

SYSTEMATICS, TAPHONOMY, AND PALEOECOLOGY OF  
MILLERICRINIDS (MILLERICRINIDA, ARTICULATA, CRINOIDEA)  
FROM THE LATE JURASSIC OF SPAIN

BY

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*Abstract* — Millericrinids constitute an order of extinct articulate crinoids that range from the Middle Triassic to the Late Cretaceous. Based on partially articulated material comprising calyces, columns, and holdfasts, six species (one of them new) belonging to five different genera are described from the Late Jurassic of Spain for the first time. They include *Angulocrinus tomaszi* n. sp. from the Yatova Formation (middle-upper Oxfordian); and *Millericrinus milleri*, *Liliocrinus polydactylus*, *Pomatocrinus hoferi*, *Pomatocrinus* cf. *mespiliformis*, and *Apiocrinites* cf. *parkinsoni* from the Sot de Chera Formation (Kimmeridgian). *A. tomaszi* n. sp. lived in association with sponges and other invertebrates in relatively shallow, open platform areas, with variable depths near storm wave base. The assemblage from the Sot de Chera Formation is more diverse and preliminary taphonomic and sedimentological information suggest that these millericrinids lived in high-energy conditions from shore-face environments and were transported and buried to the off-shore basin due to successive storm events. These faunas have a high number of specimens colonized by diverse sclerobionts, that combined with the presence of eroded material belonging to columnals suggest a prolonged biostratinomic phase for some specimens. Additionally, some specimens have swollen stems likely recording parasitism. The reported taxa also provide important data on the palaeobiogeographic distribution of millericrinids during the Jurassic showing that the Iberian material has affinities with other European localities.

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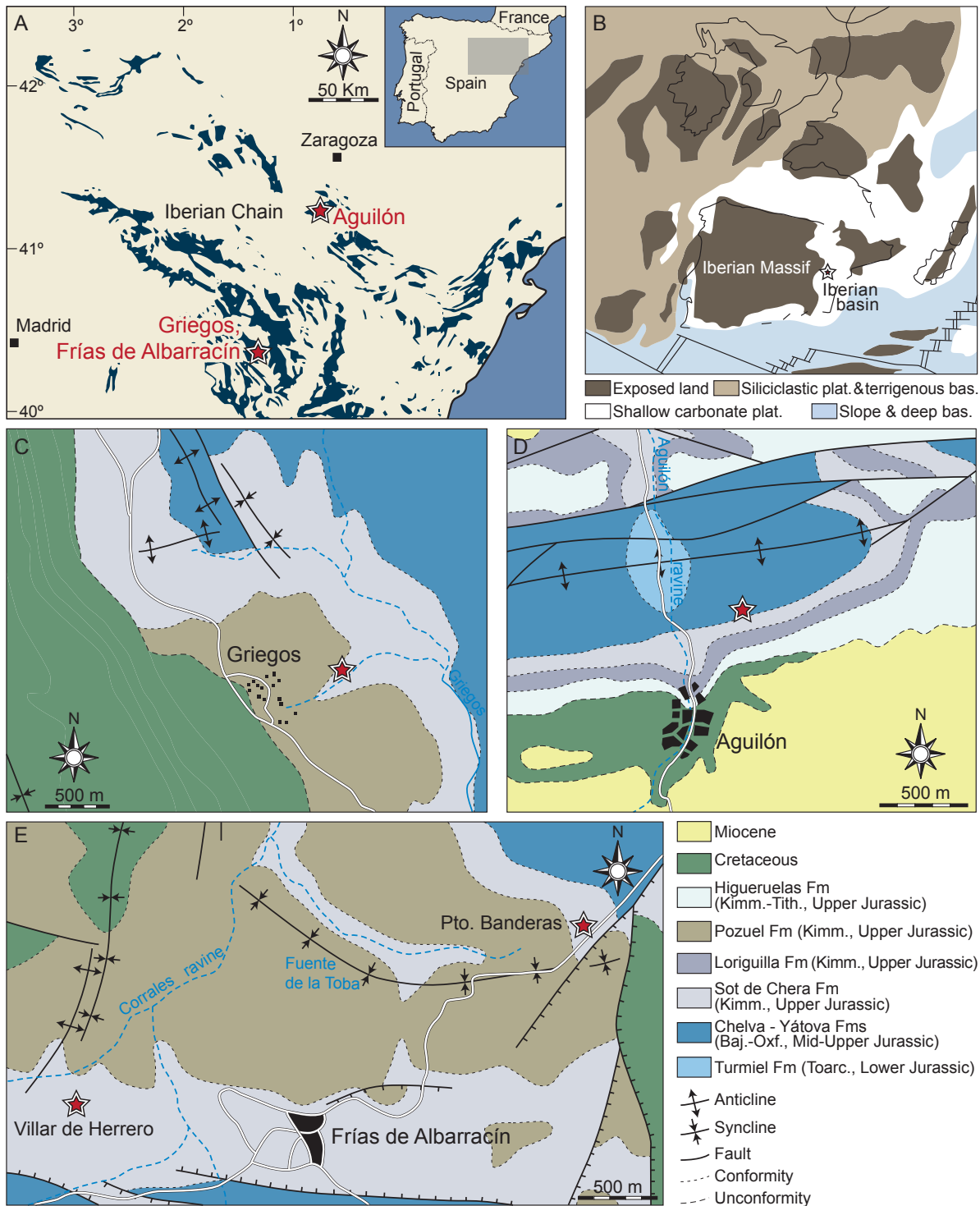


FIGURE 1 — A, distribution of Jurassic outcrops (blue) in NE Spain with indication of studied localities (red stars) (modified from Aurell et al., 2010, fig. 2). B, paleogeography of Western Europe during the Late Jurassic (modified from Dercourt et al., 1993, map 6 Early Kimmeridgian). C–E, geological maps of the studied outcrops with detailed indication of main localities. Abbreviations: Baj., Bajocian; bas., basins; Kimm., Kimmeridgian, Oxf., Oxfordian; plat., platforms; Tith., Tithonian; Toarc., Toarcian.



FIGURE 2 — Field photographs of the studied outcrops. **A**, section in the road-cut of Puerto de las Banderas. Fossiliferous levels containing crinoids appear in the marly intervals of the top of the Sot de Chera Formation. **B**, **C**, Villar de Herrero outcrop (**B**), with indication of some stem fragments by arrows (**C**). **D**, locality of Griegos with indication of the two fossiliferous levels containing crinoids. **E**, locality of Aguilón 5 with fossiliferous levels of the Yatova Formation that contain crinoid material (outcrop indicated by an arrow). **F**, partially buried specimen of *Millericrinus milleri* from the Griegos 1 locality. **G**, complete calyx of *Liliocrinus polydactylus* from the Puerto de las Banderas locality. Note that resedimented oolites are common in the surrounding sediment. **H**, partially articulated calyx of *Apiocrinites* cf. *parkinsoni* and stem fragments from the Villar de Herrero locality.

## INTRODUCTION

Post-Palaeozoic crinoids includes most post-Paleozoic taxa traditionally considered articulate, including approximately 600 extant species (Wright, et al., 2017). This group comprises eight orders (sensu Hess and Messing, 2011), some of which are present in modern marine ecosystems (Comatulida, Isocrinida, Hyocrinida, Cyrtocrinida) and some including only extinct forms (Holocrinida, Encrinida, Millericrinida, Roveacrinida). Molecular clocks estimate that Articulata resulted from the diversification of a lineage that passed through the Permian-Triassic extinction event (Rouse et al., 2013). Whereas recent phylogenetic studies start to clarify the position of modern groups (Rouse et al., 2013), extinct taxa are more problematic; however, fossils provide an important source of morphological and palaeobiogeographical information helping us understand the whole evolutionary history of crinoids.

Millericrinids are characterized among other features by five basals, five radials, a column cylindrical with radiating crenulae, and absence of cirri (sensu Hess and Messing, 2011). Species identification based on incomplete material lacking dorsal cups is problematic (Salamon and Zatoń, 2005; Krajewski et al., 2019). The problem increases with the presence of a cylindrical column with radiating crenulae is also a feature convergent with other crinoid lineages such as isocrinids (Oji and Kitazawa, 2008), posing more problems in the systematics of crinoids based on isolated columns. Thus, calyx material and proximal columns are the most diagnostic parts in millericrinid systematics (Hess and Messing, 2011).

Millericrinids range from the Anisian (Triassic) to the Cenomanian (Cretaceous; Stiller, 2000; Gorzelak and Salamon, 2006; Hagdorn, 2011; Hess and Messing, 2011) and are a typical component in the Jurassic assemblages from Europe. In the Cretaceous, the group experienced a significant decline in diversity and they have been reported in only a few assemblages from France, Switzerland, Spain, Poland, and UK (Rasmussen, 1961; Gorzelak and Salamon, 2006; Hess and Gale, 2010). During the late Jurassic, shallow epicontinental seas covered wide areas of Western Europe (Fig. 1B) with carbonate sedimentation dominating the Iberian Basin, facing the Tethys Ocean to the west on the western margin of the Iberian Plate (e.g., Dercourt et al., 1993). This was an ideal area for the development of shallow carbonate platforms hosting a wide diversity of benthic organisms, including crinoids (Pomar et al., 2015). Although crinoids are an important component in Jurassic marine assemblages, the Iberian fauna has received little attention. Millericrinids are common during the Late Jurassic, but few general papers have cited their presence in Spain. These include Olagüe (1936) and Fezer (1988), who cited *Millericrinus* and *Apiocrinus* respectively in the Upper Jurassic. Several geological map memoirs from the Spanish Geological Survey also commented on the presence of millericrinids in several areas (see Abril and Rubio, 1977, among others). Hess and Messing (2011) also cited the presence of *Pomatocrinus* and *Apiocrinites* in Spain, but never figured any material. Finally, Zamora

et al., (2018) first reported and figured a rich Late Jurassic fauna comprising cyrtocrinids, comatulids, isocrinids and millericrinids, but none of them received detailed systematic treatment.

The aim of this work is to formally describe the millericrinid fauna of the Late Jurassic of Northeastern Spain, which include calyx material and proximal columns. A large number of columnals and holdfast are also present in the described localities, and they provide important paleoecological and taphonomical information that increase our understanding of the occurrence of these crinoids. Because millericrinids constitute an extinct order of crinoids, their description will provide morphological information that can improve the knowledge of their systematic position, palaeoecology, and palaeobiogeographical distribution.

## MATERIAL AND METHODS

Specimens described in this study were surface collected directly from the outcrops as macrofossils during the last decade (Fig. 2F–H). Crinoid remains are very common in the sampled outcrops, but thecal material, especially complete calyces, are rare. For perspective, if one person collects intensely for eight hours they will recover one specimen on average. Most specimens were covered by marly material and were prepared using potassium hydroxide (KOH), and later neutralized with hydrochloric acid (10%). Specimen were photographed using a Nikon D7100 equipped with AF-S Micro NIKKOR 60 mm objective after coating with ammonium chloride to increase contrast. Specimens are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ; Canudo, 2018).

Most specimens from the Sierra de Albarracín localities have sclerobionts on skeletal elements that indicate postmortem colonization. Clear examples include sclerobionts on articulating surfaces of the brachials, columnal articulations, and attachment parts of the roots. Some others appear intensively eroded and have rounded edges. The encrustation and erosion observations point to a complex taphonomic history (see discussion below) and not in situ burial of specimens.

## GEOLOGICAL SETTING AND LOCALITIES

All specimens come from two formations and areas in the Iberian Ranges (Fig. 1A). Specimens of *Angulocrinus tomaszi* n. sp. were collected from the Yatova Formation (Upper Jurassic) in the surroundings of Aguilón (Zaragoza, Iberian Range). This corresponds with locality Aguilón 5 of Meléndez (1989) or its lateral equivalent (Fig. 1D, 2E). Although millericrinid columnals are common in the Yatova Formation, only this locality has provided important diagnostic material comprising the proximalmost columnal. This formation is a sponge-limestone dominated unit, which has been dated as middle-upper Oxfordian and contains abundant echinoderm remains, including a diverse crinoid fauna (Zamora et al., 2018). Here, the Yátova Formation

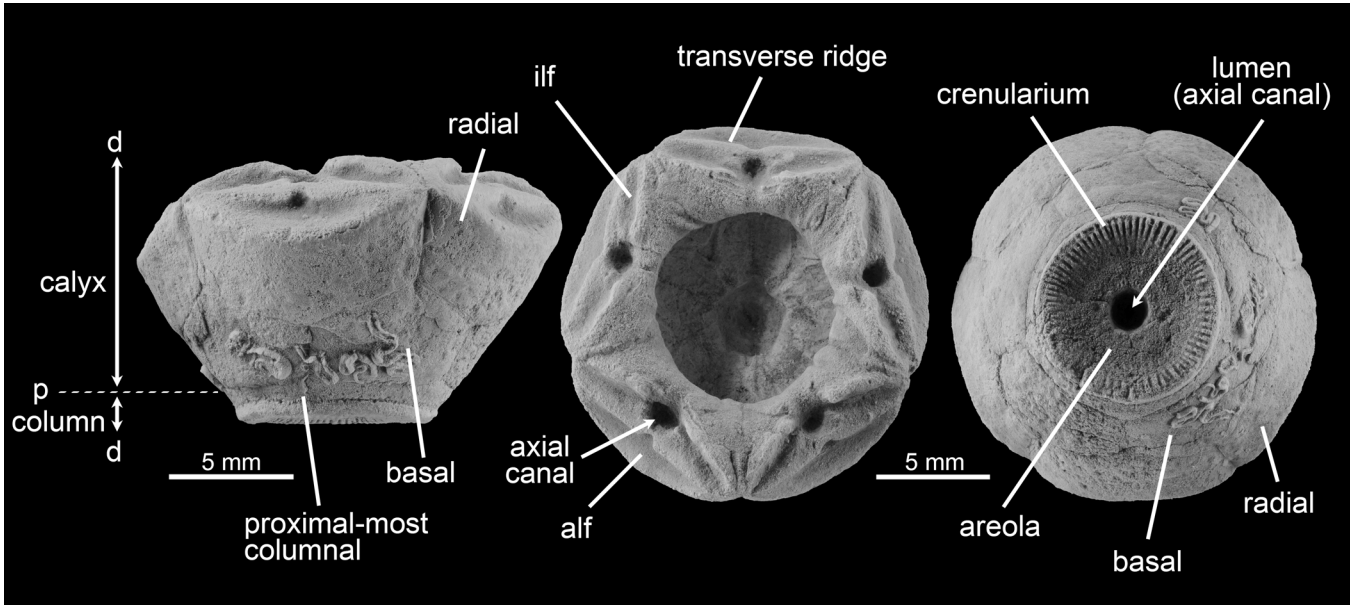


FIGURE 3 — Terminology for millericrinids used in the text. Terms follow Hess and Messing (2011). This is a photograph of *Liliocrinus polydactylus* (specimen MPZ2021/180). Abbreviations: *alf*, aboral ligament fossae; *d*, distal; *ilf*, interarticular ligament fossae; *p*, proximal.

consists of tabular to nodular limestone with marly interbeds, locally forming decimeter to meter-thick, upward-thickening sequences (Ramajo and Aurell, 2008). The main components are siliceous sponges (*Dictyida*, *Lychniskida*, and *Lithistida*, in descending order of abundance: e.g., Deusch et al., 1990) of variable morphologies (dish, cup, and tubular), typically broken and preserved in graded beds. They are associated with a microbial crust and encrusting organisms such as annelids (serpulids, *Terebella*), bryozoans, benthic foraminifera (nubecularids, *Bullopora*), and *Tubiphytes*. Also common are tuberoids and encrusted fragments of sponges. Locally, ammonites, belemnites, bivalves, brachiopods, echinoids, asterozoans, foraminifera, ostracodes, ahermatypic corals, and crinoids can be common. The maximum age range of the Yátova Formation is middle Oxfordian (i.e., lower Transversarium Biozone) to upper Oxfordian (i.e., lower Planula Biozone, Planula Subzone). The locality of Aguilón 5 represents a small outcrop that includes the transition between the Bifurcatus and Bimammtum Biozones, which corresponds with the middle-upper Oxfordian transition (sensu Meléndez, 1989).

Other described material comes from the Sot de Chera Formation (Upper Jurassic) in Griegos and Frías de Albarracín (Teruel, Iberian Range; Fig. 1A). Two localities in Frías de Albarracín (namely Puerto de las Banderas and Villar de Herrero) and two stratigraphic levels in Griegos (Griegos 1 and 2) have provided most of the described material (Fig. 1C, E; 2A–D). The localities of Villar de Herrero (Fig. 2B, C) and Griegos (Fig. 2D) are stratigraphically lower in the Sot de Chera Formation, and Puerto de las Banderas consists of the higher levels of the Sot de Chera Formation (Fig. 2A). This formation consists of thick marly dominated successions,

including decimeter-thick siliciclastic and skeletal-rich limestone intercalations. In the three localities, crinoids are abundant in skeletal-rich horizon, which includes ammonites of Galar subzone (Planula Zone) (see Zamora et al., 2018). This horizon also contains resedimented ooids from more proximal and shallow carbonate shoal environments (Pomar et al., 2015), which have implications to explain the occurrence of the crinoid material (see below). The studied bioclastic and marly intervals contain abundant echinoderm remains, including a diverse crinoid fauna. Here, the Sot de Chera Formation consists of a marly progradational wedge-shaped deposits with siliciclastics derived from the emergent areas located to the west, including abundant graded skeletal accumulations interpreted as tempestites (Aurell et al., 2003, 2010). The main skeletal components found in these mid-ramp deposits are bivalves, echinoderms, gastropods, brachiopods, siliceous sponges, serpulids, benthic foraminifera, ahermatypic colonial and solitary corals, belemnites, and ammonites. Species of crinoids per locality are summarized in Table 1.

### SYSTEMATIC PALEONTOLOGY

Descriptive terminology follows Rasmussen (1978) and Hess and Messing (2011). Classification follows Hess and Messing (2011). Main morphological terms are synthesized in Figure 3.

Class CRINOIDEA Miller, 1821  
 Subclass ARTICULATA Miller, 1821  
 Order MILLERICRINIDA Sieverts-Doreck, 1952  
 Family MILLERICRINIDAE Jaekel, 1918

TABLE 1 — Occurrence of millericrinid crinoid genera in the different localities. The locality of Pozuel correspond to the data presented in Zamora et al. (2018). \*: present as articulated specimens. +: present as disarticulated material from the calyx. -: absent.

Locality	Taxa				
	<i>Apiocrinites</i>	<i>Liliocrinus</i>	<i>Millericrinus</i>	<i>Pomatocrinus</i>	<i>Angulocrinus</i>
Pto. Banderas	*	*	-	+	-
Villar Herrero	*	-	-	*	-
Griegos 1	-	-	*	+	-
Griegos 2	-	-	-	+	-
Pozuel	-	-	-	*	-
Aguilón	-	-	-	-	*

*Diagnosis.*— Cup low cone, bowl, or globe shaped. Sharp distinction between cup and column in most forms. Few or generally no interradial plates (*sensu* Hess and Messing, 2011).

*Remarks.*— This family of only Jurassic forms include genera such as *Millericrinus*, *Angulocrinus*, and *Liliocrinus* among others. *Millericrinus*, *Pomatocrinus*, and *Orbignycrinus* have a very expanded calyces which clearly differ from the conical shape expressed in *Angulocrinus*, *Ailsacrinus*, and *Liliocrinus*. All forms with the exception of *Ailsacrinus* have large, modified attachment structures (Taylor, 1983; Hunter et al., 2016).

Genus *Angulocrinus* Rollier, 1911

*Type species.*— *Millericrinus nodotianus* d'Orbigny, 1841 by original designation.

*Diagnosis.*— Cup truncated conical, not tumid, increasing in diameter upward from edge of enlarged uppermost columnal, which is more or less included as a rounded to 5-sided proximale in cup with a 5-sided pyramidal proximal facet toward the basals. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Proximal part of column 5-sided with columnals that may alternate in height and diameter. Mesistele mostly cylindrical, commonly ornamented with tubercles, spines, or strands of stereom attached to each other; attachment by radicular cirri as creeping roots or runners along the substrate but also by terminal root. Columnal articular facets with radiating crenulae commonly arranged in five groups, especially in proximal part of the column. Crenulae may in some species, be restricted to a marginal zone of facet (*sensu* Hess and Messing, 2011).

*Remarks.*— The present material is assigned to *Angulocrinus* based on the presence of enlarged uppermost columnal and crenulae arranged in five groups present in the proximal column. Hess and Messing (2011) indicated that

proximal part of the column is pentagonal, but in the studied material only the proximalmost columnal facet is slightly pentagonal. Its distal facet is circular in outline.

*Angulocrinus tomaszi* n. sp.

Fig. 4

2018 Millericrinida indet. Zamora et al., p. 787, fig. 8C

*Etymology.*— Species honoring Professor Tomasz Baumiller (University of Michigan) for a lifetime dedicated to the study of modern and fossil crinoids; and for his generosity advising and encouraging me to work on post-Palaeozoic crinoids from Spain.

*Type material.*— Holotype includes a proximalmost columnal with second columnal (MPZ2018/472) (Fig. 4A-C). Paratype MPZ2021/178 is a fragment of a column preserving two and a half columnals (Fig. 4D-E).

*Type locality.*— Locality Aguilón 5 from Meléndez (1989).

*Type horizon.*— Yatova Formation, in the transition between the Bifurcatus and Bimammtum Biozones, middle to upper Oxfordian.

*Material.*— Single proximal columnal with second columnal attached and fragment of a column comprising two and a half columnals.

*Diagnosis.*— Proximalmost columnal flanged with five deep aureola separated by large ridges. Deep crenulae restricted to the margins of the areola and separated in five groups.

*Description.*— Proximal facet of the proximalmost columnal flat with a diameter of 8 mm, and 4.5 mm in height, and pentalobate in shape with a wide pentagonal lumen (ca. 2 mm). Five deep articular facets (areolas) with crenularium deep and restricted to the margins. Scattered granules in the areolas. Margins smooth without ornamentation. Distal

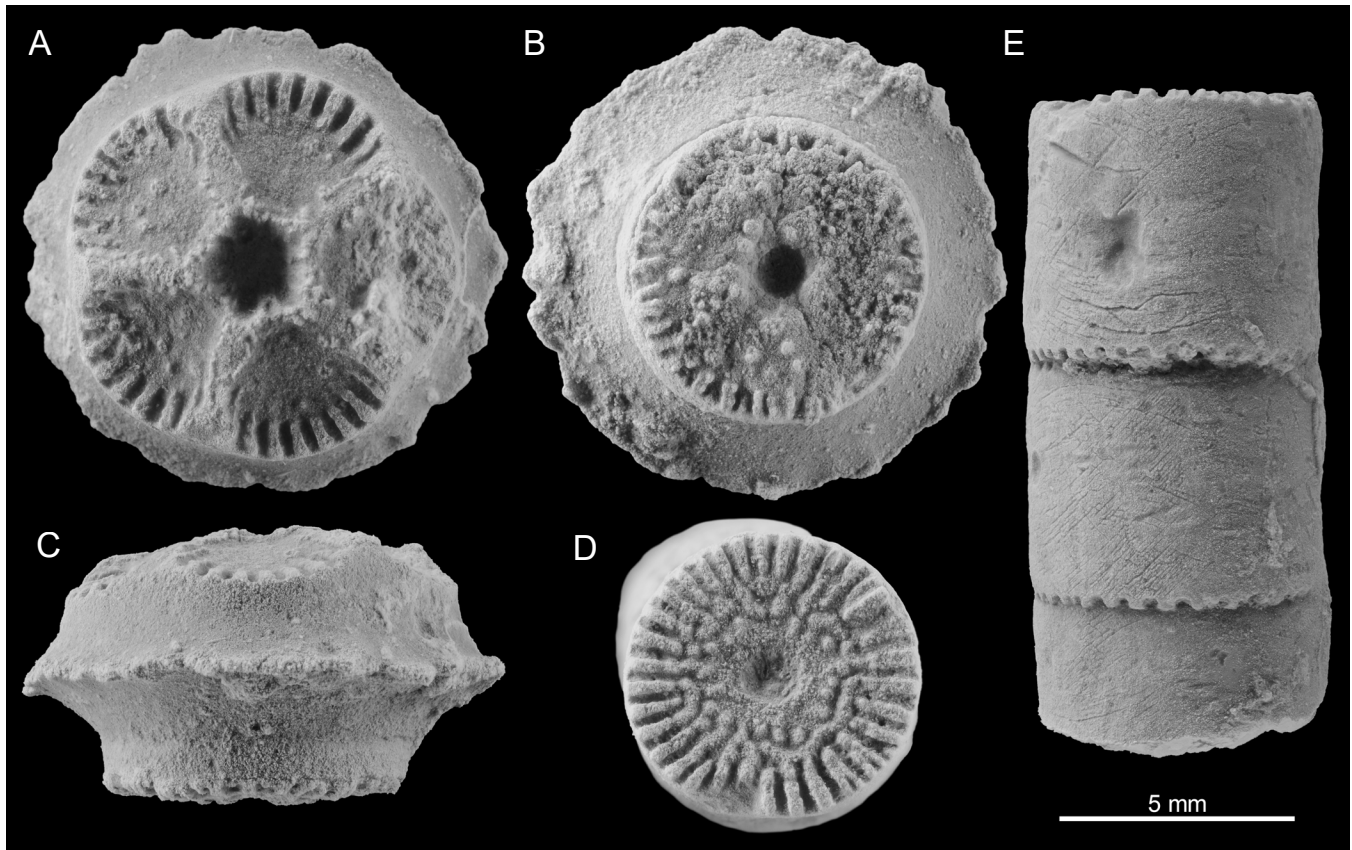


FIGURE 4—*Angulocrinus tomaszi* n. sp., photographs of specimens from the Aguilón 5 locality in the Yatova Formation (Oxfordian, Late Jurassic). A–C, photographs of specimen MPZ2018/472 that corresponds to a proximal-most stem columnal with second columnal attached in proximal (A), distal (B), and lateral (C) views. D, E, photographs of specimen MPZ2021/178 that corresponds to columnals in axial (D) and lateral views (E).

facet of the proximalmost columnal unknown, but probably circular in outline and with marginal crenulae. Distal facet of first columnal circular in outline, with crenularium restricted to the margins and circular, wide lumen. Granules scattered in the articular facet.

Column externally smooth, with columnals that are slightly higher than wide; marginal crenularium that transform into granules to the lumen.

*Remarks.*— Only the proximal column with first columnal and one additional columnal is preserved. In the same level providing the proximalmost columnal there are also columnals with typical crenulae and morphology of millericrinids; but only the figured specimens agree with the granules and crenulae observed in the described first columnal attached to the proximal columnal, thus this is a strong argument suggesting that this column belong to the same taxa. *Angulocrinus nodotianus*, the type species, lack a flanged proximal columnal, but has a column that has in some specimens flanged nodals (see de Loriol, 1884). Proximal part of uppermost columnal is pentagonal and with crenulae arranged in five groups, similar to *A. tomaszi* n. sp. *A. orbigny* (figured in de Loriol, 1884, pl. 116, 1c) also preserves

proximal most columnal and basals; *A. tomaszi* n. sp. differs from the later in having a flanged proximal columnal. Proper comparison with most species assigned to *Angulocrinus* based on columns only is problematic, especially because Hess and Messing (2011) pointed out that columns are highly variable.

#### Genus *Millericrinus* d'Orbigny, 1840

*Type species.* *Encrinites milleri* Schlotheim, 1823, under original designation.

*Diagnosis.*— Cup large and pentagonal, very low and wide. Basals form horizontal underside of cup; radials steep (*sensu* Schweigert et al., 2008).

*Remarks.*— *Millericrinus* is a name that has been traditionally used to many millericrinids either based on calyx or stem fragments only. Currently it includes two accepted species based on calyx material. *M. milleri* is the most represented and well-known species, having been recorded in many European localities (see Hess and Messing, 2011). *M. charpyi* is poorly known based on a few specimens described by de Loriol (1884) and considered in Rasmussen (1978).

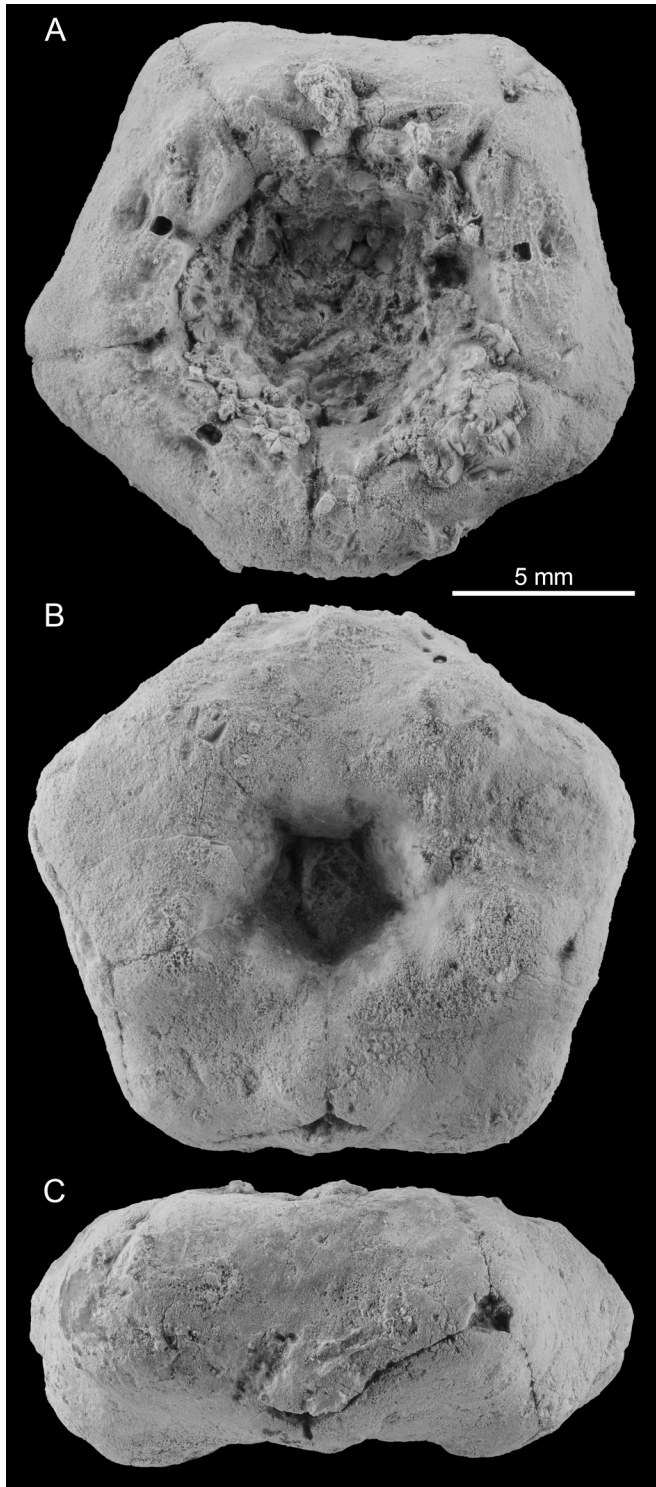


FIGURE 5 —*Millericrinus milleri*, photograph of specimen (MPZ2021/179) from the Griegos 1 locality in the Sot de Chera Formation (Kimmeridgian, Late Jurassic). A–C, complete calyx in oral (A), aboral (B), and lateral (C) views.

*Millericrinus milleri* Schlotheim (1823)

Fig. 5

2008 *Millericrinus milleri* Schweigert et al., fig. 2 (with previous synonymies)

*Material.*— Only one specimen representing a complete calyx (MPZ2021/179).

*Diagnosis.*— Large pentagonal and low cup, with basals forming the floor of the calyx and radials occupying most of the sides of the calyx. Lumen clearly pentagonal. External part of proximal-most columnal lacking bosses.

*Remarks.*— *Millericrinus milleri* is characterized by a large and pentagonal cup which is very low (compared with other millericrinids) and wide. The basal plates form the horizontal underside of the cup. The Spanish specimen follows the aforementioned features and is thus included in this species. De Loriol (1889) figured specimens in different ontogenetic stages in plates 95-96. Large specimens have proportionately smaller facets compared with the total length of the radial plates and large proximal projections (in lateral view) in the articulation of two adjacent radials. Smaller specimens have lower radials and larger arm facets. The described specimen here is very similar to the small specimens described by de Loriol (1889) in its plates 95-96. This was also emphasized by Roux (1978) who did a comparative ontogenetic study of different millericrinids and showed that the shape of the calyx in *M. milleri* is highly dependent on its size. According to Schweigert et al., (2008), *M. charpyi* de Loriol, is the most similar form to *M. milleri*; however, the occurrence of ten oval bosses covering the lateral surface of the cup of *M. charpyi* is the most important diagnostic feature distinguishing this taxon from *M. milleri*.

Genus *Liliocrinus* Rollier, 1911

*Type species.*— *Millericrinus polydactylus* d'Origny, 1841

*Diagnosis.*— Cup low conical to bowl shaped, not tumid, increasing in diameter upward from edge of rather wide, uppermost columnal. Basals and radials large. Radial articular facet low and wide. Synostosis with marginal crenulae between primibrachials 1 and 2, synarthry between secundibrachials 1 and 2. Column cylindrical, proximal columnals slightly increasing in diameter toward cup, not 5-sided. Columnal articular facets covered by radiating crenulae not separated in groups. Proximal articular facet of uppermost columnal more or less pyramidal or conical to almost flat. Attachment by root (sensu Hess and Messing, 2011).

*Remarks.*— Desor (1845) demonstrated that the species first recorded was ambiguous. Later Rasmussen (1978) designated *M. polydactylus* as the type species; a view followed by Hess and Messing (2011) and here. Hess and Messing (2011) distinguished two species in this genus: *L. polydactylus* and *L. munsterianus*. Based on the holotype of *L. polydactylus* (Fig. 7D-F) and comparison with the well-



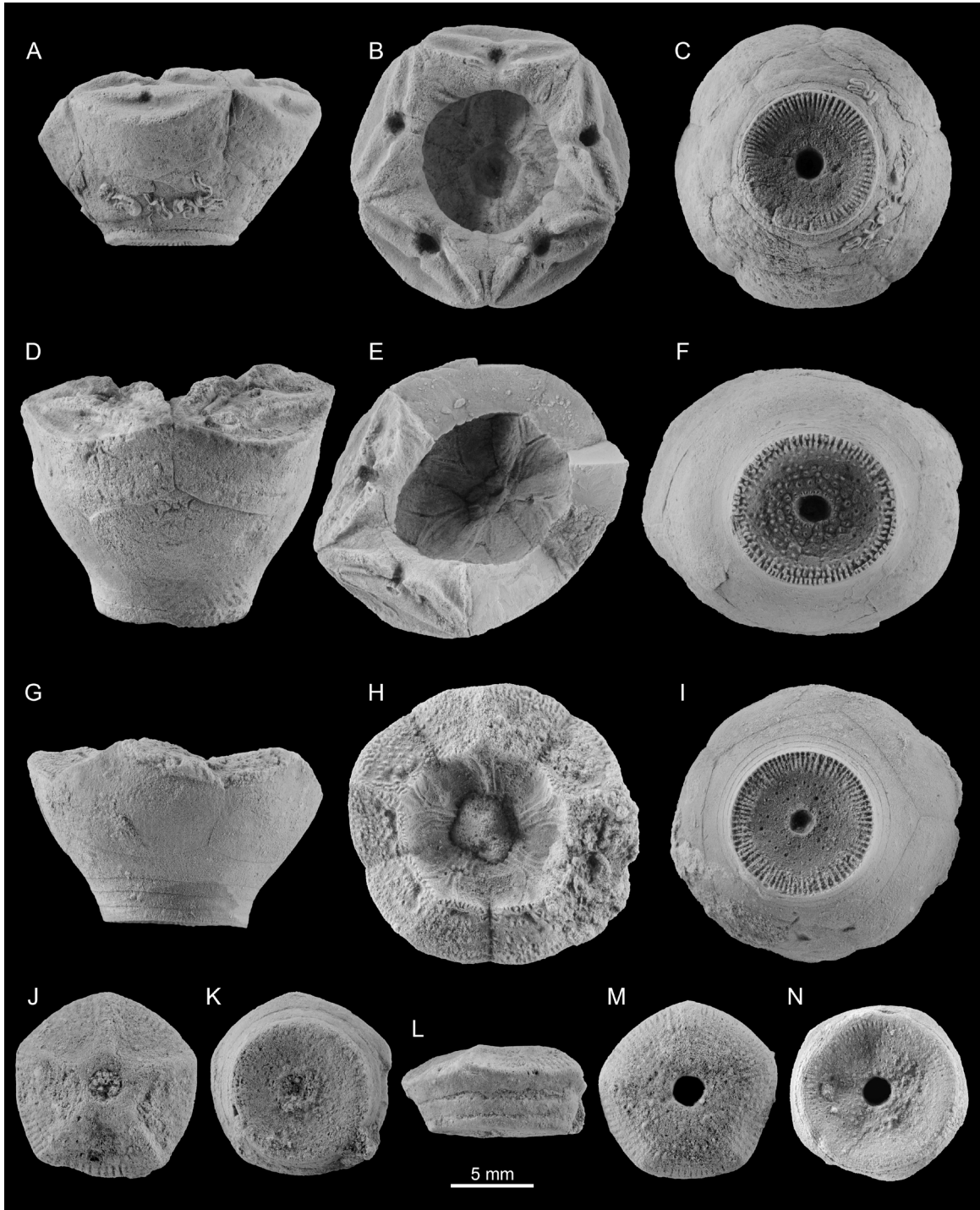


FIGURE 6 — *Liliocrinus polydactylus*, photographs of specimens from the Puerto de las Banderas locality of the Sot de Chera Formation (Kimmeridgian, Late Jurassic). A–C, MPZ2021/180 a complete calyx with first columnal in lateral (A), oral (B), and aboral views (C). D–F, MPZ2021/181, a partially complete calyx with five basals and two radials preserved, and two proximalmost columnals preserved in lateral (D), oral (E), and distal (F) views. Note granules in the articulation facet. G–I, MPZ2021/182, a partial calyx preserving the five basal plates in lateral (G), oral (H), and aboral (I) views. J–L, MPZ2021/183, a proximalmost columnal and second and third columnal in oral (J), aboral (K), and lateral (L) views. M–N, MPZ2021/184, a proximalmost columnal in oral (M) and aboral (N) views.

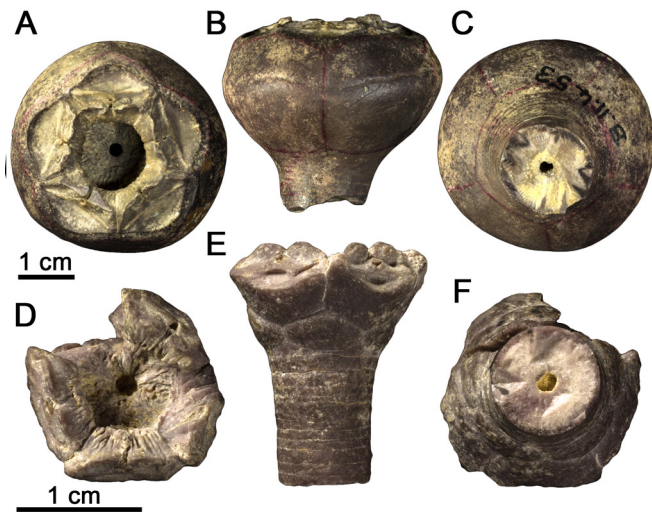


FIGURE 7 — Crinoid specimens from the Late Jurassic of Pointe-du-Chay (France) in the d'Orbigny collection of the MNHN. A–C, holotype of *Pomatocrinus fleuriausianus* (MNHN.F.B11453) in oral (D), lateral (E), and aboral (F) views. D–F, syntype of *Liliocrinus polydactylus* (MNHN.F.R62602) in oral (D), lateral (E), and aboral (F) views. Images courtesy of the Muséum National d'Histoire Naturelle (Paris)

figured material of *L. munsterianus* by de Loriol (1877), it became evident that shapes of the theca in the later is quiet variable in terms of basal and radial morphologies. For these reasons, *L. munsterianus* is treated here as a junior synonym of *L. polydactylus*. *L. polydactylus* is then considered the sole species of *Liliocrinus*.

*Liliocrinus polydactylus* (d'Origny, 1841)

Fig. 6

1877 *Millericrinus munsterianus* de Loriol, pl.VII, figs. 1–15 (with previous synonymies).

1884 *Millericrinus polydactylus* de Loriol, pl. 109, figs. 1–2 (with previous synonymies).

1978 *Liliocrinus polydactylus* Rasmussen, fig. 551, 2h, m.

1978 *Liliocrinus munsterianus* Rasmussen, fig. 551, 2j, k.

2011 *Liliocrinus polydactylus* Hess and Messing, fig. 80, 1a–b.

2011 *Liliocrinus munsterianus* Hess and Messing, fig. 80, 1c–g.

**Material.**— Several complete calyxes (MPZ2021/180, 181, 182) (Fig. 6A–I) with proximal most columnals, and some proximal columnals (MPZ2021/183, 184, 185, 186) (Fig. 6J–N) and a single radial plate (MPZ2021/187). Measurements of calyx material are given in Table 2.

**Remarks.**— Spanish material consists of well-preserved calyxes, proximal columns and probably roots. The calyx material is variable in shape. There are specimens from same

locality and stratigraphic level that have basals higher than radials; and others that have basals lower than radials. This is also observed in the material figured by de Loriol (1877, plate 7). Proximalmost columnal facets have five ridges that separate articulations for the five basals and marginal crenulae. In distal facets of proximal columnals the crenulae turn into fine granules toward the lumen. Granules are also present in the articulation between basals and radials.

Genus *Pomatocrinus* Desor, 1845

**Type species.**— *Encrinites mespiliformis* von Schlotheim, 1820 by original designation.

**Diagnosis.**— Cup large, globe shaped, thick walled, comprised of very large basals, smaller radials, and a rather large proximale surrounding an almost spherical central cavity. Sutures distinct. All cup plates with flat, slightly rough facets. No trace of infrabasals. Radial articular facet large, plenary; articulation with distinct fulcral ridge, aboral and interarticular ligament fossae, and small adoral muscle fossae. Primibrachials meet laterally. Arms divided at primibrachials 2 and more distally; first pinnule on secundibrachial 2. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Proximal most columnal 5-sided, forming aboral pole of spherical cup, and continued as high, 5-sided, truncated pyramid inside basal cirlet to bottom of central cavity; underside has a concave, circular, articular facet to receive finely granulated proximal facet of next columnal, which together with a few succeeding, very low columnals form very short, slightly conical transition to cylindrical column. Columnal articular facets with fine, radiating crenulae, closely placed, not in separate groups; crenulae might be modified to granules in central area (sensu Hess and Messing, 2011).

**Remarks.**— The genus *Pomatocrinus* include several species mostly described by d'Orbigny (1840) and de Loriol (1884, 1887) that have different development of basals and radials (Roux, 1978). Based on the currently known species and apparent changes in ontogeny, it is necessary to perform a morphometric analysis in order to understand changes in shape within and between different species. This is beyond the scope of the current work. Specimens described here include complete calyx, fragments of columns, and holdfasts. Disarticulated specimens including proximalmost columnal that usually appear with fused proximal columnals and isolated calyx plates are also present. Shape of the calyx in described material meets the diagnosis presented by Salamon and Zatoń (2005) and Hess and Messing (2011, see above) and should be assigned to the genus *Pomatocrinus*. The proximal part of the proximalmost columnal has the shape of a truncated pyramid which is higher than in *Liliocrinus* and also lacks crenulae in its proximal facet. These two features are important differences between two genera when only the proximal column is present. There are two clear morphotypes of *Pomatocrinus* in the described material; one includes a complete calyx plus isolated basal plates here considered as

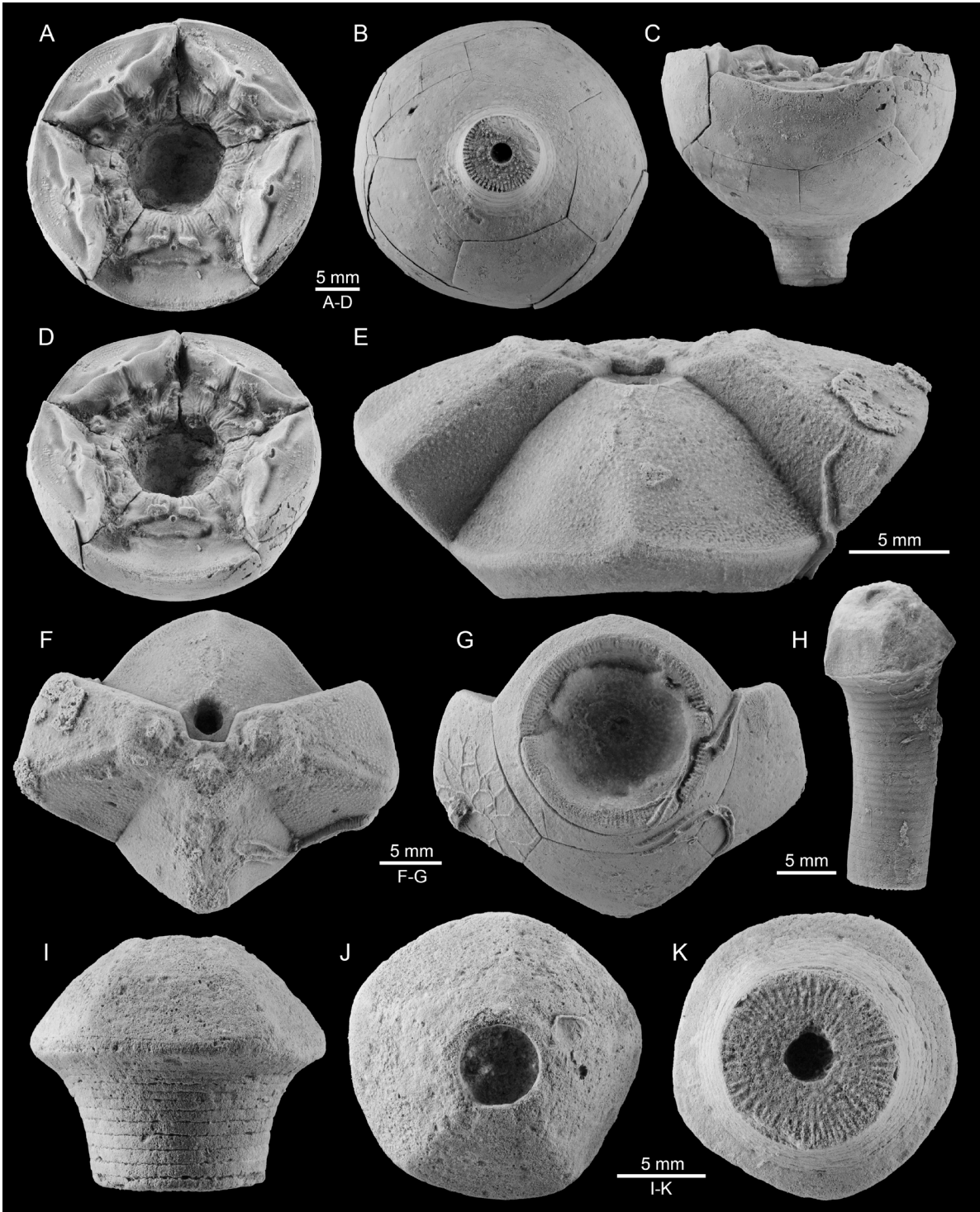


FIGURE 8—*Pomatocrinus hoferi*, photographs of specimens from the Villar de Herrero locality of the Sot de Chera Formation (Kimmeridgian, Late Jurassic). **A–D**, MPZ2021/188, a complete calyx with proximal part of the stem, five basals, five radials and four brachial plates in oral (A), aboral (B), lateral (C), and oblique (D) views. **E–G**, MPZ2021/189, a proximal-most columnal with three basal plates, in lateral (E), proximal (F) and distal views (G). Note the morphology of the proximalmost columnal as a truncated pyramid. **H**, MPZ2021/190 a proximal-most columnal with proximal column. Compare with proximal most columnal in *Liliocrinus* from figure 6. **I–K**, MPZ2018/473, a proximal stem with proximal-most columnal in lateral (I), proximal (J) and distal views (K).

TABLE 2 — Measurements of *Liliocrinus polydactylus* based on the three complete or partially completed calyx materials. All measures are in millimeters.

Measure	Specimen number		
	MPZ2021/188	MPZ2021/189	MPZ2021/190
Max. cup diameter	17	ca. 20	-
Min. cup diameter	11	12	13,5
Cup height	9	13	-
Basal height	4,8/5/4,7/5/5	6,2/-/6,5/5/6,5	7/7/7/6,8/6,5
Basal width	8/8/8/8/7,5	9/10,1/10/10/10	10,1/11,5/10,8/10,5/10,5
Radial height	4/4/4/4/4	5/4,5/-/-/-	-/-/-/-/-
Radial width	11/10/11	13/12,2/-/-/-	-/-/-/-/-

*Pomatocrinus hoferi* (Mérian, 1849). The second morphotype is *Pomatocrinus* cf. *mespiliformis* (von Schlotheim, 1820) including only basal plates.

*Pomatocrinus hoferi* (Mérian, 1849)  
Fig. 8, 9E-H

1760 *Trochita pentagonus* Hofer, p. 202, pl. 8, fig. 19–21.

1849 *Millericrinus* (*Pomatocrinus*) *hoferi* Mérian p. 28.

1862 *Millericrinus hoferi* Thurmann and Étallon p. 345, pl. XLIX, fig. 7.

1878 *Millericrinus hoferi* de Loriol p. 62, pl. X, figs. 1–12.

1882–84 *Millericrinus hoferi* de Loriol pl. 105, figs. 1, 2.

*Material.*— Complete calyx preserving proximal columnals and four brachial plates (MPZ2021/188) (Fig. 8A–D), one partial calyx (MPZ2021/189) (Fig. 8E–G), several proximalmost columnals (MPZ2018/473, MPZ2021/190) (Fig. 8H–K) and several isolated basal plates (MPZ2021/196–202) (Fig. 9E–H).

*Diagnosis.*— Species of *Pomatocrinus* with a bowl-shaped calyx, basals slightly higher than radials. Pentagonal basal plates, with poorly developed external curvature, proximal facets straight and internal apex acute.

*Remarks.*— *Pomatocrinus hoferi* was first described by Hofer (1760) as *Trochita pentagonus*. Mérian (1849) first observed important differences in the basal plates compared to *P. mespiliformis* and erected the new species *Millericrinus* (*Pomatocrinus*) *hoferi*, but never figured the specimens (sensu Thurman and Etallon, 1862). All later authors have recognized Mérian as the author of *P. hoferi*, a view followed here, pending further research on this topic. Specimens are properly figured in de Loriol (1878, plate X fig. 1–12) (reproduced here in Fig. 9J–L) and de Loriol (1882–84, plate 105 figs.

1, 2); who maintained assignment to *Millericrinus*. Neither Mérian nor de Loriol provided a proper diagnosis, which is reported here for the first time (see above). The descriptions and illustrations of de Loriol are enough to assign the Spanish material to *P. hoferi*. The species are considered valid here and transferred to *Pomatocrinus* according to characters described by Rasmussen (1978).

*Pomatocrinus hoferi* differs from *Pomatocrinus mespiliformis* in the shape of the basal plates (Fig. 9). These are pentagonal in *P. hoferi* and with flat sutures. For contrast, in *P. mespiliformis* they are more bulbous, with a more convex external surface, crenularium present in the articulation with proximal columnal, and double distal facet with a clear ridge in the middle.

*Pomatocrinus* cf. *mespiliformis* (von Schlotheim, 1820)  
Fig. 9A–D

*Material.*— About five specimens (MPZ2021/191–195) of basal plates (Fig. 9A–D). No complete calyces have been yet reported.

*Remarks.*— Basal plates described here are externally very curved and have double proximal concave facets identical to those of *P. mespiliformis* figured by Rasmussen (1978, fig. 552.1a; refigured here in Fig. 9I). This typical shape of the basals suggest inclusion in *Pomatocrinus* cf. *mespiliformis* pending further and more complete material. According to Salamon and Zatoń (2005), *P. mespiliformis* and *P. fleuriausianus* (Fig. 7A–C) are distinguished by the shape of the radials and basals respectively which agree with the figures of Rasmussen (1978). In *P. fleuriausianus* radials are very low and only relegated to the uppermost part of the calyx, whereas in *P. mespiliformis* they contribute to the spherical shape of the calyx. For contrast, most of the shape of the calyx

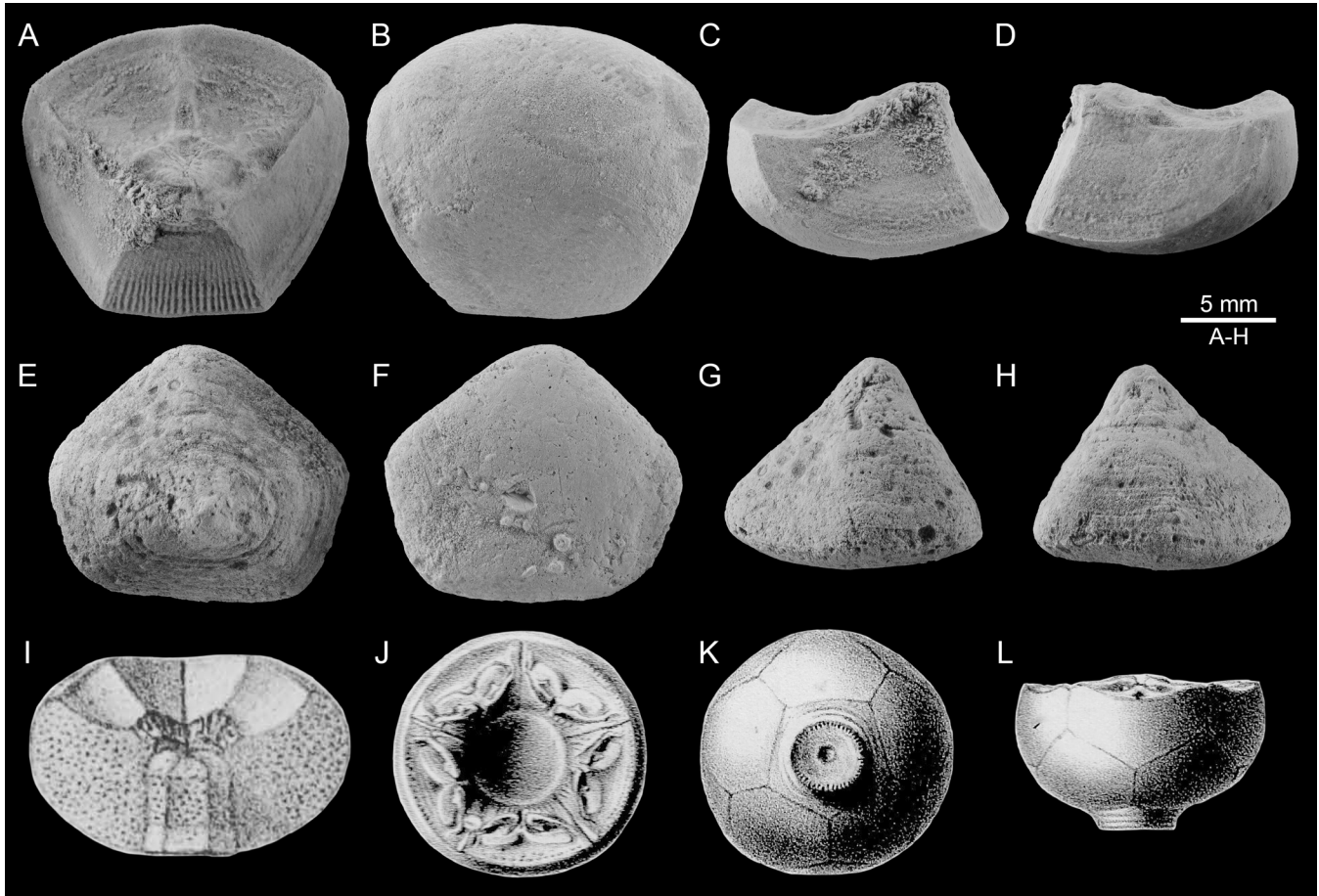


FIGURE 9 — A–D, *Pomatocrinus* cf. *mespiliformis*, photographs of the basal plate from the Puerto de las Banderas locality of the Sot de Chera Formation (Kimmeridgian, Late Jurassic). MPZ2018/473, in internal (A) (note the double facets for radials), external (B), lateral right (C), and lateral left views (D). E–H, *Pomatocrinus hoferi*, photographs of the basal plate from the Griegos 1 locality of the Sot de Chera Formation (Kimmeridgian, Late Jurassic). MPZ2021/196, in internal (E), external (F), lateral right (G), and lateral left views (H). I, specimen of *Pomatocrinus mespiliformis* figured in Rasmussen (1978, fig. 552. 1a). Note the shape of the basal plates and compare with A. J–L, specimen of *Pomatocrinus hoferi* figured in de Loriol (1878, pl. X, fig. 1) in oral (J), aboral (K) and lateral (L) views.

in *P. fleuriausianus* is related with the huge development of the basal plates. In the later the basals also have an external ridge that is very characteristic. This ridge is absent in *Pomatocrinus* cf. *mespiliformis*. The main differences in the latter with *P. hoferi* are related with the shape of the basal plates (see above).

#### Family APIOCRINITIDAE d'Orbigny, 1840

*Diagnosis.*— Cup very large, bowl to globe shaped, medium to high, very thick walled. Interradial plates variable in number, smaller plates may be concealed, wedge between other plates and reaching surface. Variable number of proximal columnals with increasing diameter form conical transition between cup and column (sensu Hess and Messing, 2011).

*Remarks.*— From all the features diagnosed by Hess and Messing (2011), the presence of proximal columnals that increase in diameter proximally is probably the most diagnostic feature of the family. This is very obvious for *Apiocrinites*. *Guettardicrinus*, the second genus included in the family also has this feature in the proximal columnals, but it has a calyx shape similar to the family Millericrinidae.

#### Genus *Apiocrinites* Miller, 1821

*Type species.*— *Encrinites parkinsoni* von Schlotheim, 1820 by original designation.

*Diagnosis.*— Cup typically globe- or pear-shaped to ovoid; greatest diameter at basal or radial circlet. Variable height of radials and basals. Primibrachials meet laterally, with or without a few small, polygonal, interradian plates. Synarthry

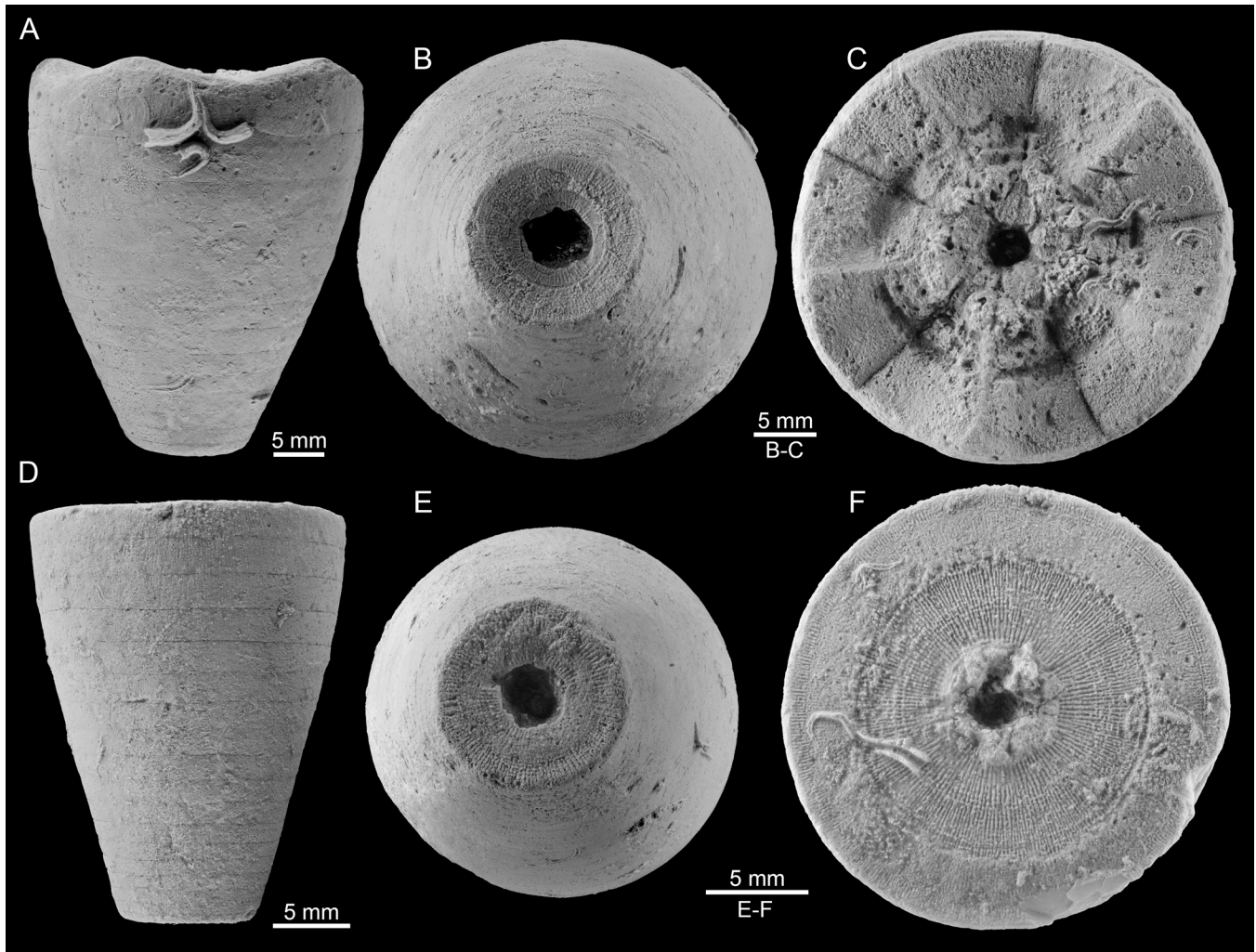


FIGURE 10 — *Apiocrinites cf. parkinsoni*, photographs of specimens from the Villar de Herrero locality of the Sot de Chera Formation (Kimmeridgian, Late Jurassic). **A–C**, MPZ2018/472, a proximal stem with the five basals but lacking radials in lateral (A), distal (B) and proximal (C) views. **D–F**, MPZ2021/203, a proximal stem showing increase in columnal diameters to the proximal part in lateral (D), distal (E) and proximal views.

or synostosis with marginal crenulae between primibrachials 1 and 2, synarthry between secundibrachials 1 and 2. All or most secundibrachials free. Arm divided at primibrachial 2, and in some species, further divided once or twice with variable interval. First pinnule on secundibrachial 2. Proximal column of thin, discoidal columnals increasing gradually in diameter to form long, smoothly conical transition from column to cup. Proximal columnals typically with flat proximal articular facet and concave distal facet, leaving empty central space between columnals. Proximal facet of uppermost columnal with 5 radiating ridges separating facets facing basals (sensu Hess and Messing, 2011 with modifications from Ausich and Wilson, 2012).

*Remarks.*— *Apiocrinites* is easily differentiated from *Guettardicrinus* by the general shape of the calyx and by the presence in the latter of radials and proximal brachials separated by several, small interrachial plates.

*Apiocrinites cf. parkinsoni* von Schlotheim, 1820  
Fig. 10

*Material.*— One calyx preserving proximal columnals and basals (MPZ2018/470; Fig. 10A–C). Other specimens include proximal columnals that are expanded and fused (MPZ2021/203) (Fig. 10D–F). Other specimens are partial proximal part of stems (MPZ2021/204–206).

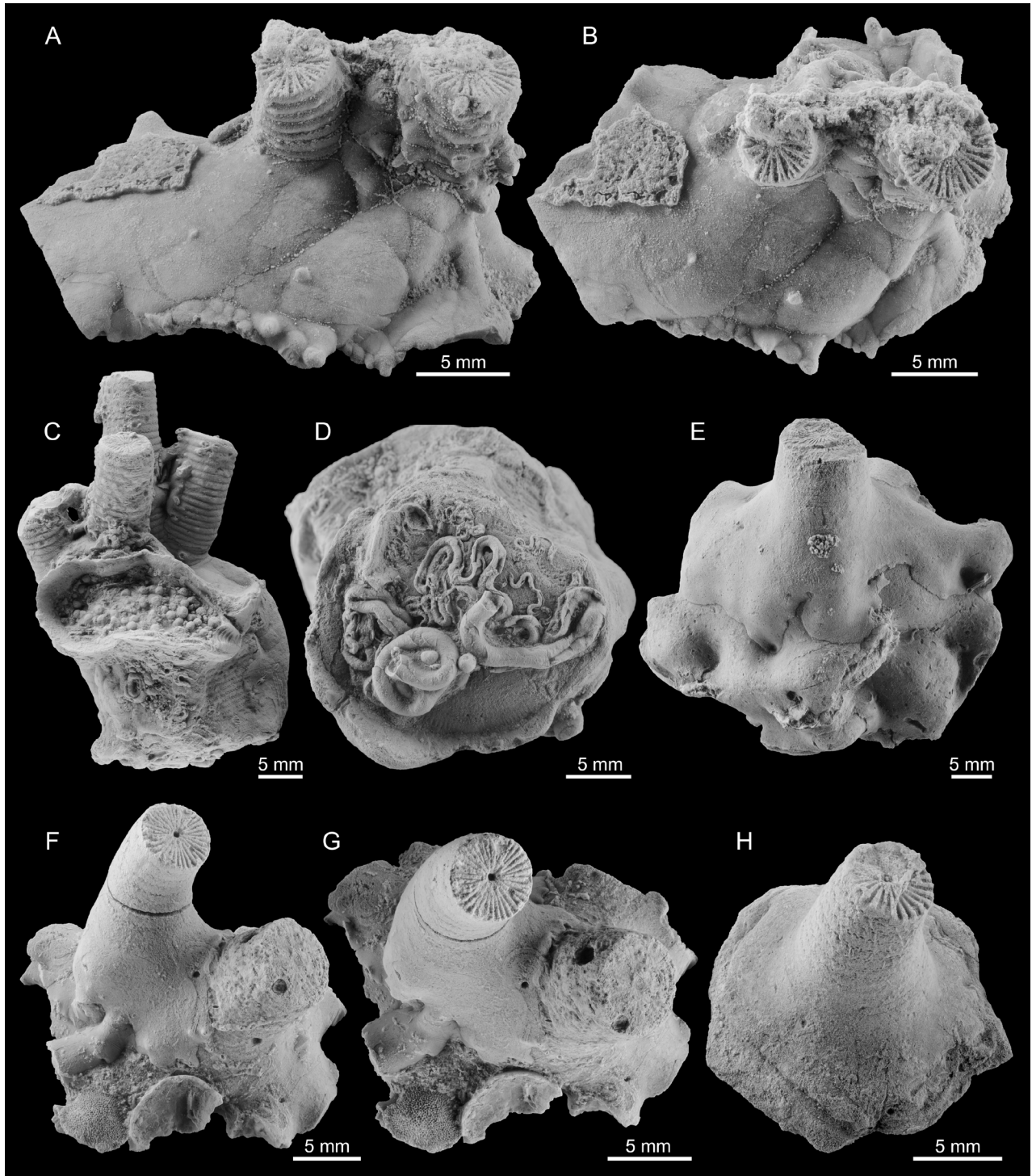


FIGURE 11 — A–H, attachment structures of millericrinids from the Sot de Chera Formation (Kimmeridgian, Late Jurassic). A–B, MPZ2021/207, is a double holdfast in lateral and proximal views from Griegos 2 locality. C–D, MPZ2021/208, are four holdfasts in the same cluster in lateral and distal views, from Griegos 2 locality. Note that the attachment surface is covered with serpulids (D). E, MPZ2021/209, is a specimen of holdfast overlapping a previous attachment structure from Villar de Herrero. F–G, MPZ2021/210, is a double holdfast from the Puerto de las Banderas locality. Note the different state of preservation of both individuals that suggest the left specimen was alive while the other died in the colony. H, MPZ2021/211, is a single holdfast from the Villar de Herrero locality.

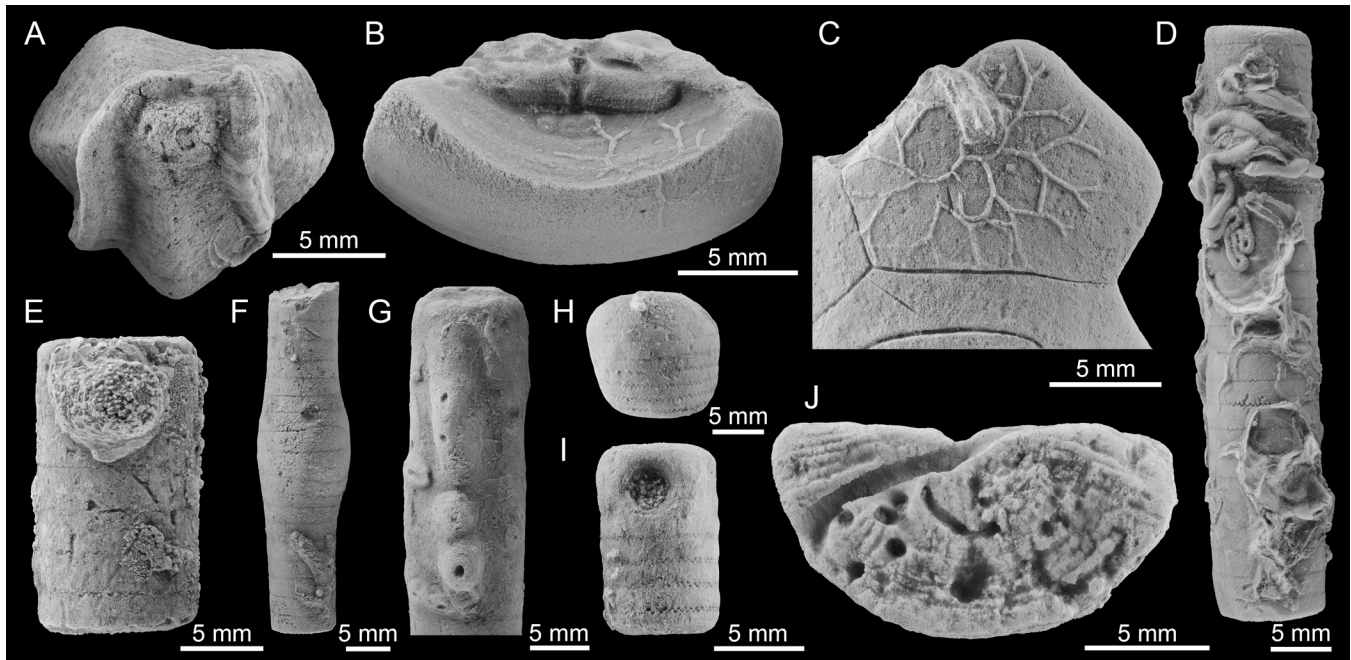


FIGURE 12 — Taphonomy of millericrinid material from the Villar de Herrero (A, C, H) and Puerto de las Banderas (B, D-G, I, J) localities of the Sot de Chera Formation (Kimmeridgian, Late Jurassic). A, MPZ2021/214, is a basal plate of *Pomatocrinus hoferi* with a large serpulid in the facets. B, MPZ2021/215, is a radial plate of a millericrinid indet. with a colonial organism growing in the attachment to brachial plate. C, MPZ2021/189, is a lateral view of a basal plate of *Pomatocrinus hoferi* with the bryozoan *Stomatopora* attached on its surface. Note a serpulid overlapping both, crinoid plate and *Stomatopora*. D, MPZ2021/216, is a stem fragment colonized by oysters and serpulids. E, MPZ2021/217, is a stem fragment with a small sponge attached on its surface. F, MPZ2021/218, is a stem fragment showing *Oichnus* isp. and a gall. G, MPZ2021/219, is a stem fragment infested with parasites showing crinoid reaction in life. H, MPZ2021/220, is a stem fragment highly eroded. I, MPZ2021/221, is a stem fragment showing *Oichnus* isp. J, MPZ2021/222, is a fragment of a columnal fully covered with bioerosion trace fossils.

*Remarks.*— Material is assigned to *A. cf. parkinsoni* because the general shape of the calyx and the very low basal plates. If the presence of this species is confirmed with furthermore complete material this would represent the youngest occurrence of the species because type material is from the Middle Jurassic of France. Specimens from Bradford Clay (UK) also belong to the same species and age and also have very low basal plates. *A. roissyanus* d'Orbigny from the Oxfordian of France has by comparison very high basal plates that are more comparable to those appearing in *Pomatocrinus mespiliformis*. More recently Ausich and Wilson (2012) described *A. negevensis* from the Middle Jurassic of Israel that also has high basals comparable in height to radials. Basals in *A. negevensis* are very similar to those in *A. roissyanus* but higher than in *A. cf. parkinsoni*. Further material from Spain preserving both basals and radials would confirm if *A. cf. parkinsoni* belongs to *A. parkinsoni* or to a different and new species. Wilson et al. (2014) described a second species from Israel as *A. feldmani* but figured specimens that have radial and basal plates of similar heights which seem very similar to those observed in *A. parkinsoni*. The basals in *A. feldmani* are also similar to those of *A. cf. parkinsoni*.

## ATTACHMENT

Most stalked crinoids require permanent attachment as adults. When complete material is available from the calyx to the attachment system (see examples in Hess et al., 1999) it is easy to assign a calyx to columns and attachment structure, but when only disarticulated material is available this is a risky inference. In special cases when dealing with low diversity faunas it is sometimes possible to correlate the calyx with the rest of the animal (see Salamon and Zatoń, 2005 as a possible example), based on its morphology. Millericrinids were permanently attached by means of complex root systems or holdfast that cemented on substrates (de Loriol, 1877; Palmer and Fürsich, 1974). The column is constructed of cylindrical columnals that lack cirri, and the holdfast is the only way these crinoids attached on the substrate. In the studied material there are several types of holdfast preserved that inform about substrate preferences and attachment.

Assignment of each type of holdfast to the species of crinoids described is difficult, because they all come from the same stratigraphic horizons and coexisted. Only a few examples have been described of millericrinids in the



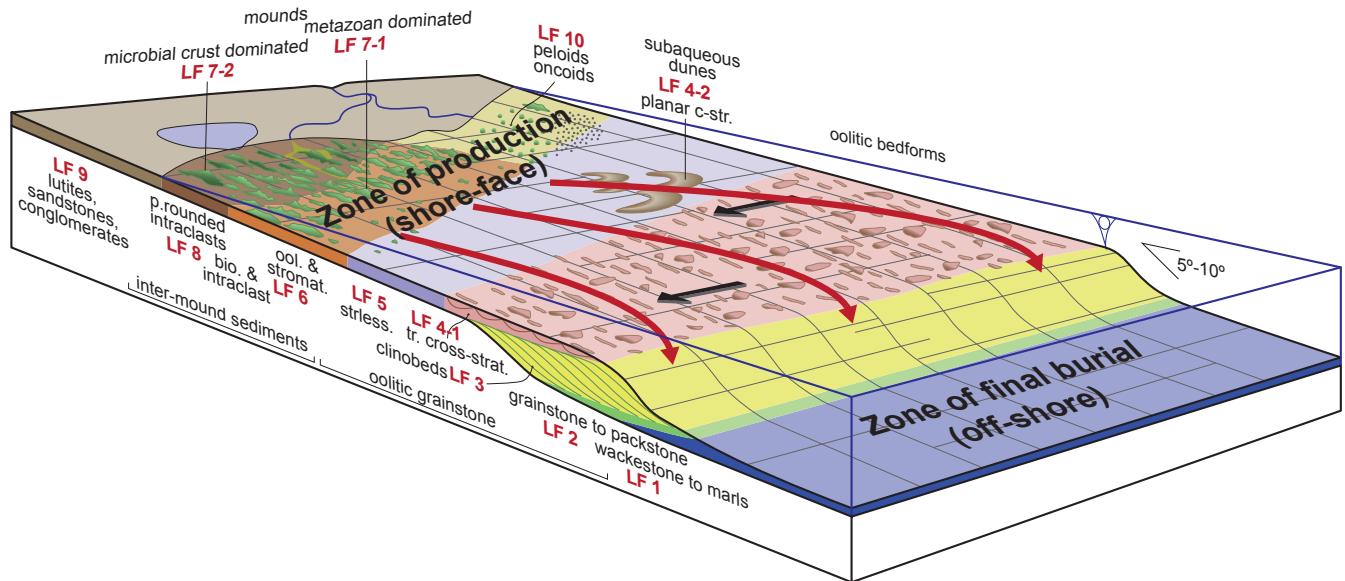


FIGURE 13 — Depositional model for the Pozuel Formation (Kimmeridgian, Late Jurassic). Studied crinoids were probably living in shore-face facies (Zone of production). Most disarticulation processes and erosion probably occurred in the high energetic oolitic grainstones. Final burial and preservation of specimens occurred in the off-shore basin, lithofacies 1 (Zone of final burial). Specimens were transported to the basin by storm-induced events. Modified from Pomar et al. (2015; fig. 11). Abbreviations: *bio.*, bioclasts; *c-str.*, cross-stratification; *ool.*, oolites; *p.*, poorly; *stromat.*, stromatolites; *strless.*, structureless; *tr. cross-strat.*, trough cross-stratification.

literature with the calyx, stem, and holdfast articulated. *Liliocrinus munsterianus* (*L. polydactylus* here) from the Swiss Jura developed a column up to 2 meters high that ended in a massive, cemented root; but alternatively, also developed roots on soft sediment that first attached on a hard object (Hess et al., 1999; p. 6). Specimens of *Apiocrinites parkinsoni* from the British Jurassic also developed massive holdfast that attached on hard grounds but had a considerable shorter column (Palmer and Fürsich, 1974; Hess et al. 1999 p. 198). Salamon and Zatoń (2005) figured a holdfast and column that they assigned to *Pomatocrinus mespiliformis*, and these holdfasts are notably very massive structures. Scheweigert et al., (2008) figured a specimen of *Millericrinus milleri* with a long portion of the stem preserved but lacked distal attachment structure. Based on this evidence it is impossible to correlate the described calyces with stems and holdfasts with certainty. This is especially true in the material presented here, where more than one species cooccur in the same assemblage. All columns are rather similar having millericrinid-like features such as circular outline, lack of cirri and presence of radial crenulae. Moreover, some millericrinids change the general shape of the column through ontogeny and from proximal to distal parts posing extra problems to assign column to a specific calyx. Further articulated material might clarify this issue.

Some of the reported holdfasts (Fig. 11) had more than one individual living in the same cluster (Fig. 11A, C, F). One of the specimens has up to four specimens clustered together (Fig. 11C). This suggests a gregarious lifestyle for

millericrinids but also points out the possibility that space for attachment was limited. Alternatively, some restricted places were more optimal than others for attachment.

All specimens with the exception of one example (MPZ2021/212) appear unattached from the original substrate, thus determining the original substrate preferences is difficult. The sole specimen that seems attached to a fragment of rock corresponds to a large holdfast that has distal radices attached to a certain type of lithified carbonate grainstone, which is different from the marly sediment that covers the rest of the specimen. Another specimen overgrew a bivalve shell (MPZ2021/213) but have some broken radices suggesting they attached on some sort of soft substrate. These two specimens will be treated in a different paper but they suggest that millericrinids attached to either a lithified grainstone or shell fragments, supporting previous observations (Palmer and Fürsich, 1974; Hess et al., 1999).

Attachment structures are diverse in the studied material (see below) and range from very gracile structures to relatively massive ones. This probably reflects the diversity of millericrinids in the studied material. Some clusters of holdfast provide evidence that some specimens were still alive in the colony while others were dead (Fig. 11F, G). This is supported by the presence of excellently preserved specimens coexisting with other poorly preserved material in the same cluster. Attachment structures also support long post-mortem exposures with specimens preserving sclerobionts and bioerosion trace fossils that were formed after the death of the crinoids (Fig. 11D).

## TAPHONOMIC OBSERVATIONS

Most of the crinoid material presented in this work comes from the Sot de Chera Formation. For this reason, the taphonomic observations and palaeoecological implications will focus only on this specific assemblage. Material from the Yatova Formation was considered in Zamora et al., (2018) and does not need to be repeated here. Crinoid material includes mostly columnals and column fragments, attachment structures, isolated brachials, and rarely partial or complete calyces. Specimens range from excellently preserved material to extremely abraded specimens (Fig. 12H), and sclerobionts, including bryozoans, serpulids, bivalves, and sponges, are common on many specimens (Fig. 12A-E). Bioerosion trace fossils are also present (Fig. 12F, G, I, J). There are also specimens of stem fragments that are swollen (Fig. 12F, G, I). Some of the sclerobionts are compatible with interactions in life, but many are located on parts that were covered with other plates in life such as brachial facets or columnal articulations (Fig. 12A, B). There are also examples of attachment structures covered with sclerobionts on the attachment surface (Fig. 11D). Similar sclerobionts on crinoids from the Jurassic have been described for the Callovian Matmor Formation (Feldman and Brett, 1998; Wilson et al., 2010). Swollen columnals in millericrinids have been previously interpreted as signs of parasitism (Wilson et al., 2014); and they show external pits with increase in steroom thickness that are interpreted as a crinoid reaction to parasitism (Fig. 12F, G). The massive roots of millericrinids offered benthic “islands” for obligate encrusters as has been demonstrated in previous observations (Seilacher and Macclintock, 2005; Lach et al., 2014), and in the many examples figured here (Fig. 11). Quantification of sclerobionts and bioerosion trace fossils has not been performed yet and will require further detailed study, but based on preliminary observations some important information can be provided. The presence of post-mortem epibiont material and abrasion suggest a long and complex taphonomic history (Zamora et al., 2018). Many specimens have evidence of abrasion that changed their original shape suggesting resedimentation in coarse grained sediment like that provided by ooids preserved with the crinoid material (see above). Size and variety of sclerobionts also support the idea that most crinoid material was on the sea floor for long periods of time (Feldman and Brett, 1998). Exceptions of rapid burial probably resulted in the preservation of complete cups having brachials in place. The theca of millericrinids was probably rigidly sutured and some of the plates were probably fused because there are examples of *Apiocrinites* and *Pomatocrinus* with the basals still present but with the articulations to radials fully covered by sclerobionts (Figs. 8E, 10A–C).

## ENVIRONMENTAL INTERPRETATION

Pomar et al., (2015) provided the reconstruction of shallow carbonate platforms in the studied area. They

recognized ten different lithofacies. Constructional organisms like corals, stromatoporoids, and crinoids appear associated to mounds and oolitic-skeletal grainstones of lithofacies 6 and 7. Lithofacies 3–5 are dominated by oolitic grainstones in which high energetic condition and coarse sediment favored erosion of bioclastic material. These lithofacies were developed in proximal shoreface environments. For contrast the material here described is abundant in lithofacies 1 which corresponds to basinal offshore marls (see Fig. 13).

Based on the reconstruction provided by Pomar et al., (2015); two possibilities are most suitable for the crinoids. One possibility points that most organisms including crinoids were living on shoreface meadows and were transported with the ooidal material to the lithofacies 1. A second possibility suggests that crinoids were living at the base of the talus and beginning of the basin, between lithofacies 1 and 2; and were finally buried in lithofacies 1. Based on the grade of abrasion of most material and the degree of colonization by sclerobionts the first option is most probable. Crinoids probably lived in highly energetic environments were attached in colonies to hardgrounds or small mounds (zone of production). Shortly after death, individuals rapidly disarticulated and some specimens were resedimented with the ooids in the proximal environments for long periods of time, resulting in highly abraded specimens and increase of encrusting possibilities. Finally, all the material including time-averaging assemblages was transported to the basin and buried in marly sediments (zone of final burial). This model explains the co-existence between well preserved specimens and others that are highly abraded or colonized by sclerobionts. This also explains why millericrinids are not present elsewhere in the Sot de Chera Formation and only concentrate in certain localities. Storm-driven down-welling and geostrophic currents that evolved into gravity flows at the slope (Pomar et al., 2015) were probably responsible for transporting specimens and bioclastic material from the zone of production to the zone of final burial (see direction of arrows in Fig. 13).

## CONCLUSIONS

Millericrinid crinoids have been largely ignored in the Late Jurassic rocks from Spain. A rich assemblage from the Yátova and Sot de Chera Formations provides important information on the systematics, taphonomy, and palaeoecology of this important extinct clade of crinoids. Only material comprising relatively articulated specimens is described, but the diversity of millericrinids can be increased if disarticulated material is further described in the future. One taxon from the Yátova Formation is described as *Angulocrinus tomaszi* n. sp. The remaining taxa include *Millericrinus milleri*, *Liliocrinus polydactylus*, *Pomatocrinus hoferi*, *Pomatocrinus* cf. *mespiliformis* and *Apiocrinites* cf. *parkinsoni*, and are all described from the Sot de Chera Formation. The later assemblage also provides important taphonomic data on syn-vivo and postmortem interactions with other organisms. These crinoids experienced a long biostratinomic phase with long periods of exposure to erosion and colonization.

Taken together this information provides clear evidence demonstrating that millericrinids lived in relatively high energetic shore-face conditions and were transported and finally buried in deeper off-shore meadows. This provides important information to reconstruct ancient habitats from shoreface energetic meadows that rarely preserve in the fossil record.

#### ACKNOWLEDGMENTS

I would like to dedicate this work to Prof. Tomasz Baumiller (University of Michigan) because after a visit in 2016 he first encouraged me to describe some of the material of Post-Palaeozoic crinoids from Spain that the author collected over the last decade. Specimens studied have been collected with the help of students from the University of Zaragoza including Victoria Barrios and Fernando Ari Ferratges. The latter also helped preparing some critical specimens. Juan Carlos García Pimienta (Gobierno de Aragón, Spain) helped with field work. Isabel Pérez did incredible photography assistance. Important discussions have been taken on the sedimentology of the area with Marcos Aurell and Beatriz Bádenas, both from the University of Zaragoza. Luis Moliner classified some of the ammonites associated with the crinoids. Meg Veitch (University of Michigan) helped finding very old literature that was important to review the described species. Two reviewers, Mark A. Wilson (The College of Wooster) and Mariusz A. Salamon (University of Silesia), and editor William I. Ausich (The Ohio State University) have provided important comments that improved the resulting manuscript. Jen Bauer, editor, (University of Michigan) did a grammatical correction of an early draft of this manuscript. This is a contribution to project E18\_20R “Aragosaurus: Recursos geológicos y paleoambientales” from the Government of Aragón.

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*Contributions from the Museum of Paleontology, University of Michigan* is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum. Jennifer Bauer and William Ausich, Guest Editors; Jeffrey Wilson Mantilla, Editor.

Publications of the Museum of Paleontology are accessible online at: <http://deepblue.lib.umich.edu/handle/2027.42/41251>  
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ISSN 0097-3556