A shallow-water cyrtocrinid crinoid (Articulata) from the upper Albian of the Western Pyrenees, North Spain

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ABSTRACT

The cyrtocrinid crinoid *Proholopus holopiformis* (Remeš, 1902) is described from the upper Albian succession that may be included in the Albeniz unit to the east of Iruñea-Pamplona (Navarre, Western Pyrenees, Spain). Although based on partially disarticulated material, this taxon preserve calyx, stem, attachment structure, and brachial plates from the arms. *Proholopus holopiformis* was previously described from the Upper Jurassic-Lower Cretaceous of the Czech Republic and Lower Cretaceous of France and Crimea, thus the occurrence from Spain represents the youngest of the species. This allows a better characterization of the family Proholopodidae that was originally described based on calyx morphology only and expands its distribution to the upper Albian. *Proholopus holopiformis* inhabited the fore-reef areas of coral-sponge bioconstructions. Based on coral types, crinoids are thought to have dwelled near the euphotic-oligophotic zones transition and, thus, thrive in shallow depths. Most specimens have bite marks compatible with cidaroid predation. This represents one of the youngest occurrences of cyrtocrinids inhabiting shallow marine environments before their migration to the deep sea due to the ongoing Mesozoic Marine Revolution.

1. Introduction

Cyrtocrinids are a small clade of extant articulate crinoids (Rouse et al., 2013) that include a handful of species (i.e. *Holopus rangii*) living in deep bathyal environments (Donovan and Jakobsen, 2004). They are relatively small crinoids and typically attach on hardgrounds or bioclasts forming large colonies (Hess and Messing, 2011). Cyrtocrinids typically have short, rigid stems, and thick short arms with few branches, although the stem is absent in some taxa (i.e., *Cyathidium*). The group has a long evolutionary history that originated during the Late Triassic-Early Jurassic (De Loriol, 1882−1889; Manni and Nicosia, 1990; Hess, 2006; Salamon et al., 2009), and fossil cyrtocrinids occupied a wide range of environments from shallow marine sponges reefs (Hess and Spichiger, 2001; Salamon and Gorzelak, 2007) to deeper conditions (Hess, 2006; Zatón et al., 2008). By the Middle and Late Jurassic, cyrtocrinids mostly occupied sponge meadows and were abundant and diverse (Zatón et al., 2008; Hess and Messing, 2011; Zamora et al., 2018). After the Jurassic, cyrtocrinids dramatically dropped in diversity, and only few species have been documented from the late Mesozoic and Cenozoic (Rasmussen, 1961; Jäger, 1982; Donovan and Jakobsen, 2004; Salamon et al., 2007; Hess and Messing, 2011). Few references document cyrtocrinids living in shallow marine environments after the Jurassic, which is probably the result of 1) lack of sedimentological information associated with systematic papers (Zitt, 1974), 2) species inhabited deep water environments by that time (Donovan and Jakobsen, 2004), or 3) they were very rare in shallow water environments due to the ongoing Mesozoic Marine Revolution (Whittle et al., 2018).

Herein, we report an upper Albian cyrtocrinid crinoid from Spain that belongs to the family Proholopodidae Žitt, 1974. This family has a poorly known fossil record that consists of one genus and species *Proholopus holopiformis* from the Late Jurassic and Lower Cretaceous of Crimea, Czech Republic, France, and Hungary (Hess and Messing, 2011). The material from Spain

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contains specimens that preserve calyx, arm brachials, columnals, and holdfast. This allows a better understanding of the morphology of this family. Material has been collected from the Albian reef facies of the Basque-Cantabrian basin (near Pamplona, Spain) allowing a better understanding of its palaeoecology and demonstrating that some cyrtocrinids inhibited shallow marine environments by the Middle Cretaceous. Some specimens also are preserved with pits and scratches that are interpreted as evidence of predation.

2. Material and methods

Most specimens described in this study were surface collected directly from outcrops, but a few were isolated from bulk sediment samples (~10 kg). The latter were placed in buckets containing water and hydrogen peroxide (H_2O_2) that dissolved the rock. After two days of soaking, the material was washed for ca. 16 h until clean. Crinoid remains larger than 1 mm were separated for analyses.

Most specimens were prepared using potassium hydroxide (KOH) and later neutralized with hydrochloric acid (10%).

Specimens were photographed using a Nikon D7100 equipped with AF-S Micro NIKKOR 60 mm objective. Specimens were coated with ammonium chloride to increase contrast.

Specimens are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ) (Canudo, 2018). All figured specimens and important non-figured specimens have a museum number (MPZ2021/347−365). There are also extra crinoid material and associated invertebrate fauna that have been deposited under acronyms EMPZ2021/49, 50.

The stratigraphy is based on a new cartography of the fossil-bearing facies, field-sedimentological observations, and analysis of thin sections of key intervals.

3. Geological setting and stratigraphy

Limestones located to the north of the Irañeta locality (Navarre) crop out in the southern flank of the Aralar Mountains folded area, which is part of the present-day inverted Basque-Cantabrian Basin. Aralar is mainly an E-W oriented anticline 30 km long bounded by two almost parallel main reverse faults with northward and southward convergence (Fig. 1A). Limestones of the Aralar southern flank dip between 60 and 70° toward the south.

The studied limestones are part of the shallow marine carbonate platforms of Aptian-Albian age that form the main peaks in the Aralar Mountains. The Aptian is characterized by extensive platforms with mainly micritic facies rich in rudists transitional to siliciclastic tidal troughs. During the late Aptian and Albian the siliciclastic input increased, and carbonate platforms record a transition from ramps to rimmed platforms. This change is also conditioned by the differential subsidence after an important tectonic control basinwide (e. g., García-Mondéjar et al., 1996). Carbonate platform sedimentation was then developed on shallow marine highs bounded by active faults, especially during the late Albian when shallow carbonates developed on comparatively reduced areas subjected to an increasing tectonic subsidence and large siliciclastic input from the south (e. g. García-Mondéjar et al., 2004). Consequently, downthrown blocks became deeper marine troughs where shallow to deeper marine siliciclastic sedimentation took place. Almost the entire shallow marine carbonate sedimentation terminated before the latest Albian due to the incapability of the shallow carbonate producers to keep up with the increasing subsidence and the environmental stress caused by siliciclastic input (e. g., López-Horgue et al., 1993).

3.1. Stratigraphy

Figure 1B represents the main stages of carbonate platform development during the early Albian to late Albian transition recorded to the north of the Irañeta locality in the Maddalenaitz-Aitzondo peaks area. The figure is an improved version of a figure in Zamora et al. (2018, fig. 5). After a lower Albian carbonate ramp stage, both the development of unconformities bounding middle and basal upper Albian units and the sedimentation of carbonate breccias testify to the creation of a deeper trough whose origin is likely linked to tectonic activity (Lertxundi and García-Mondéjar, 1998). Consequently, from the middle to upper Albian, the shallow marine carbonate sedimentation is only represented on the borders of the trough, being especially thicker in the western portion during the middle Albian. The studied interval corresponds to the upper Albian succession. During this time, the trough expands to the west where the shallow marine carbonate sedimentation was areally reduced and the siliciclastic input increased. The carbonate succession in the Maddalenaitz area (corresponding with Irañeta 1 locality) is approximately 400 m thick, whereas in Aitzondo area (corresponding with Irañeta 2 locality) coeval limestones and overlying silty marls are approximately 475 m thick (Fig. 1B). The trough silty succession is slightly thicker in the middle part with approximately 500 m. Crinoid-bearing beds occur in the lower part of this succession (Figs. 1B and 2). The age of this succession is early late Albian based on ammonoids from correlative successions to the east and west (Wiedmann, 1962; López-Horgue et al., 1996, 1997; López-Horgue and Owen, in prep.) This succession is included herein in the Albeniz unit (López-Horgue et al., 1996 erected this to group the upper Albian carbonates and their coeval siliciclastic sediments of the Alsasua-Irurtzun area; Fig. 1A).

## 4. Main facies associations and environments of the upper Albian

4.1. Facies associations

Shallow marine limestones to the east of the Maddalenaitz (Fig. 3-FA 1) area occur as micritic beds centimeters−meters thick interlayered with cm-thick intervals of marly limestones. Corals, rudists, and green algae are the dominant fossils; orbitolinids and other bivalves are the main components of the marly intervals. Coeval coralline micritic limestones dominate the transition toward the deeper siliciclastic trough forming build-ups some meters thick and tens of meters wide interbedded with biostromic coral-rudist packstones (FA 2). Farther toward the trough, the limestones are mainly comprised of platy corals (microsolenids), sponges, red algae, orbitolinids, and echinoderm fragments interbedded with silty marls, with clinoform depositional dips less than 15-20° (FA 3).

In the area of Aitzondo peak (Fig. 3), coeval limestones have the same constructional facies associations, but the sedimentary area is only 400 m wide and the transition to the trough is marked by more inclined clinoforms (less than 40° dip).

Trough sedimentation was characterized by calcareous siliciclastic mudstones (silty marls) with sporadic breccia (debrite)-calcarenite intervals at the fore-reef slope of the shallow marine limestones (FA 4), and interlayered very fine grained and thin siliciclastic tempestites occurred mainly in the central part of the trough (FA 5). Calcispheres are common in FA 3 and 4. Siliciclastic calcareous mud is the background sediment in the trough, being almost devoid of fossils, but with scarce *Chondrites*-like burrows and occasional ammonites with anatomical details finely preserved.

The studied crinoid fauna (Fig. 4C, D) occurs in two debrite beds (Fig. 2; Fig. 3-FA 4) as mm-sized loose clasts together with red
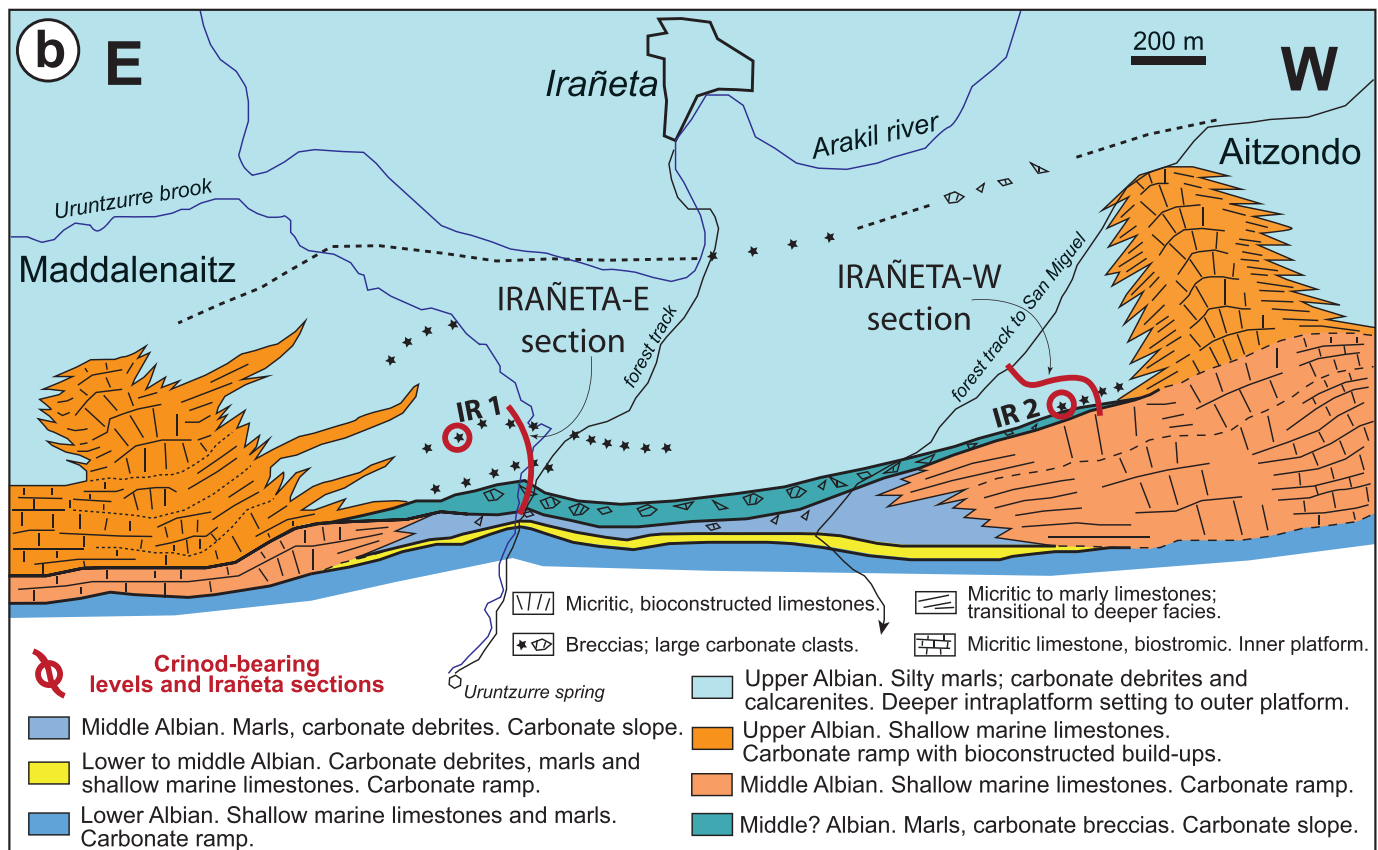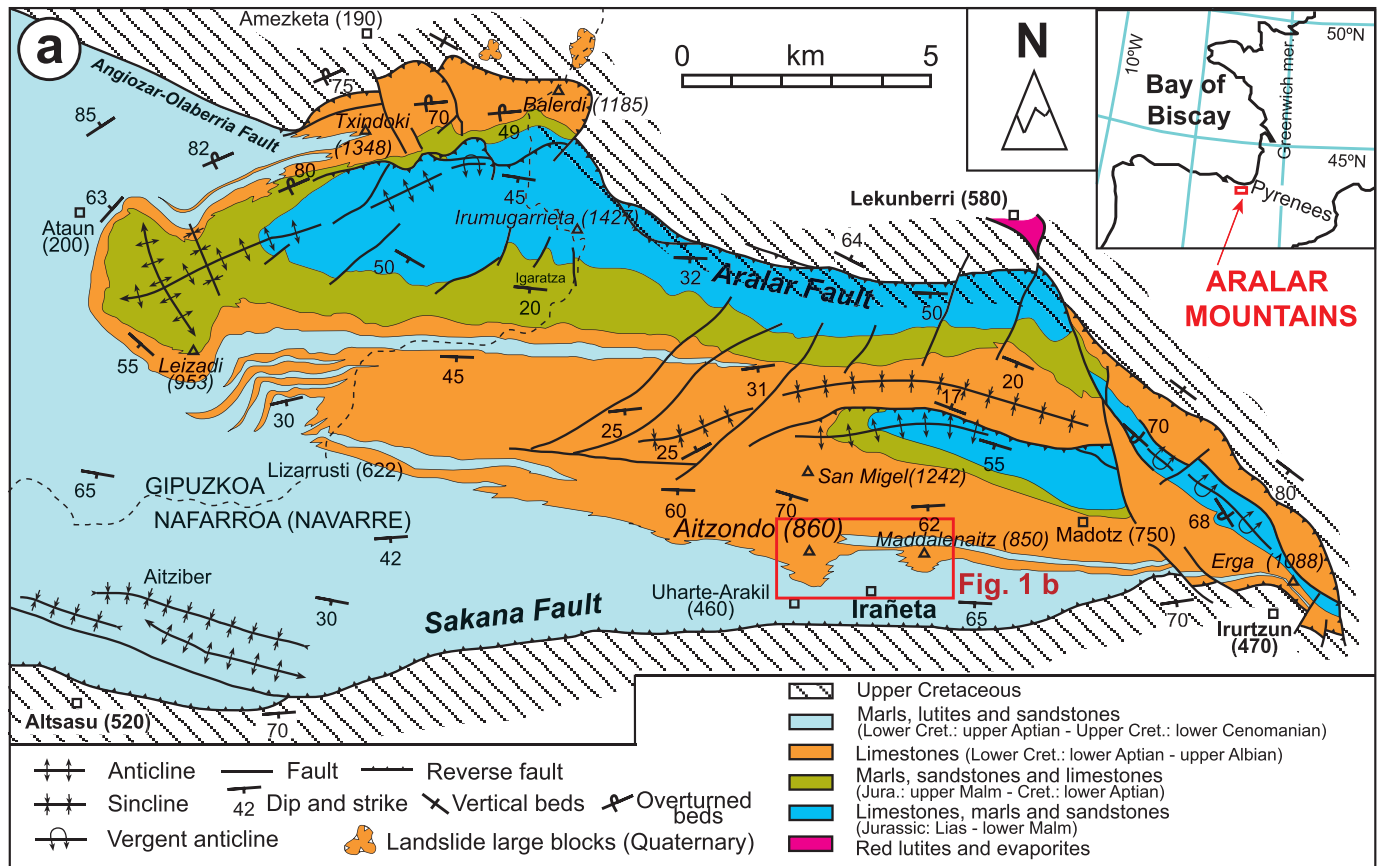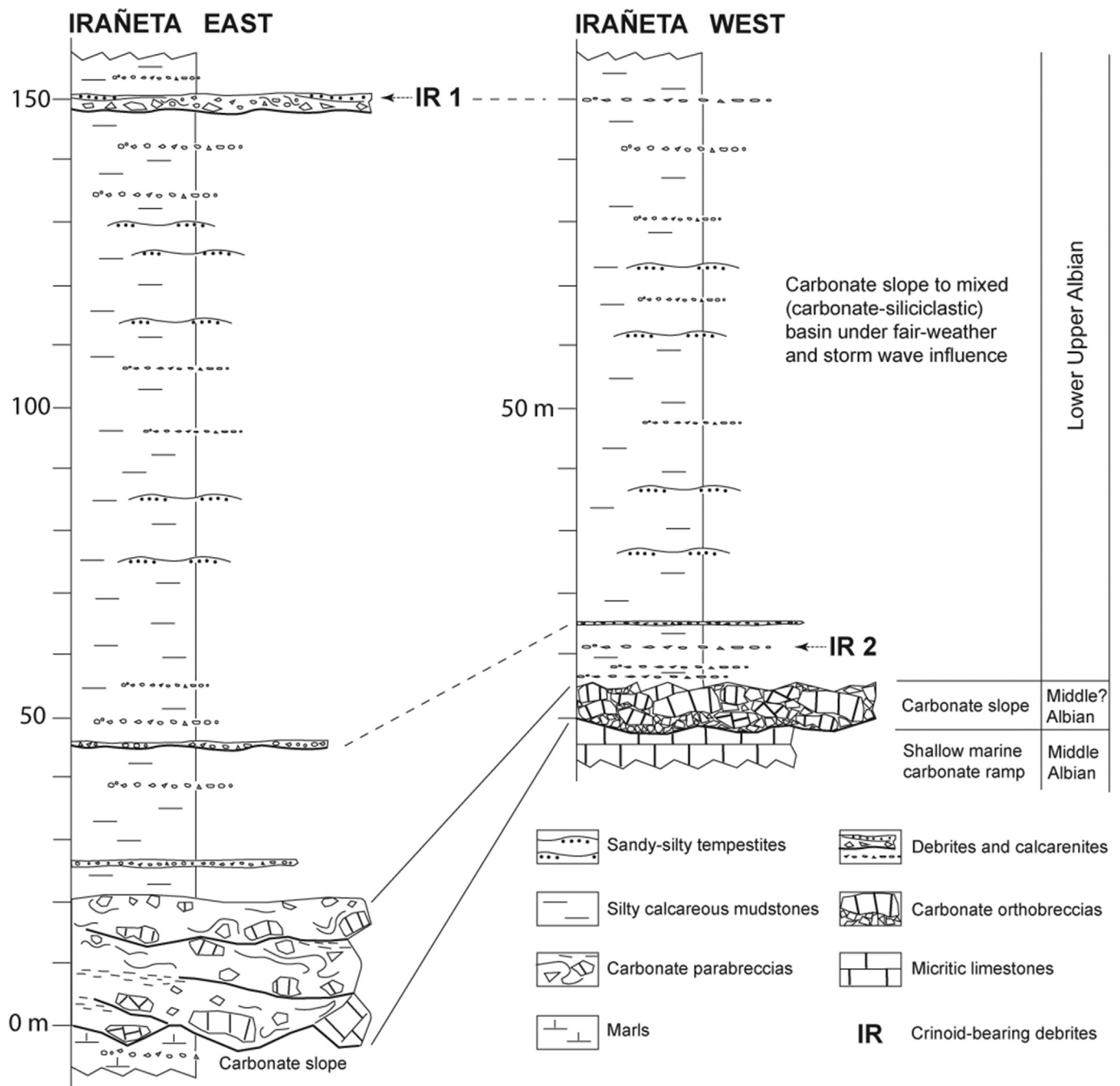
Fig. 2. Synthetic stratigraphic sections of the lower part of the trough sediments equivalent to the Maddalenaitz and Aitzondo limestones near Irañeta locality. Crinoid-bearing beds occur in two stratigraphical levels, with IR 2 being the oldest one. Correlation is based both on facies analysis and bedding correspondance in the field. See Fig. 1 for sections location.

algae, sponges (Fig. 4E, 5D), encrusting bryozoans (Fig. 5B), brachiopods, other echinoderms (cidaroid remains (Fig. 5I, J) and isocrinid crinoids (Fig. 5C, E, F-H)), orbitolinids, benthic foraminiferans (*Involutina hungarica*), crustacean remains, and intraclasts with sponges (Figs. 4, 5). This facies bears microsparitic cement but also conspicuous micritic matrix in places. These deposits are arranged in breccia to calcarenite beds 0.2 to 1.5 m thick that are interlayered with meter-thickness silty marls.

4.2. Environments

FA 1 limestones of the eastern part of the studied succession (Maddalenaitz area) are interpreted as having originated in a shallow inner platform environment in normally euphotic conditions. Their transition to FA 2 and FA3 suggests a gradual dipping in the depositional profile toward the west possibly with a slightly elevated area where carbonae build-ups (sensu

Fig. 1. Geological maps of the studied area. A. Simplified geological map of the Aralar mountains in the Gipuzkoa and Navarre provinces of the Western Pyrenees, North Spain. Most of the outcropping units are of Early Cretaceous age. Irañeta area with crinoid-bearing levels is highlighted. Modified from López-Horgue (2004). B. Detailed geological map of the Irañeta studied area with the main stratigraphy and ages. Modified from Zamora et al. (2018, Fig. 5). Ir 1 and Ir 2 correspond to the two sampled localities of Irañeta 1 and 2.
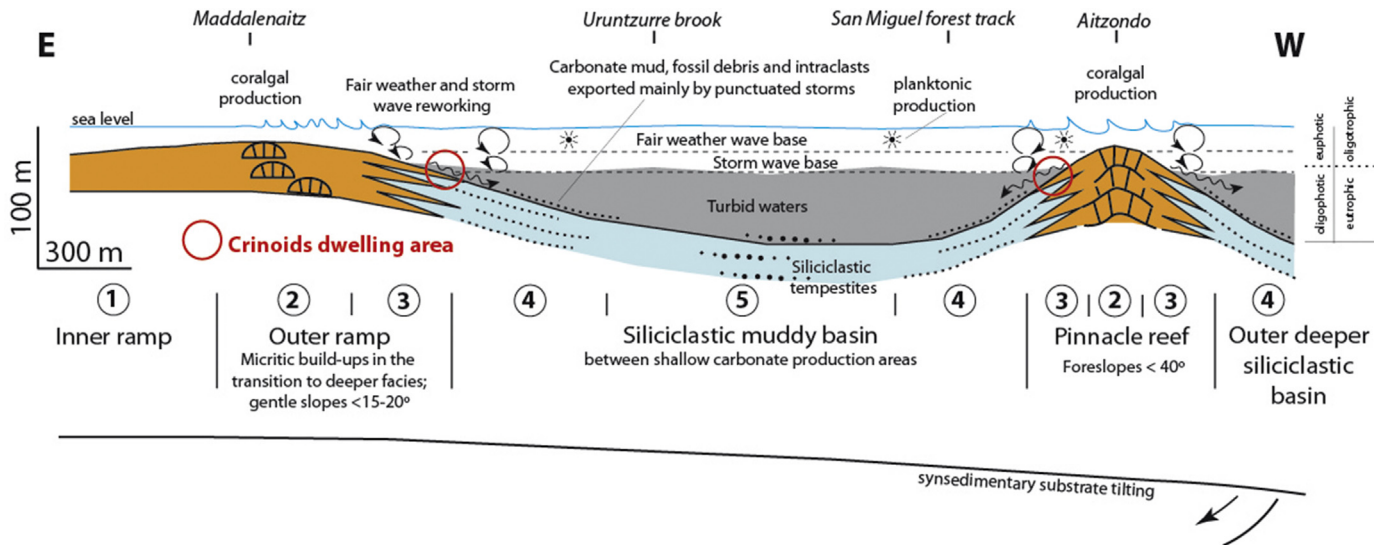
Fig. 3. Sedimentary model of the lower upper Albian interval near the Irañeta locality based on stratigraphical and sedimentological data, with indication of the distinguished facies associations and the suggested main controls on sedimentation. Crinoid preferential habitats are the fore-reef areas at the transition of both euphotic-oligophotic and oligotrophic-eutrophic zones in the water column, below fair-weather wave base.

Fig. 4. Field photographs of the studied outcrops and *in situ* fossils. A. General view of an abandoned quarry (Irañeta 2). Arrow indicates marly levels providing crinoid material. B. Detail of the marly levels with interbedded carbonate debrites (AF 4). C, D. Detail of nearly complete cyrtocrinids. E. In-situ inverted sponge atop of one of the debrite beds.
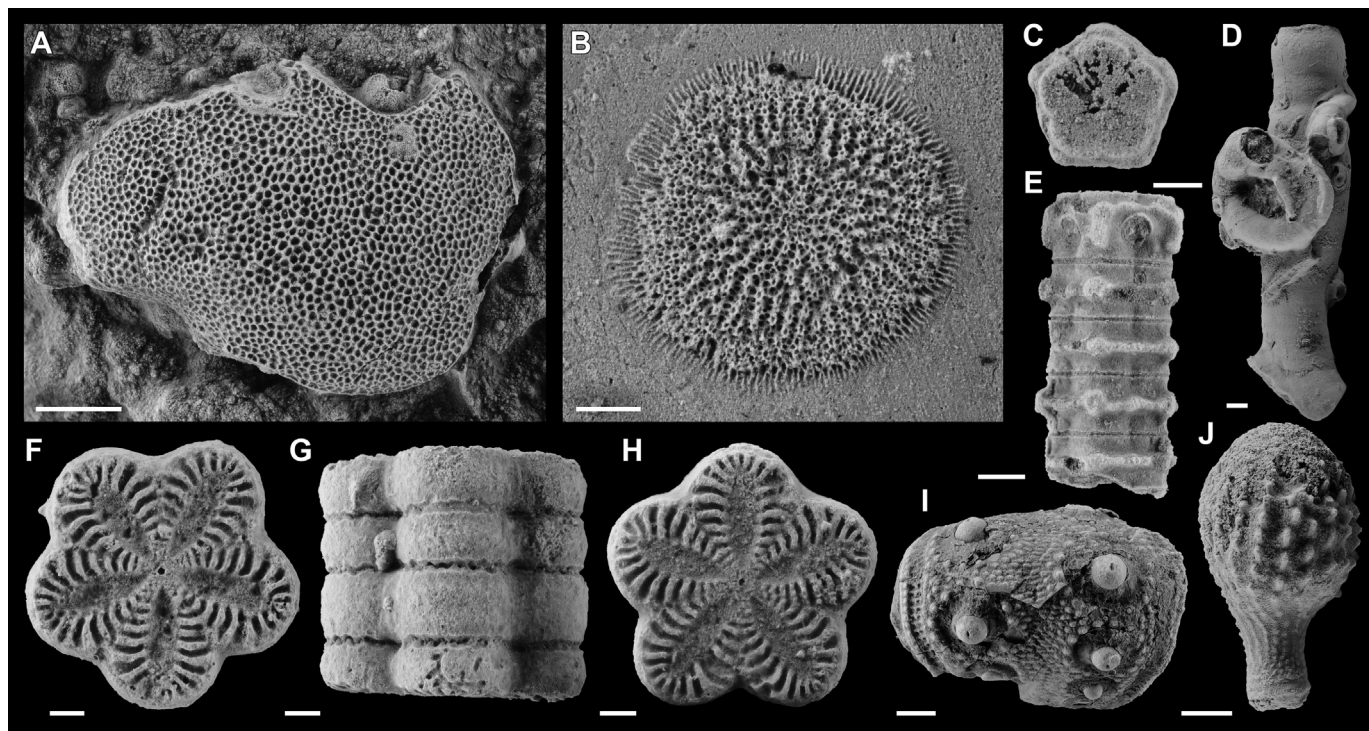
Fig. 5. Associated fauna in the levels containing the studied crinoid, Albeniz unit, Albian, Navarre, Spain. A. Stromatoporoid attached on a hardground. Specimen MPZ2021/359. B. Bryozoan encrusting an oyster shell. Specimen MPZ2021/360. C, E. Isocrinid crinoid *Isocrinus*? sp. A. Specimen MPZ2021/361. D. Conical sponge with encrusting serpulids. Specimen MPZ2021/363. F—H. Isocrinid crinoid *Isocrinus*? sp. B. Specimen MPZ2021/362. I. Fragment of an indeterminate Cidarinae. Specimen MPZ2021/364. J. *Tylocidaris* sp. spine. Specimen MPZ2021/365. All specimens are from Irañeta 2. Scale bars represent 5 mm in A; 2 mm in D, H-J; 1 mm in C, E-H.

Stanton, 1967) formed (in the euphotic zone; e. g., Pomar, 2001). FA 3 is interpreted as *in situ* deposition under lower light conditions and slightly turbid; but quiet waters are suggested by platy corals, sponges, and undisturbed siliciclastic mud. In any case, micrite preservation indicates a zone near or below fair-weather wave base. In the Aitzondo area, despite the clinoforms with higher depositional dips, *in-situ* facies dominate in the limestones.

Debrite (breccia)-calcarenite beds of FA 4 suggest resedimentation down the depositional slope at the edges of the limestone units. Bioclasts, intraclasts, and micritic matrix suggest the downslope transport of FA 3 facies. Intraclasts indicate lime mud consolidation. These deposits punctuate the background siliciclastic muddy sedimentation in the trough, suggesting episodic higher turbulence capable of eroding the bottom. These data and the occurrence of thin tempestites in the center of the basin indicate episodic turbulence related to storms affecting both limestones and silty marls. Additionally, marine sedimentation during the late Albian of the Basque-Cantabrian Basin was affected by typical storm generated currents (e. g., Lopez-Horgue et al., 1993, 1999). As suggested above, the trough sediments are indicative of mud settling under low energy conditions in turbid waters (oligophotic zone); mud particles are almost absent in FA 2 suggesting limpid waters and normal light penetration (euphotic zone; e. g., Pomar, 2001). In these conditions episodic high turbulence (storms) was capable of transport of carbonate particles to the trough. The occurrence of calcispheres (Versteegh et al., 2009), both in the shallow limestones and in the trough, indicates planktonic carbonate production. This may be the main source of carbonate mud (Berkyová and Munnecke, 2010) in the trough facies because carbonate dispersal from the shallow carbonate areas to the trough was probably only episodic.

The muddy siliciclastic input would also have been responsible for a high nutrient input conditioning the settlement of bioconstructors in the trough (e.g., Fabricius, 2011); sponges, orbitolinids, and red algae of FA 3 represent this mesotrophic to eutrophic scenario (e. g., Hallock, 1988; Vilas et al., 1995; Pomar, 2001). The scarcity of infauna in the silty muds supports the interpreatation of an oxygen-depleted muddy bottom.

According to the data discussed above, depth differences from the reef core (approximately 20—30 m deep at most), to the siliciclstic trough (approximately 70—80 m deeper, are reasonable.

Lertxundi and García-Mondéjar (1998) suggested the synsedimentary tilting of the substrate due to tectonic activity. Both tectonism and siliciclastic input may have been major controls in the development of the bioconstructed limestones affecting productivity by eutrophication and deepening of the area. The pinnacle reef structure formed in the Aitzondo area may be explained as a keep-up (Wright and Burchette, 1996) bioconstruction that terminated after controlling factors exceeded its growth rate and drowned the area.

4.3. Crinoid preferential environment

Crinoid specimens were transported down the carbonate slope, so they represent resedimented associations (FA 4) but were likely from the fore-reef, where autochthonous limestones of FA 3 were deposited. The fact that crinoids were just transported a bit farther from their living area is also supported by the low abrasion on specimens, absence of sorting, and the high degree of articulation. The fact that some of them still preserve articulated parts (i. e. calyx with some columnals) suggests that they were rapidly buried. They also have predation marks (see below) that may be attributed to

cidaroids, typical dwellers of shallow reefal areas. All these data suggest a crinoid habitat in the fore-slope areas of the carbonate bioconstructions in the transition from euphotic to the oligophotic water zones, under sporadic storm influence (below fair-weather wave base) and oligotrophic to euthrophic conditions, in approximate 30–50 m depths.

5. Systematic palaeontology

Descriptive terminology follows Hess (2006) and Hess and Messing (2011) (Fig. 6). Details for cup measurements as in Salamon (2008). Classification follows Hess and Messing (2011).

Class Crinoidea Miller, 1821
Subclass Articulata Miller, 1821
Order Cyrtocrinida Sieverts-Doreck, 1952
Suborder Cyrtocrinina Sieverts-Doreck, 1952
Family Proholopodidae Žítt, 1974

Discussion. The family Proholopodidae was erected by Žítt (1974) to include the single genus *Proholopus*. Hess and Messing (2011) accepted the creation of the Proholopodidae. Romano et al. (2016) developed a first rigorous phylogenetic analysis of cyrtocrinids demonstrating that there is little consensus between traditional classifications and phylogenetic analysis. Their strict consensus tree had *Proholopus* in a large polytomy, but the tree obtained from the gap-weighting method suggested *Proholopus* is the sister taxon of *Gammarocrinites* and *Paragammarocrinites*. If the latter is confirmed, the Proholopodidae would not be recognized in future classifications. Herein, we maintain traditional classification pending future phylogenetic work on this topic.

Genus *Proholopus* Jaekel, 1907

Diagnosis (enmend.). Funnel-shaped asymmetric theca with a large radial cavity. Articular facets are horizontal or slope slightly outward, laterally in contact with each other. First primibrachial as an axilliary and strongly convex aborally. Secundibrachials with a dome-shaped aboral surface. Columnals smooth and cylindrical, proximalmost columnal wider than high, probably three remaining columnals higher than wide, ending on a cemented holdfast.
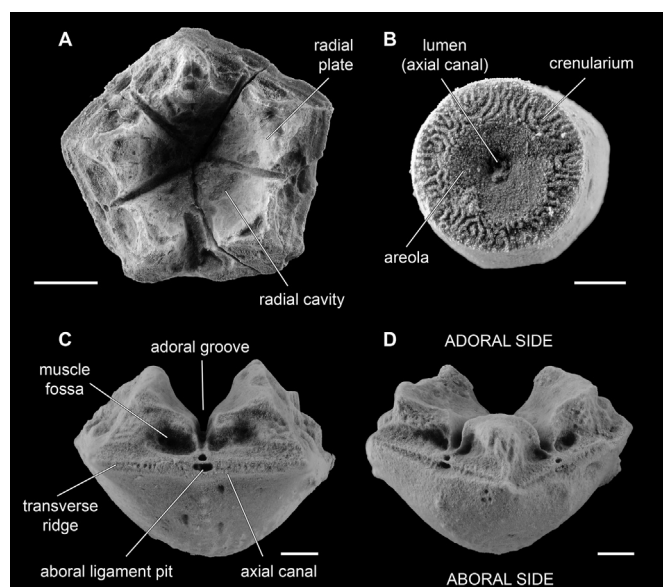

Fig. 6. Terminology for cyrtocrinids used in the text. Terms follow Hess and Messing (2011). A. Oral view of a calyx. B. Columnal articulation. C, D. Brachial plate in proximal (C) and distal view (D). Scale bars represent 2 mm in the upper left specimen and 1 mm in the remainder specimens.

Type species: Eugeniacrinus holopiformis Remeš, 1902 by original designation.

Proholopus holopiformis (Remeš, 1902)
Figs. 7-9

1901 *Eugeniacrinus holopiformis* Remeš, pl. 2
1902 *Eugeniacrinus holopiformis* Remeš, p. 203, pl. 19 fig. 4–6
1902 *Eugeniacrinus cupuliformis* Remeš, p. 203, pl. 19 fig. 7
1907 *Proholopus holopiformis* (Remeš) — Jaekel, p. 292, fig. 17
1961 *Proholopus holopiformis* (Remeš) — Rasmussen, p. 220, pl. 32, fig. 3
1974 *Proholopus holopiformis* (Remeš) — Arendt, p. 98, pl. V, fig. 6–10, pl. VI, fig. 1–14
1974 *Proholopus holopiformis* (Remeš) — Žitt, p. 28, pl. 5, figs. 1–12
1978 *Proholopus holopiformis* (Remeš) — Rasmussen, p. 833, fig. 559.4
1992 *Proholopus holopiformis* (Remeš) — Manni et al. p.117, fig. 3, pl. 1, figs. 1, 2
2011 *Proholopus holopiformis* (Remeš) — Hess and Messing, p. 185, fig. 90.1
2018 *Proholopus* sp. Zamora et al. fig. 10D

Diagnosis. As for a monotypic genus.
Material. Several cups, some with columnals still attached (MPZ2018/484, MPZ2021/347–351), stem fragments (MPZ2021/352), holdfast (MPZ2021/357, 358), and several brachials (MPZ2021/253–356). Additional material is under repository EMPZ2021/49, 50.
Description. Available cups of similar size (ca. 10 mm in diameter) and variable shape, from more conical (Fig. 7B) to bowl-shaped (Fig. 7G). They are comprised of five slightly elongate, slightly asymmetric radials that form a wide cone. The sutures between the radials are mostly visible from the interior, but they are poorly defined from the exterior. Radial articular facets equal in size and pleneplenary (Fig. 7H, J). The cup articulates to a barrel-like first columnal. Ornamentation with small granules disposed in rows that continue to the first columnal (Fig. 7B) and brachials (Fig. 8A). As many as three columnals (probably four) that increase in height distally ending in a cemented holdfast (Fig. 7A, F; 9). External surface of second and third columnals and the holdfast smooth. Large lumen, wide smooth areola and crenularium comprised of curved rows restricted to the margins of the columnal facet (Fig. 7D). The material also contains a number of brachials that undoubtedly belong to this species based on the size and ornamentation (Fig. 9). All brachials reveal deep muscle fosase. First primibrachial axillary, with single proximal facet and doubled distal facet (Fig. 8A, B). Primibrachials variable in size and with a deep adoral groove that splits distally (Fig. 8F). Primibrachials have large transverse ridge in the proximal part that occupy the total length of the brachial. They are also nodose and ornamented by granules in the aboral surface (Fig. 8E). Secundibrachials comparatively smaller in size, slightly ornamented with granules, and with a very nodose aboral surface (Fig. 8G-L).
Remarks. Proholopus holopiformis
was first described as a species of *Eugeniacrinus* by Remeš, 1902, who figured a well-preserved calyx. Jaekel (1907) first recognized differences with *Eugeniacrinites* and *Holopus* in the calyx and arm articulations and erected the new genus *Proholopus* with a single species. He also provided information on the most proximal columnal. Material from Spain is assigned to *Proholopus holopiformis* based on the general morphology of the calyx, which is comparable to material originally described by Remeš (1902) and later authors. Primibrachials in the described material are consistent between different specimens, but dimensions are rather different with some being higher than wide in plan view and others wider than high. Compared with specimens from Crimea described by Arendt (1974), the ornamentation of this species is very variable. Crimean material has external ridges, whereas the calyx in the Spanish
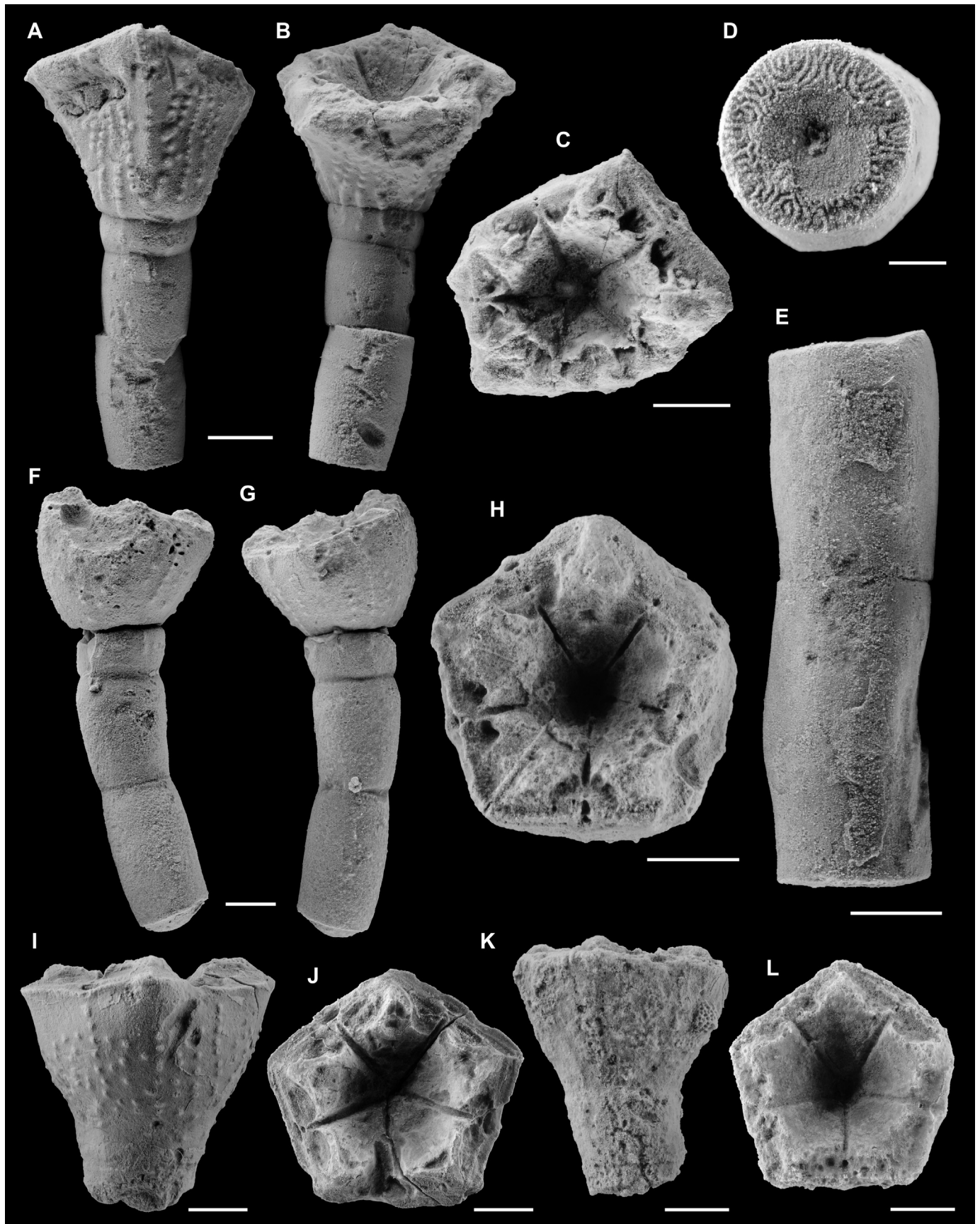
Fig. 7. *Proholopus holopiformis* from the Albian Albeniz unit (Navarre, Spain). A–C. Complete calyx with three columnals attached in lateral (A), oblique (B), and oral (C) views. Note columnals increase in lón height distally (specimen MPZ2021/348). D, E. Column comprised of two joining columnals in axial (D) and lateral (E) views (specimen MPZ2021/352). F–H.
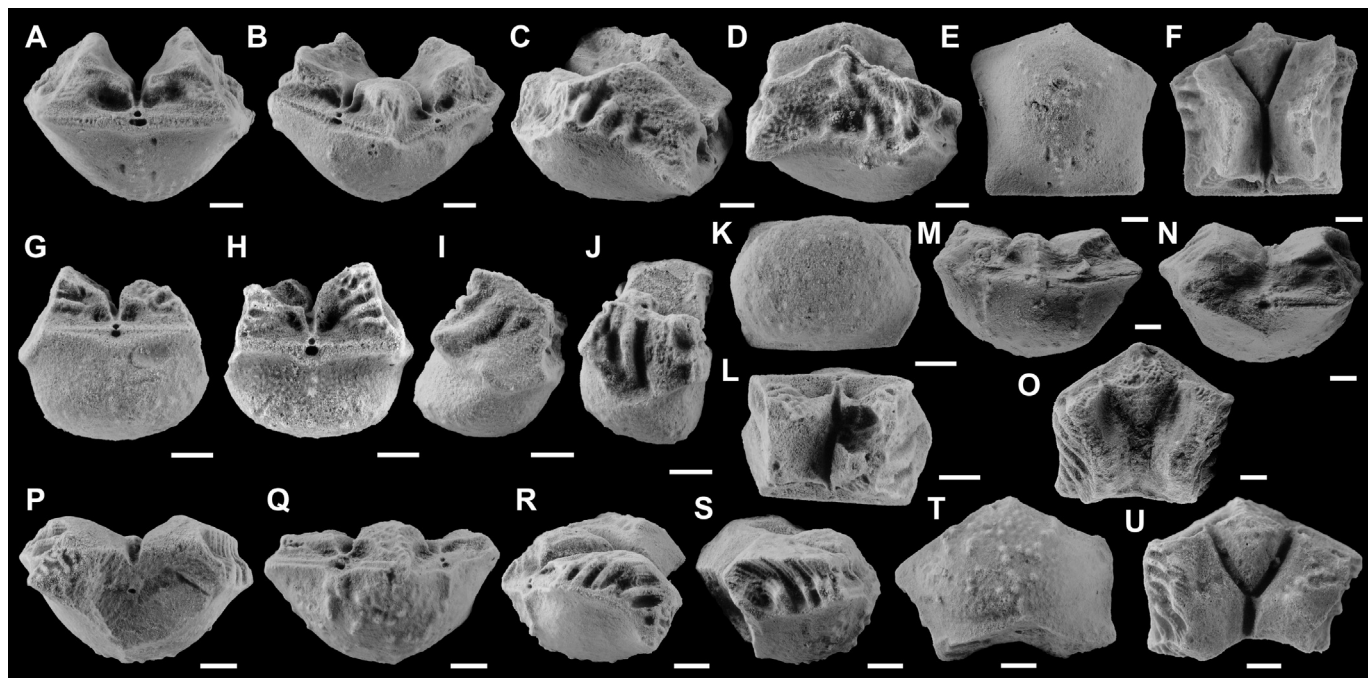
Fig. 8. Brachial plates of *Proholopus holopiformis* from the Albian Albeniz unit (Navarre, Spain). A-F. First primibrachial in proximal (A), distal (B), lateral left (C), lateral right (D), aboral (E), and adoral (F) views (specimen MPZ2021/353). G-L. Secundibrachial in distal (G), proximal (H), lateral right (I), lateral left (J), aboral (K), and adoral (L) views (specimen MPZ2021/354). M-O. First primibrachial in distal (M), proximal (N) and adoral (O) views (specimen MPZ2021/356). P−U. First primibrachial in proximal (P), distal (Q), lateral left (R), lateral right (S), aboral (E), and adoral (F) views (specimen MPZ2021/355). All specimens from Irañeta 2 with exception of M−O which is from Irañeta 1. Scale bars represent 1 mm.

material is ornamented by rows of ridges. Only one specimen described by Arendt (1974, pl. V, Fig. 9) seems to have comparable ornamentation to the Spanish material. The shape of the theca is also very variable in the population suggesting this form was strongly dependent on ecological conditions.

Occurrence. Upper Jurassic of the Czech Republic and Hungary (Manni et al., 1992), Hauterivian of France (Rasmussen, 1961), Oxfordian, Valanginian−Barremian of Crimea (Arendt, 1974), Albian of Spain (herein).

6. Discussion

Crinoids were an important component of Mesozoic marine assemblages (Hess and Messing, 2011) and have been used as an example of the impact of the Mesozoic Marine Revolution on marine invertebrates (Bottjer and Jablonski, 1988; Baumiller et al., 2010). Stalked isocrinid crinoids were displaced into deeper water by the Late Cretaceous and replaced by more motile stalkless crinoids (Gorzelak et al., 2012; 2016), apparently due to the increase of predation pressure in shallow-water environments. Nevertheless, recent studies on Cenozoic isocrinids from the Southern Hemisphere have demonstrated that the timing of migration to the deep sea was not synchronous globally (Whittle et al., 2018). The same is true for some bourgeticrinids that remained in shallow water into the Cenozoic (Zamora et al., 2018). Thus, the impact of the MMR on crinoids is different depending on the order of crinoids in question and the geographic area. In the case of cyrtocrinids, there is little information about their evolutionary history.

All specimens in which a complete calyx is available preserve pits and scratches on the stereom surface (Fig. 10). These pits are elliptical in shape and sometimes appear in pairs with a dimension of ca. 2 mm in length. They are on both the stem (Fig. 10C) and the calyx (Fig. 10A, B). Similar marks in modern and ancient crinoid assemblages have been interpreted as bite marks compatible with those produced by modern cidaroids (Baumiller et al., 2010); although as Gorzelak and Salamon (2009) pointed out the differentiation between cidaroid damage and damage by others predators has not been well identified, and other durophages cannot be excluded. In fact one of the studied specimens (Fig. 7A, B) consists of a cup with articulated columnals that has bites in both cup and columnals. This might be interpreted as a result of fish predation similar to cases described by Salamon and Gorzelak (2010, Fig. 6A-C). In the faunas studied here, cidaroids appear commonly in the same formation (Fig. 5I, J), and they are likely one of the main modern predators of crinoids (Baumiller et al., 2010). The fact that all studied cyrtocrinids appear with associated marks strongly suggest that predation was very common in the shallow marine environments where they lived.

Modern forms of cyrtocrinids all inhabited relatively deep areas exceeding 100 m and reaching 900 m deep (Donovan and Pawson, 2004). During the Jurassic the habitats of cyrtocrinids were rather different with forms living in relatively deep water exceeding 200 m depth in some cases (Hess, 2006; Charbonnier et al., 2007; Zatón et al., 2008) but also ranging into shallow environments (Hess and Spichiger, 2001; Salamon and Gorzelak, 2007). Cretaceous cyrtocrinids from the Albian onward are rare fossils. Shallow-water high energetic deposits like the Shenley Limestone (England) have contain cyrtocrinid taxa associated with millericrinids and isocrinids (Hess and Gale, 2010), but the sedimentological interpretation of the Shenley Limestone is controversial (see discussion in Hess and Gale, 2010). The presence of cyrtocrinids associated

Complete calyx with three columnals attached in lateral (F, G) and oral (H) views (specimen MPZ2021/347). I, J. Calyx in lateral (I) and oral (J) views (specimen MPZ2018/484). Note characteristic ornamentation. K, L. poorly preserved calyx in lateral (K) and oral (L) views (specimen MPZ2021/349). Specimens D-E, I-J are from Irañeta 1. Specimens A-E, F−H, K-L are from Irañeta 2. Scale bars represent 2 mm in A-C, E-L; 1 mm in D.
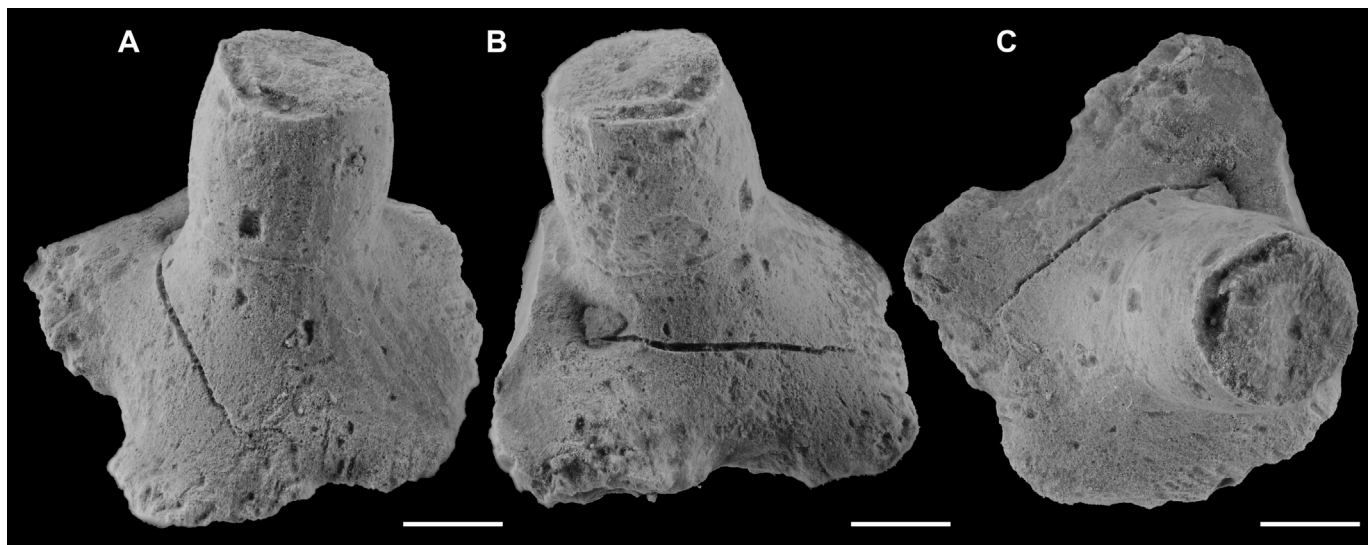
Fig. 9. Attachment structure of *Proholopus holopiformis* from the Albian Albeniz unit (Navarre, Spain) (specimen MPZ2021/357, from Irañeta 2), in lateral (A, B) and proximal (C) views. Scale bar represents 5 mm in A; 2 mm in D, H-J; 1 mm in C, E-H. Scale bars represent 2 mm.
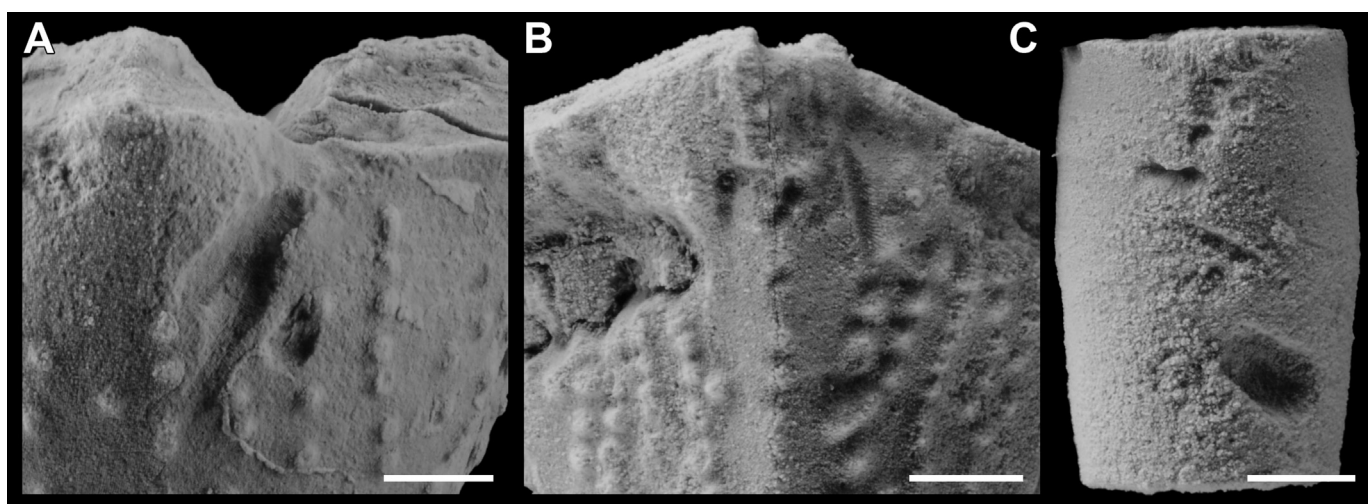

Fig. 10. Pits and scratches in *Proholopus holopiformis* from the Albian Albeniz unit (Navarre, Spain). A. Pair of deep scratches and subcircular pit in the proximal part of the calyx (specimen MPZ2018/484). B. Scratches in the suture of radial plates (specimen MPZ2021/348). C. Pair of scratches and deep oval tip in the third columnal (specimen MPZ2021/348). Scale bars represent 1 mm.

with isocrinids reported herein suggests that both groups still inhabited shallow marine reef environments by the Albian (see above). *Proholopus holopiformis* from Spain was one of the last cyrtocrinid species from shallow marine environments before the migration of the entire order to the deep sea by the Cenozoic (Donovan and Jakobsen, 2004; Eagle, 2005). This might be in part was driven by the Mesozoic Marine Revolution, but further data are necessary to corroborate such an hypothesis.

7. Conclusions

Stalked crinoids from the subclass Articulata are an important component of modern deep sea ecosystems, and they are absent in shallow marine environments. For contrast, the situation in the past is rather different with Articulata being diverse in a wide range of environments. Understanding the distribution of crinoids in the fossil record is sometimes problematic and requires exhaustive complementary information, especially sedimentological analysis.

In the current research we document an exceptional case of the cyrtocrinid crinoid *Proholopus holopiformis* from the Albian successions of Western Pyrenees (Spain). Well preserved specimens complement previous descriptions. Sedimentological data suggest that this is one of the youngest cyrtocrinid crinoids living in shallow water conditions that are estimated to be less than 50 m deep. Specimens with evidence of bites by cidaroid echinoids and durophagous fishes indicate that predation was high for these crinoids in shallow marine environments during the Albian. This support the idea that stalked crinoids migrated to the deep sea as a result of the ongoing Mesozoic Marine Revolution.

References

Arendt, J.A., 1974. Morskije liliji cirtokrinidy (The sea lilies cyrtocrinid). Trudy Paleontologicheskogo Instituta 144, 1–251. (in Russian).

Baumiller, T., Salamon, M., Gorzelak, P., Mooi, R., Messing, C., Gahn, F., 2010. Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. Proceedings of the National Academy of Sciences of the United States of America 107 (13), 5893–5896. https://doi.org/10.1073/pnas.0914199107.

Berkyová, S., Munnecke, A., 2010. "Calcispheres" as a source of lime mud and peloids - evidence from the early Middle Devonian of the Prague Basin, the Czech Republic. Bulletin of Geosciences 85 (4), 585–602. Czech Geological Survey, Prague. https://doi.org/10.3140/bull.geosci.1206.

Bottjer, D.J., Jablonski, D., 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. Palaios 3, 540–560. https://doi.org/10.2307/3514444.

Canudo, J.I., 2018. The collection of type fossils of the Natural Science Museum of the University of Zaragoza (Spain). Geoheritage 10, 385–392.

Charbonnier, S., Vannier, J., Gaillard, C., Bourseau, J.-P., Hantzpergue, P., 2007. The La Voulte Lagerstätte (Callovian): Evidence for a deep water setting from sponge and crinoid communities. Palaeogeography, Palaeoclimatology, Palaeoecology 250, 216–236. https://doi.org/10.1016/j.palaeo.2007.03.013.

De Loriol, P., 1882–1889. Paléontologie française, Sér. 1, Animaux invertébrés. Terrain jurassique: 11, Crinoïdes, Pt. 1 (1882–84) 627 pp.; pt. 2 (1884–89). G. Masson, Paris, p. 580.

Donovan, S.K., Jakobsen, S.L., 2004. An unusual crinoid–barnacle association in the type area of the Danian (Paleocene), Denmark. Lethaia 37, 407–415. https://doi.org/10.1080/00241160410002126.

Eagle, M.K., 2005. A new genus of a fossil crinoid (Cyrtocrinidia: Sclerocrinidae) from Chatham Island, New Zealand. Records of the Auckland Meseum 42, 35–47. https://www.jstor.org/stable/42905875.

Fabricius, K.E., 2011. Factors determining the resilience of coral reefs to eutrophication: a review and conceptual model. In: Dubinsky, Z., Stambler, N. (Eds.), Coral Reefs: An Ecosystem in Transition. Springer Science+Business Media B. V., pp. 493–505. https://doi.org/10.1007/978-94-007-0114-4_28

García-Mondéjar, J., Agirrezabala, L.M., Aranburu, A., Fernández-Mendiola, P.A., Gómez-Pérez, I., López-Horgue, M.A., Rosales, I., 1996. Aptian-Albian tectonic pattern of the Basque-Cantabrian Basin. Geological Journal 31, 13–45. https://doi.org/10.1002/(SICI)1099-1034(199603)31:1<13::AID-GJ689>3.0.CO;2-Y.

García-Mondéjar, J., Fernández-Mendiola, P.A., Agirrezabala, L.M., Aranburu, A., López-Horgue, M.A., Iriarte, E., Martínez de Rituerto, S., 2004. El Aptiense-Albiense de la Cuenca Vasco-Cantábrica. In: Vera, J.A. (Ed.), Geología de España. SGE-IGME, Madrid, pp. 291–296.

Gorzelak, P., Salamon, M.A., 2009. Signs of benthic predation on Late Jurassic stalked crinoids, preliminary data. Palaios 24, 70–73. https://doi.org/10.2110/palo.2008.p08-032r.

Gorzelak, P., Salamon, M.A., Baumiller, T.K., 2012. Predator-induced macroevolutionary trends in Mesozoic crinoids. PNAS 109 (18), 7005–7007. https://doi.org/10.1073/pnas.1201573109.

Gorzelak, P., Salamon, M.A., Trzęsiok, D., Lach, R., Baumiller, T.K., 2016. Diversity dynamics of post-Palaeozoic crinoids–in quest of the factors affecting crinoid macroevolution. Lethaia 49, 231–244. https://doi.org/10.1111/let.12141.

Hallock, P., 1988. The role of nutrient availability in bioerosion: Consequences to carbonate buildups. Palaeogeography, Palaeoclimatology, Palaeoecology 63 (1–3), 275–291.

Hess, H., 2006. Crinoids (Echinodermata) from the Lower Jurassic (Upper Pliensbachian) of Arzo, southern Switzerland. Schweizerische Paläontologische Abhandlungen 126, 1–144.

Hess, H., Spichiger, P.U., 2001. *Argoviacrinus rarissimus* n. g. n. sp., a new crinoid (Echinodermata) from the Middle Oxfordian of northern Switzerland. Eclogae Geologicae Helvetiae 94, 489–494.

Hess, H., Gale, A.S., 2010. Crinoids from the Shenley Limestone (Albian) of Leighton Buzzard, Bedfordshire, UK. Journal of Systematic Palaeontology 8 (3), 427–447. https://doi.org/10.1080/14772019.2010.484942.

Hess, H., Messing, C.G., 2011. In: Selden, P. (Ed.), Treatise on Invertebrate Paleontology Part T, Echinodermata 2, Revised, Crinoidea 3. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 1–261.

Jaekel, O., 1907. Ueber die Korperform der Holopocriniten. Neues Jahrbuch fuer Mineralogie, Geologie, Palaontologie, Festband 1907, 272–309.

Jäger, M., 1982. Seltene Crinoiden aus der Oberkreide der Umgebung von Hannover. Berichte der naturhistori-schen Gesellschaft Hannover 125, 61–87.

Lertxundi, D., García-Mondéjar, J., 1998. Facies and constructional dynamics of an Albian carbonate pinnacle (Aitzondo buildup, Aralar, Basque-Cantabrian Basin). 15th International Sedimentological Congress, Alicante. In: Cañaveras, et al. (Eds.), Abstracts of the 15th Sedimentological Congress, pp. 500–501.

López-Horgue, M., 2004. Geología de Aralar, p. 17. http://barandiaran.aranzadi.eus/ineditos.htm.

López-Horgue, M., Aranburu, A., Fernández-Mendiola, P.A., García-Mondéjar, J., 1993. Existencia de una plataforma carbonatada entre materiales terrígenos de mar somero (Karrantza-Trucíos, Bizkaia). Geogaceta 13, 65–68.

López-Horgue, M.A., Hernández-Samaniego, A., Baceta-Caballero, J.I., Faci-Paricio, E., Larrañaga-Sancena, M.J., 1997. Mapa geológico de Navarra a escala 1: 25.000, hoja 114-II (Uharte-Arakil). Gobierno de Navarra, servicio de obras públicas, Pamplona.

López-Horgue, M.A., Lertxundi-Manterola, D., Baceta-Caballero, J.I., 1996. Evolución sedimentaria del episodio mixto carbonatado-terrígeno del Albiense Superior-Cenomaniense Inferior entre Altsasu (Nafarroa) y Asparrena (Araba): la Unidad Albeniz. Príncipe de Viana 14–15, 81–96.

López-Horgue, M.A., Owen, H.G., Rodríguez-Lázaro, J., Orue-Etxebarria, X., Fernández-Mendiola, P.A., García-Mondéjar, J., 1999. Late Albian-Early Cenomanian stragigraphic succession near Estella-Lizarra (Navarra, central northern Spain) and its regional and interregional correlation. Cretaceous Research 20, 369–402. https://doi.org/10.1006/cres.1999.0162.

López-Horgue, M.A., Owe, H.G. in prep. Early late Albian Mortoniceratinae (Ammonitina, Brancoceratidae) from the Basque-Cantabrian Basin (Western Pyrenees).

Manni, R., Nicosia, U., 1990. *Psalidocrinus zitti* n. sp., cyrtocrinid crinoid from the Lower Tithonian of the Central Apennines. Geologica Romana 24, 79–86.

Manni, R., Nicosia, U., Szabó, J., 1992. Late Jurassic crinoids from the Eperkés-hegy (Bakony Mts., Hungary). Fragmenta Mineralogica et Palaeontologica 15, 115–137.

Miller, J.S., 1821. A natural history of the Crinoidea or lilyshaped animals, with observation on the genera Asteria, Euryale, Comatula, and Marsupites. Bryan & Co., Bristol, p. 274.

Pomar, L., 2001. Types of carbonate platforms: a genetic approach. Basin Research 13, 313–334.

Rasmussen, H.W., 1961. A monograph on the Cretaceous Crinoidea. Biologiske Skrifter udgivet af Det Kongelige Danske Videnskabernes Selskab 12 (1), 1–428.

Rasmussen, H.W., 1978. Articulata. In: Moore, R.C., Teichert, C. (Eds.), Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea 3, T813- T928, T938-T1027. Geological Society of America & University of Kansas Press, Boulder & Lawrence.

Remeš, M., 1902. Nachträge zur Fauna von Stramberg, VI. Crinoiden-. Asteriden- und Echinoiden-resten aus dem Weissen Kalsktein von Stramberg. Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients 14, 195 (Wien).

Romano, M., Manni, R., Nicosia, U., 2016. Phylogenetic analysis of cyrtocrinid crinoids and its influence on traditional classifications. Journal of Mediterranean Earth Sciences 8, 1–21. https://doi.org/10.3304/JMES.2016.001.

Rouse, G.W., Jermiin, L.S., Wilson, N.G., Eeckhaut, I., Lanterbecq, D., Oji, T., Young, C.M., Browning, T., Cisternas, P., Helgen, L.E., 2013. Fixed, free, and fixed: the fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian–Triassic origin. Molecular Phylogenetics and Evolution 66, 161–181. https://doi.org/10.1016/j.ympev.2012.09.018.

Salamon, M.A., 2008. Jurassic cyrtocrinids (Cyrtocrinida, Crinoidea) from extra-Carpathian Poland. Palaeontographica Abt. A 285, 77–99. https://doi.org/10.1127/PALA/285/2008/77.

Salamon, M.A., Gorzelak, M.A., 2007. Evidence of shallow-water cyrtocrinids (Crinoidea) from the Callovian of Poland. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 244, 257–260. https://doi.org/10.1127/0077-7749/2007/0244-0257.

Salamon, M., Gorzelak, P., 2010. Late Cretaceous crinoids (Crinoidea) from Eastern Poland. Palaeontographica Abt. A 291, 1–43. https://doi.org/10.1127/pala/291/2010/1.

Salamon, M.A., Gajerski, A., Gorzelak, P., Łukowiak, M., 2007. A new plicatocrinid crinoid, *Tetracrinus jagti*, from the Cenomanian (Upper Cretaceous) of southern Poland. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 245, 179–183. https://doi.org/10.1127/0077-7749/2007/0245-0179.

Salamon, M.A., Gorzelak, P., Zatoń, M., 2009. In quest of cyrtocrinid origins: Evidence from Late Triassic ossicles from the Tatra Mountains. Acta Palaeontologica Polonica 44 (1), 171–174. https://doi.org/10.4202/app.2009.0119.

Sieverts-Doreck, H., 1952. Millericrinida. In: Moore, R.C., Lalicker, C., Fischer, A.G. (Eds.), Invertebrate Fossils. McGraw-Hill, New York, p. 614.

Stanton Jr., R.J., 1967. Factors controlling shape and internal facies distribution of organic carbonate buildups. Bulletin of the American Association of Petroleum Geologists 51, 2462–2467.

Versteegh, G.J.M., Servais, T., Streng, M., Munnecke, A., Vachard, D., 2009. A discussion and proposal concerning the use of the term calcispheres. Palaeontology 52 (part 2), 343–348. https://doi.org/10.1111/j.1475-4983.2009.00854.x.

Vilas, L., Masse, J.P., Arias, C., 1995. Orbitolina episodes in carbonate platfrom evolution: the early Aptian model from SE Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 119, 35–45. https://doi.org/10.1016/0031-0182(95)00058-5.

Wiedmann, J., 1962. Ammoniten aus der Vascogotischen Kreide (Nordspanien), I. Phylloceratina, Lytoceratina. Palaeontographica Abt. A 118, 119–237.

Whittle, R.J., Hunter, A.W., Cantrill, D.J., McNamara, K.J., 2018. Globally discordant Isocrinida (Crinoidea) migration confirms asynchronous Marine Mesozoic Revolution. Communications Biology 1 (46), 1–10. https://doi.org/10.1038/s42003-018-0048-0.

Wright, V.P., Burchette, T.P., 1996. Shallow water carbonate environments. In: Reading, H.G. (Ed.), Sedimentary Environments: Processes, Facies and Stratigraphy. Blackwell Science Ltd., Oxford, pp. 325–394.

Zamora, S., Aurell, M., Veitch, M., Saulsbury, J., Lopez-Horgue, M.A., Ferratges, F.A., Arz, J.A., Baumiller, T.K., 2018. Environmental distribution of post-Palaeozoic crinoids from the Iberian and south-Pyrenean basins (NE Spain). Acta Palaeontologica Polonica 63, 779–794. https://doi.org/10.4202/app.00520.2018.

Zatoń, M., Salamon, M.A., Kaźmierczak, J., 2008. Cyrtocrinids (Crinoidea) and associated stalked crinoids from the Lower/Middle Oxfordian (Upper Jurassic) shelfal deposits of southern Poland. Geobios 41, 559–569. https://doi.org/10.1016/j.geobios.2007.10.009.

Žítt, J., 1974. Sclerocrinus Jaekel, 1891 and Proholopus Jaekel, 1907. (Crinoidea, Cyrtocrinida) from the Lower Cretaceous of Stramberk (Czechoslovakia). Sborník Geologických Věd: Paleontologie 16, 7–32.