 | 0 | 0 |
| COR-1 | 1148 | 72,2 | 27,8 | 1,8 | 8,5 | 29,9 | 17,2 | 3,9 | 20,2 | 28,7 | 80 | 14,3 | 5,7 | 56,1 | 43,9 | 41,2 | 0,4 | 58,4 | 0,8 | 1 |
| COR-D | 438 | 78,5 | 21,5 | 0 | 8,9 | 50,2 | 49,1 | 0 | 30,1 | 0 | 65,3 | 26,7 | 8 | 96,6 | 3,4 | 89,5 | 4,4 | 6,1 | 0 | 0 |
| PS-2 | 218 | 66,8 | 33,2 | 2,8 | 5,1 | 40,6 | 59,4 | 0 | 15,7 | 0 | 27,3 | 25,7 | 47 | 97,7 | 2,3 | 97,2 | 1,9 | 0,9 | 0 | 3,2 |
| VERT | 180 | 55 | 45 | 0 | 25,5 | 59,5 | 40,5 | 0 | 0 | 0 | 79 | 21 | 0 | 100 | 0 | 100 | 0 | 0 | 0 | 0 |
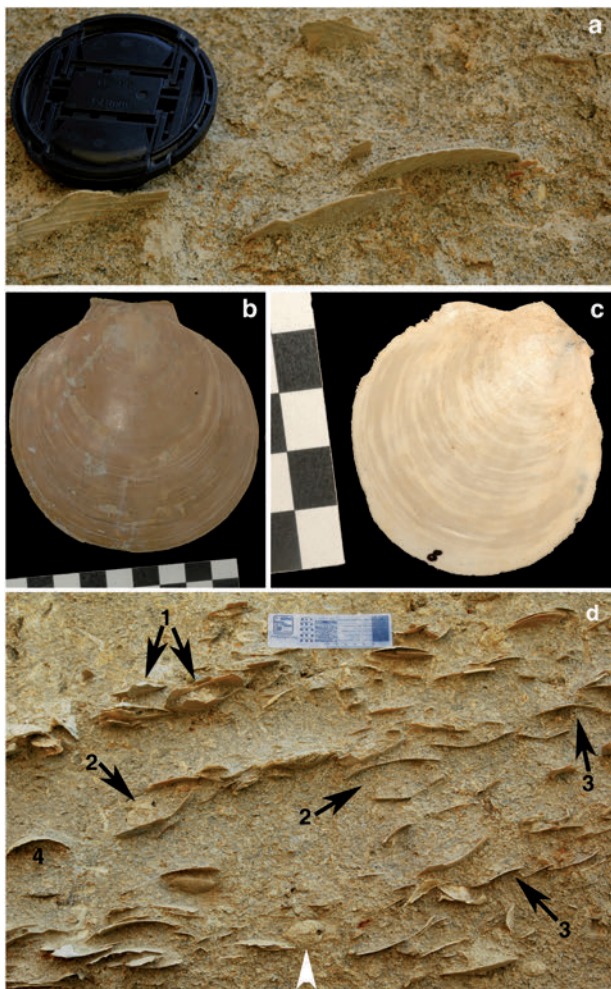


**Figure 5. a)** Disarticulated, but complete, *Amusium* shells from the Vertedero section. The radial ribs are visible in the inner surface of the shells. Lens cap = 58 mm. **b-c)** Isolated shells of *Amusium cristatum* preserving traces of the original colour pattern and the lustre **(c)**. **d)** *Amusium* concentration from Vertedero section (VERT in Fig. 2). Numerous shells are disarticulated but show sharp edges. Numbers 1 to 4 indicate different stages of disarticulation, from paired bivalves (1) to completely disarticulated shells (4) (see text for an explanation). The arrowhead indicates the internal cast of an articulated bivalve.

# 6. DISCUSSION

## 6.1. Type of shell beds and palaeoenvironmental interpretation

Kidwell *et al.* (1986) categorized shell concentrations as intrinsic or extrinsic accumulations. The former concentrations are the result of biological processes, i.e. due to gregarious behaviour of organisms, while the latter are the result of either sedimentary processes or of the activity of living organisms using/interacting with other skeletonized hard parts of death organisms (Kidwell *et al.*, 1986). The taphonomic implications and the palaeoecological significance of the two types of

concentrations are different. In particular, the biological accumulations can be non-time-averaged autochthonous (or parautochthonous) shell concentrations that were suddenly buried (Kidwell *et al*., 1986). Therefore, they constitute unique windows to assess ecological processes, such as population dynamics or community structures, which are very often distorted due to time averaging and taphonomic feedback (Kidwell *et al*., 1986; Kidwell & Bosence, 1991; Kidwell, 1991a, 1991b). In marine settings, these accumulations typically imply intervals of reduced or no sedimentation, favouring the colonization of the seabed followed by catastrophic entombment (i.e. Aguirre & Jiménez, 1997, 1998; Aguirre *et al*., 2008; Bassi *et al*., 2015).

Sedimentologic accumulations differ from the biological ones, since they are related to physical processes, such as hydraulic processes, producing reworked and allochthonous shell beds. In these cases, shells behave as sedimentary particles that remain in the taphonomic active zone (TAZ) for a long period of time, and are often subjected to reworking and transport. Typical examples are tempestites due to storms, or shell beds due to higher hydraulic energy events such as hurricanes or tsunamis (Aigner, 1985; Seilacher & Aigner, 1991; Nummedal, 1991; Héquette & Hill, 1993; Boyajian & Thayer, 1995; Dattilo *et al*., 2008), as well as hiatal concentrations due to bypass (Beckvar & Kidwell, 1988; Kidwell, 1989, 1991b, 1993; Rivas *et al*., 1997). These types of concentrations have a valuable sedimentary and sequence stratigraphic significance, since they form in particular settings and during particular sea-level conditions (Kidwell, 1986, 1988, 1989, 1991a, 1991b, 1993; Fürsich, 1995; Aguirre & Yesares-García, 2003; Aguirre & Méndez-Chazarra, 2010; Patzkowsky & Holland, 2012).

In the Almería-Níjar Basin, *A. cristatum* can be a major constituent in shell beds intercalated in shallower settings, such as distal delta front or proximal prodelta facies (Aguirre *et al*., 1996). However, the monospecific-paucispecific *A. cristatum* shell beds are mostly interbeded in silt and very fine-grained sands in the central part of the basin. Benthic foraminiferal assemblages in these sediments are highly diversified and characterized by species preferentially distributed in the middle shelf (Aguirre *et al*., 2006). Occasionally, *in situ* preserved clumps of *Neopycnodonte navicularis* are present in these facies (Aguirre, 1998). This bivalve typically inhabits deep-water settings (Wissak *et al*., 2009), thus reinforcing the palaeoenvironmental interpretation.

Taphonomic analysis shows that *Amusium cristatum* did not undergo significant alteration or destruction. The ligament in *A. cristatum*, as well as in general in all pectinids, is small and prone to rapid decay. Therefore, a high percentage of articulation suggests low-energy conditions and limited exposure on the TAZ due to rapid entombment. Absence of bioerosion/encrustations, high

proportion of complete shells and low abrasion, as well as the preservation of colour patterns in some *Amusium* shells, are all taphonomic features consistent with rapid burial. Advance of the prodelta facies to the centre of the basin guaranteed rapid burial of these shell concentrations. The sediment supply, in turn, also negatively affected these filter-feeding bivalves, causing their massive death. In short, taphonomic analysis shows that *A. cristatum* concentrations in the lower Pliocene deposits of the Almería-Níjar Basin can be interpreted as biological concentrations *sensu* Kidwell *et al*. (1986).

## 6.2. Origin of the biological concentrations of *A. cristatum*

Numerous scallop species tend towards gregarious behaviour, forming large and dense concentrations of individuals (Dredge, 1988; Stokesbury & Himmelman, 1993; Hatcher *et al*., 1996; Brand, 2006; Orensanz *et al*., 2006; Kangas *et al*., 2006). Formation of these dense settlements depends upon complex interactions of physical and biological factors affecting the standing stock of adult populations, their spawning, their recruitment, and their larval dispersal (see a summary in Orensanz *et al*., 2006). Nonetheless, the proximal ecological causes behind this gregarious behaviour in particular cases are not well understood. In this respect, Young *et al*. (1990, p. 80), studying the recruitment of *Pecten fumatus* populations, stated "*that while the size of the population of larvae competent to settle is related to the parental stock, the number actually settling on the bottom is dependent upon some, as yet unknown, characteristics of the physical and biological environment at the settlement site*".

It has been speculated, based on the capacity to actively swim, that aggregations of recent *A. balloti* could be related to long-distance displacements or migrations (Yonge, 1936; Baird, 1954; Morton, 1980; Chapman, 1981). These massive migrations would produce large concentrations of individuals. Nonetheless, Joll (1989) demonstrated that *A. balloti*, which is the best swimmer among scallops, was unable to maintain a sustained swim. In a study of 55 individuals of *A. balloti*, 46 of them (83%) remained resting on the bottom after two swims, with only one individual being able to swim up to four times. In addition, the longest distance achieved by all scallops was 30.8 m (Joll, 1989). Therefore, these results do not support the idea of large-distance migrations (Joll, 1989; Brand, 2006).

In many cases, scallop aggregations follow irregular and unpredictable pulses of population blooms followed by dramatic reductions. Global-regional temperature variations and/or oceanographic patterns most likely account for these sporadic changes in abundance (Orensanz *et al*., 2006). Recent *A. balloti* produces dense populations distributed for kilometres in sheltered areas of the Shark Bay, western

Australia (Dredge, 1990; Joll, 1990; Kangas *et al.*, 2006; Mueller *et al.*, 2012). Here, the species undergoes abrupt changes in population dynamics that have been linked to the Leeuwin Current, which is in turn influenced by the El Niño-Southern Oscillation (ENSO) events (Joll & Caputi, 1995b). According to these authors, an intensification of the Leeuwin Current produces a corresponding dramatic reduction in *A. balloti* populations.

Other authors have proposed that the recent massive occurrences of *Amusium* may be related to the preferential orientation of individuals with water currents based on the large-scale morphology of the aggregations (Heald & Caputi, 1981; Dredge, 1985b). It has been noted that long and thin concentrations of *A. balloti* are parallel to tidal currents, suggesting that larvae settled within strong current areas (Brand, 2006). This author also stated that these concentrations could be the result of active downstream swimming following the strong currents.

In our study case, it is difficult to apply any of these actualistic approaches to account for the massive occurrences of *A. cristatum*. It is possible, however, to discard the distribution of *Amusium* concentrations following a particular water current, since they formed in silty deposits without any evidence of high-energy currents. However, the spatial distribution of the beds, the palaeogeographic configuration of the Almería-Níjar Basin during the early Pliocene, and additional microfossil data help to envisage the origin of these shell beds.

Although the presence of *Amusium cristatum* is widespread in the lower Pliocene deposits of the Almería-Níjar Basin, the monospecific-paucispecific biological concentrations formed by this species are restricted to the central part of the basin. Palaeogeographically, the basin was a semi-enclosed bay mainly open to the south during the early Pliocene (Fig. 3). Coincidently, recent large and massive occurrences of *Amusium* species are in partially enclosed bays, such as the well-known examples of extensive *A. balloti* beds in the protected areas of the Shark Bay (W Australia) (Joll, 1989; Kangas *et al.*, 2006; Mueller *et al.*, 2012). Here, these beds develop in water between 10 and 75 m deep. The Pliocene *A. cristatum* biological beds were preserved in mid-shelf settings, as inferred from the benthic foraminiferal assemblages found in the prodelta facies (Aguirre *et al.*, 2006). Pérez-Muñoz *et al.* (2001) inferred a maximum water depth of ~100 m for the silts along the northern margin of the Almería-Níjar Basin. This depth is close to, or even slightly greater than, the water-depth range of the recent *A. balloti* in western Australia. It is reasonable to assume that *A. cristatum* also formed biological concentrations in shallower waters, as *A. balloti* does today. Nevertheless, storm events might distort these concentrations and lead *A. cristatum* shells to be part of tempestites as shell fragments.

In addition, the benthic foraminiferal assemblages indicate a mesotrophic environment shown by a mixture of species from eutrophic and oligotrophic conditions (Aguirre *et al.*, 2006). The supply of nutrients and food particles by the deltas outflowing into the basin accounts for the establishment of mesotrophic conditions widespread in the centre of the basin (Aguirre *et al.*, 2006). The continuous supply of food would have triggered demographic blooms of *A. cristatum* populations, forming extensive concentrations. Similarly, dense populations of *A. balloti* in the Shark Bay are favoured when water eddies linked to oceanographic conditions concentrate food particles in localized areas of the basin (Heald & Caputi, 1981; Orensanz *et al.*, 2006).

The continuous source of nutrients and food particles to the bottom of the basin eventually produce disoxyc conditions (Aguirre *et al.*, 2006). These events of oxygen reduction on the sea floor could trigger massive death of local populations of *A. cristatum*. Therefore, the sporadic depletion of oxygen close to the water-sediment interface, together with the continuous sediment supply due to delta progradation, guaranteed catastrophic death of local populations and sudden burial, leading the exceptional preservation of shells in the *A. cristatum* monospecific-paucispecific biological concentrations.

# 7. CONCLUSIONS

1. The pectinid *Amusium cristatum* formed monospecific-paucispecific dense concentrations in very fine-grained sand and silt of the Almería-Níjar Basin (SE Spain) during the early Pliocene. These sediments correspond to distal prodelta sediments deposited in mid-shelf settings.

2. Upper and lower contacts of the beds are sharp. Quantitative taphonomic analysis indicates relatively high percentage of articulation, low fragmentation, and almost absence of abrasion. Many shells preserve the patterns of the original colouration. Disarticulated shells occur concave-up and down, sorting is very poor and they are unaffected by encrusting organisms or borings. These taphonomic signatures indicate nearly *in situ* preservation without reworking and exceptional preservation due to rapid burial. They represent biological concentrations *sensu* Kidwell *et al.* (1986).

3. *Amusium cristatum* beds formed in the centre of the Almería-Níjar Basin, a wide and relatively sheltered palaeobay. Benthic foraminiferal assemblages found in the prodelta sediments suggest mesotrophic conditions with a supply of nutrients and food particles from the continent due to the progradation of delta systems. The extra supply of nutrients produced blooms of scallop populations. Then, the advance of deltas to the centre of the basin led rapid entombment of local populations.

4. The present-day scallop species *Amusium balloti* and *A. pleuronectes* form similar dense concentrations.

The former species develops large accumulations in the Shark Bay (NW Australia) from 10 to 75 m depth. The greatest water-depth distribution is similar to the palaeobathymetry inferred for the *A. cristatum* shell beds intercalated in the lower Pliocene prodelta deposits of the Almería-Níjar Basin. The recent shell beds of *A. balloti* can be considered a present-day counterpart of *A. cristatum* accumulations.

# ACKNOWLEDGEMENTS

# REFERENCES

Aguirre, J. 1995. Implicaciones paleoambientales y paleogeográficas de dos discontinuidades estratigráficas en los depósitos pliocénicos de Cádiz (SW de España). *Revista de la Sociedad Geológica de España*, 8, 161-174.

Aguirre, J. 1998. El Plioceno del SE de la Península Ibérica (Provincia de Almería). Síntesis estratigráfica, sedimentaria, bioestratigráfica y paleogeográfica: *Revista de la Sociedad Geológica de España*, 11, 297-315.

Aguirre, J. 2009. Biological concentrations of *Amusium cristatum*. *Journal of Taphonomy*, 2-3, 263-264.

Aguirre, J. & Jiménez, A.P. 1997. Census assemblages in hard-bottom coastal communities: a case study from the Plio-Pleistocene Mediterranean. *Palaios*, 12, 598-608; doi: 10.2307/3515415.

Aguirre, J. & Jiménez, A.P. 1998. Fossil analogues of the present-day ahermatypic *Cladocora caespitosa* coral banks: Sedimentary setting, dwelling community, and taphonomy (Late Pliocene, W Mediterranean). *Coral Reefs*, 17, 203-213; doi: 10.1007/s003380050119.

Aguirre, J. & Méndez-Chazarra, N. 2010. Tafonomía de los carbonatos templados pliocenos de la Cuenca de Almayate (Málaga, S de España). *Revista Española de Paleontología*, 25, 149-163.

Aguirre, J. & Sánchez-Almazo, I.M. 2004. The Messinian post-evaporitic deposits of the Gafares area (Almería, SE Spain). A new view of the "Lago-Mare" facies.

*Sedimentary Geology*, 168, 71-95; doi: 10.1016/j.sedgeo.2004.03.004.

Aguirre, J. & Yesares-García, J. 2003. Análisis tafonómico y secuencial del Plioceno inferior en el sector NE de la cuenca de Almería-Níjar (SE de España). *Revista Española de Paleontología*, 18, 61-82.

Aguirre, J., Pérez-Muñoz, A.B. & Sánchez-Almazo, I.M. 2006. Benthic foraminifer assemblages in the lower Pliocene deposits of the Almería-Níjar Basin (SE Spain). *Revista Española de Micropaleontología*, 38, 411-428.

Aguirre, J., Braga, J.C., Jiménez, A.P. & Rivas, P. 1996. Substrate-related changes in pectinid fossil assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 126, 291-308; doi: 10.1016/S0031-0182(96)00042-9.

Aguirre, J., Braga, J.C., Martín, J.M. & Betzler, C. 2012. Palaeoenvironmental and stratigraphic significance of Pliocene rhodolith beds and coralline algal bioconstructions from the Carboneras Basin (SE Spain). *Geodiversitas*, 34, 115-136; doi: 10.5252/g2012n1a7.

Aguirre, J., Martín, J.M., Braga, J.C., Betzler, C., Berning, B.B. & Buckeridge, J.S. 2008. Densely-packed concentrations of sessile barnacles (Cirripedia: Sessilia) from the early Pliocene of SE Spain. *Facies*, 54, 193-206; doi: 10.1007/s10347-007-0132-2.

Aigner, T. 1985. *Storm Depositional Systems. Dynamic, Stratigraphy in Modern and Ancient Shallow-Marine Sequences*. Springer-Verlag, Berlin.

Andrés, I. & de Porta, J. 1987. La distribución de los Pectinidae en el Neógeno de Huelva. Datos preliminaries. In: *Paleontología del Neógeno de Huelva (W. Cuenca del Guadalquivir)* (ed. Civis, J.). Dpto. de Paleontología, Universidad de Salamanca, Salamanca, 143-151.

Baird, F.T., Jr. 1954. Migration of the deep sea scallop *Pecten magellanicus*. *Maine Department of Sea Shore Fisheries Circ.*, 14, 1-8.

Bassi, D., Posenato, R. & Nebelsick, J.H. 2015. Paleoecological dynamics of shallow-water bivalve carpets from a lower Jurassic lagoonal setting, northeast Italy. *Palaios*, 30, 758-770; doi: 10.2110/palo.2015.020.

Beckvar, N. & Kidwell, S.M. 1988. Hiatal shell concentrations, sequence analysis, and sealevel history of a Pleistocene coastal alluvial fan, Punta Chueca, Sonora. *Lethaia*, 21, 257-270; doi: 10.1111/j.1502-3931.1988.tb02078.x.

Belaústegui, Z., de Gibert, J.M., Domènech, R., Muñiz, F. & Martinell, J. 2012. Clavate borings in a Miocene cetacean skeleton from Tarragona (NE Spain) and the fossil record of marine bone bioerosion. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 323-325: 68-74; doi: 10.1016/j.palaeo.2012.01.031.

Belda, C.A. & Del Norte, A.G.C. 1988. Notes on the induced spawning and larval rearing of the Asian moon scallop, *Amusium pleuronectes* (Linné), in the laboratory. *Aquaculture*, 72, 173-179; doi: 10.1016/0044-8486(88)90157-3.

Boorsma, L.J. 1992. Syn-tectonic sedimentation in a Neogene strike-slip basin containing a staked Gilbert-type delta (SE Spain). *Sedimentary Geology*, 81, 105-123; doi: 10.1016/0037-0738(92)90059-Z.

Boyajian, G.E. & Thayer, C.W. 1995. Clam calamity: a recent supratidal storm-deposit as an analogue for fossil shell beds. *Palaios*, 10, 484-489; doi: 10.2307/3515051.

Braga, J.C., Martín, J.M. & Quesada, C. 2003a. Patterns and average rates of late Neogene-Recent uplift of the Betic Cordillera, SE Spain. *Geomorphology*, 50, 3-26; doi: 10.1016/S0169-555X(02)00205-2.

Braga, J.C., Betzler, C., Martín, J.M. & Aguirre, J. 2003b. Spit-platform temperate carbonates: the origin of landward-downlapping beds along a basin margin (lower Pliocene, Carboneras basin, SE Spain). *Sedimentology*, 50, 553-563; doi: 10.1046/j.1365-3091.2003.00564.x.

Brand, A.R. 2006. Scallop ecology: Distribution and behaviour. In: *Scallops: Biology, Ecology and Aquaculture* (eds Shumway, S.E. & Parsons, G.J.). Elsevier, Amsterdam, 651-744.

Chapman, C.J. 1981. The swimming behaviour of queens in relation to trawling. *Scottish Fishering Bulletin*, 46, 7-10.

Cropp, D.A. 1993. Development of large-scale hatchery production techniques for *Amusium balloti* (Bernardi 1861) in western Australia. *Aquaculture*, 115, 285-296; doi: 10.1016/0044-8486(93)90143-M.

Dabrio, C.J. 1987-86. Las sand waves calcareníticas del Río Alías (Mioplioceno de la Cuenca de Níjar, Almería). *Acta Geológica Hispánica*, 21-22, 159-166.

Danise, S., Dominici, S. & Betocchi, U. 2010. Mollusk species at a Pliocene shelf whale fall (Orciano Pisano, Tuscany). *Palaios*, 25, 449-456; doi: 10.2110/palo.2009.p09-139r.

Dattilo, B.F., Brett, C.E., Tsujita, C.J. & Fairhurst, R. 2008. Sediment supply *versus* storm winnowing in the development of muddy and shelly interbeds from the Upper Ordovician of the Cincinnati region, USA. *Journal of Canadian Earth Sciences*, 45, 243–265; doi: 10.1139/E07-060.

Demarq, G. 1990. Pectinidés Néogènes: proposition d'échelle biostratigraphique pour la Méditerranée. *Geobios*, 23, 149-159; doi: 10.1016/S0016-6995(06)80047-1.

Dominici, S., Cioppi, E., Danise, S., Betocchi, U., Gallai, G., Tangocci, F., Valleri, G. & Monechi, S. 2009, Mediterranean fossil whale falls and the adaptation of mollusks to extreme habitats. *Geology*, 37, 815-818; doi: 10.1130/G30073A.1.

Dredge, M. 1985a. Estimates of natural mortality and yield-per-recruit for *Amusium japonicum balloti* Bernardi (Pectinidae) based on tag recoveries. *Journal of Shellfish Research*, 5, 103-109.

Dredge, M. 1985b. Growth and mortality in an isolated bed of saucer scallops, *Amusium japonicum balloti* (Bernard). *Queensland Journal of Agricultural Animal Science*, 42, 11-21.

Dredge, M. 1988. Recruitment overfishing in a tropical scallop fishery? *Journal of Shellfish Research* 7, 223-239.

Dredge, M. 1990. How far can a scallop population be pushed? In: *Proceedings of the Australasian scallop workshop* (eds Dredge, M.C.L., Zacharin, W.F. & Joll, L.M.). Hobart, Australia, 68-79.

Fürsich, F.T. 1995. Shell concentrations. *Eclogae geologicae Helvetiae*, 88, 643-655.

Gould, S.J. 1971. Muscular mechanics and the ontogeny of swimming in scallops. *Palaeontology*, 14, 61-94.

Hatcher, B.G., Scheibling, R.E., Barbeau, M.A., Hennigar, A.W., Taylor, L.H. & Windust, A.J. 1996. Dispersion and mortality of a population of sea scallop (*Placopecten magellanicus*) seeded in a tidal channel. *Canadian Journal of Fishery Aquatic Sciences*, 53, 38-54.

Hayami, I. 1991. Living and fossil scallop shells as airfoils: an experimental study. *Paleobiology*, 17, 1-18.

Heald, D.I. & Caputi, N. 1981. Some aspects of growth, recruitment and reproduction in the southern saucer scallop, *Amusium balloti* (Bernardi, 1861) in Shark Bay, Western Australia. *Fishery Research Western Australia*. 25, 1–33.

Héquette, A. & Hill, P.R. 1993. Storm-generated currents and offshore sediment transport on a sandy shoreface, Tibjak Beach, Canadian Beaufort Sea. *Marine Geology*, 113, 283–304; doi: 10.1016/0025-3227(93)90023-O.

Himmelman, J.H., Guderley, H.E. & Duncan, P.F. 2009. Responses of the saucer scallop *Amusium balloti* to potential predators. *Journal of Experimental Marine Biology and Ecology*, 378, 58-61; doi: 10.1016/j.jembe.2009.07.029.

James, N.P. 1997. The cool-water carbonate depositional realm. In: *Cool-Water Carbonates* (eds James, N.P. & Clarck, A.D.). SEMP Special Publication, 56, 1-20.

Jiménez, A.P., Aguirre, J. & Rivas, P. 2009. Taxonomic study of scallops (Pectinidae: Mollusca, Bivalvia) from Pliocene deposits (Almería, SE Spain). *Revista Española de Paleontología*, 24, 1-30.

Joll, L.M. 1989. Swimming behaviour of the saucer scallop *Amusium balloti* (Mollusca: Pectinidae). *Marine Biology*, 102, 299-305; doi: 10.1007/BF00428481.

Joll, L.M. 1990. Recruitment variation in stocks of the saucer scallop *Amusium balloti* in the Abrolhos Island area. In: *Proceedings of the Australasian scallop workshop* (eds Dredge, M.C.L., Zacharin, W.F. & Joll, L.M.). Hobart, Australia, 61-67.

Joll, L.M. & Caputi, N. 1995a. Geographic variation in the reproductive cycle of the saucer scallop, *Amusium balloti* (Bernardi, 1861) (Mollusca: Pectinidae), along the Western Australian coast. *Marine and Freshwater Research*, 46, 779-792; doi: 10.1071/MF9950779.

Joll, L.M. & Caputi, N. 1995b. Environmental influences on recruitment in the Shark Bay saucer scallop (*Amusium balloti*) fishery of Shark Bay, Western Australia. *ICES Marine Science Symposia*, 199, 47-53.

Kangas, M., Weir, V., Fletcher, W. & Sporer, E. 2006. *Shark Bay Scallop Fishery*. ESD Report Series No. 2, Department of Fisheries, Western Australia, North Beach WA.

Kidwell, S.M. 1986. Models for fossil concentrations: Paleobiological implications. *Paleobiology*, 12, 6-24; doi: 10.1017/S0094837300002943.

Kidwell, S.M. 1988. Taphonomic comparison of passive and active continental margins: Neogene shell beds of the Atlantic coastal plain and northern Gulf of California.

*Palaeogeography, Palaeoclimatology, Palaeoecology*, 63, 201-223; doi: 10.1016/0031-0182(88)90097-1.

Kidwell, S.M. 1989. Stratigraphic condensation of marine transgressive records: Origin of major shell deposits in the Miocene of Maryland. *Journal of Geology*, 97, 1-24.

Kidwell, S.M. 1991a. The stratigraphy of shell concentrations. In: *Taphonomy. Releasing the Data Locked in the Fossil Record* (eds Allison, P.A. & Briggs, D.E.G.). Topics in Geobiology. Plenum, New York, 211-290.

Kidwell, S.M. 1991b. Condensed deposits in siliciclastic sequences: Expected and observed features. In: *Cycles and Events in Stratigraphy* (eds Einsele, G., Ricken, W. & Seilacher, A.). Springer-Verlag, Berlin, 682-695.

Kidwell, S.M. 1993. Taphonomic expressions of sedimentary hiatuses: Field observations on bioclastic concentrations and sequence anatomy in low, moderate and high subsidence settings. *Geologische Rundschau*, 28, 189-202; doi: 10.1007/BF00191825.

Kidwell, S.M. & Bosence, D.W.J. 1991. Taphonomy and time-averaging of marine shelly faunas. In: *Taphonomy. Releasing the Data Locked in the Fossil Record* (eds Allison, P.A. & Briggs, D.E.G.). Topics in Geobiology. Plenum, New York, 115–209.

Kidwell, S.M., Fürsich, F.T. & Aigner, T. 1986. Conceptual framework of the analysis and classification of fossil concentrations. *Palaios*, 1, 228-238; doi: 10.2307/3514687.

Mandic, O. 2004. Pectinid bivalves from the Ground Formation (lower Badenian, middle Miocene, Alpine-Carpathian foredeep) – Taxonomic revision and stratigraphic significance. *Geologica Carpathica*, 55, 129-146.

Martín, J.M. & Braga, J.C. 1996. Tectonic signals in the Messinian stratigraphy of the Sorbas basin (Almería, SE Spain). In: *Tertiary Basins of Spain: The Stratigraphic Record of Crustal Kinematics* (eds Friend, P.F. & Dabrio, C.J.). World and Regional Geology Series, Cambridge University Press, Cambridge, 6, 387-391.

Martín, J.M., Braga, J.C. & Betzler, C. 2003. Late Neogene-Recent uplift of the Cabo de Gata volcanic province, Almería, SE Spain. *Geomorphology*, 50, 27-42; doi: 10.1016/S0169-555X(02)00206-4.

Martín, J.M., Braga, J.C., Aguirre, J. & Betzler, C. 2004. Contrasting models of temperate carbonate sedimentation in a small Mediterranean embayment: the Pliocene Carboneras basin, SE Spain. *Journal of the Geological Society, London*, 161, 387-399; doi: 10.1144/0016-764903-044.

Montenat, C., Ott d'Estevou, P. & La Chapelle, G. 1990. La bassin de Níjar-Carboneras et le couloir du bas-Andarax. In: *Les Bassins Néogènes du Domaine Bétique Oriental (Espagne): Tectonique et Sedimentation dans un Couloir de Decrochement. Premiere Partie: Etude Regionale* (ed. Montenat, C.). Documents et Travaux, Institut Geologique Albert-de-Lapparent, 12-13, 129-164.

Morton, B. 1980. Swimming in *Amusium pleuronectes* (Bivalvia: Pectinidae). *Journal of Zoology*, 190, 375-404; doi: 10.1111/j.1469-7998.1980.tb01434.x.

Mueller, U., Kangas, M., Sporer, E. & Caputi, N. 2012. Variability in the spatial and temporal distribution of

the saucer scallop, *Amusium balloti*, in Shark Bay – management implications. *Marine and Freshwater Research*, 63, 1152-1164; doi: 10.1071/MF12051.

Nummedal, D. 1991. Shallow marine storm sedimentation – the oceanographic perspective. In: *Cycles and Events in Stratigraphy* (eds Einsele, G., Ricken, W. & Seilacher, A.). Springer-Verlag, Berlin, pp. 227–248.

Orensanz, J.M., Parma, A.M., Turk, T. & Valero, J. 2006. Dynamics, assessment and management of exploited natural populations. In: *Scallops: Biology, Ecology and Aquaculture* (eds Shumway, S.E. & Parsons, G.J.). Elsevier, Amsterdam, 765-868.

Patzkowsky, M.E. & Holland, S.M. 2012. *Stratigraphic Paleobiology. Understanding the Distribution of Fossil Taxa in Time and Space*. The University of Chicago Press. Chicago, USA.

Pérez-Asensio, J.N. & Aguirre, J. 2010. Benthic foraminiferal assemblages in temperate coral-bearing deposits from the late Pliocene. *Journal of Foraminiferal Research*, 40, 61-78; doi: 10.2113/gsjfr.40.1.61.

Pérez-Muñoz, A.B., Márquez-Crespo, R., Yesares-García, J., Sánchez-Almazo, I.M. & Aguirre, J. 2001. Evolución paleoambiental durante el Plioceno inferior en la Cuenca de Almería-Níjar (SE de España) según las asociaciones de foraminíferos bentónicos. *Revista Española de Paleontología*, Nº extra, 21-34.

Postma, G. 1979. Preliminary note on a significant sequence in conglomeratic flows of a mass-transport dominated fan-delta (lower Pliocene, Almeria Basin, SE Spain). *Proceedings Kon. Nederland Akademie van Wet., Serie B*, 82, 465-471.

Postma, G. 1983. Water-scape structures in the context of a depositional model of a mass flow dominated conglomeratic fan-delta (Abrioja Formation, Pliocene, Almeria Basin, SE Spain). *Sedimentology*, 30, 91-103; doi: 10.1111/j.1365-3091.1983.tb00652.x.

Raffi, S., Stanley, S.M. & Marasti, R. 1985. Biogeographic patterns and Plio-Pleistocene extinction of Bivalvia in the Mediterranean and southern North Sea. *Paleobiology*, 11, 368-388.

Rivas, R., Aguirre, J. & Braga, J.C. 1997. *Entolium* beds: hiatal shell concentrations in starved pelagic settings (middle Liassic, SE Spain). *Eclogae geologicae Helvetiae*, 90, 293-301.

Rose, R.A., Campbell, G.B. & Sanders, S.G. 1998. Larval development of the saucer scallop *Amusium balloti*, Bernardi (Mollusca: Pectinidae). *Australian Journal of Marine and Freshwater Research*, 39, 133-160; doi: 10.1071/MF9880153.

Seilacher, A. & Aigner, T. 1991. Storm deposition at the bed, facies and basin scale: The geologic perspective. In: *Cycles and Events in Stratigraphy* (eds Einsele, G., Ricken, W. & Seilacher, A.). Springer-Verlag, Berlin, pp. 249-267.

Serrano, F. 1990. El Mioceno medio en el área de Níjar (Almería, España). *Revista de la Sociedad Geológica de España*, 3, 65-77.

Stokesbury, K.D.E. & Himmelman, J.H. 1993. Spatial distribution of the giant scallop *Placopecten magellanicus*

in unharvested beds in the Baie des Chaleurs, Québec. *Marine Ecology Progress Series*, 95, 159-168.

Tremblay, I., Samson-Dô, M. & Guderley, H.E. 2015. When behavior and mechanics meet: scallop swimming capacities and their hinge ligament. *Journal of Shellfish Research*, 34, 203-212; doi: 10.2983/035.034.0201.

Wang, S., Duncan, P.F., Knibb, W. & Degnan, B.M. 2001. Successful hatchery production and the first report of byssal attachment in the 'unusual' scallop, *Amusium balloti*. *13th International Pectinid Workshop, Coquimbo, Chile*, 71-72.

Wissak, M., López-Correa, M., Gofas, S., Salas, C., Taviani, M., Jakobsen, J. & Freiwald, A. 2009. Shell architecture, element composition, and stable isotope signature of the giant deep-sea oyster *Neopycnodonte zibrowii* sp. nov. from the NE Atlantic. *Deep-Sea Research I*, 56, 374-407; doi: 10.1016/j.dsr.2008.10.002.

Yesares-García, J. & Aguirre, J. 2004. Quantitative taphonomic analysis and taphofacies in lower Pliocene temperate carbonate-siliciclastic mixed platform deposits (Almeria-Nijar Basin, SE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 207, 83-103; doi: 10.1016/j.palaeo.2004.02.002.

Yonge, C.M. 1936. The evolution of the swimming habit in the Lamellibranchia. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique (2me series)*, 3, 77-100.

Young, P.C. & Martin, R.B. 1989. The scallop fisheries of Australia and their management. *CRC Critical Reviews in Aquatic Sciences*, 1, 615-638.

Young, P.C., Martin, R.B., McLoughlin, R.J. & West, G. 1990. Variability in spatfall and recruitment of commercial scallops (*Pecten fumatus*) in Bass Strait. In: *Proceedings of the Australasian scallop workshop* (eds Dredge, M.C.L., Zacharin, W.F. & Joll, L.M.). Hobart, Australia, 80-91.