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Stratigraphic and paleogeographic distributions of Devonian crinoids from Spain with description of new taxa from the Iberian Chains

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Abstract.—A new Lower Devonian fauna from the Iberian Chains (NE Spain) is described. Specimens have been collected from the shaley intervals of the Mariposas Formation dated as early Emsian. These include the camerates *Acanthocrinus carsli* n. sp., *Platyhexacrinus santacruzensis* n. sp., *Culicocrinus breimeri* n. sp., Camerata indeterminate, and an indeterminate eucladid. Compared with other faunas from Spain, this represents a low diversity crinoid assemblage that was probably concentrated in shallow, turbid environments. A summary of crinoids previously described from the Spanish Devonian is reported, which indicates that crinoid faunas become progressively more cosmopolitan during the Devonian.

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Introduction

During the Devonian, Iberia was situated in the northwestern margin of Gondwana and separated from Laurussia by the narrow northeastern-trending Rheic Ocean. As part of Gondwana, Iberia moved northward, reaching about 35°S during Givetian times (Scotese, 2000, 2001; Nance et al., 2012). Thus, the Devonian sediments were deposited in subtropical seas.

Devonian crinoids from the Cantabrian Zone in North Spain are well documented, and the first species were described by de Verneuil in the 19th century (de Verneuil, 1850). Several authors described crinoids from this area (Oehlert, 1897; Schmidt, 1931; Almela and Revilla, 1950; Sieverts Doreck, 1951), but the first comprehensive monograph on Spanish crinoids was Breimer (1962). He described five new genera and sixteen new species, with fourteen of these taxa previously unreported from this area. Most of the crinoids studied by Breimer were from the Lower and Middle Devonian. He also described a small number of Carboniferous species. Since, only a few species have been reported either by professional paleontologists (Le Menn, 1976; Webster, 1976; Pidal, 1984, 2008; Kammer, 2001; Zamora et al., 2015) or amateurs (e.g., Hauser, 2010, 2015; Hauser and Landeta, 2007, 2012, 2013).

Apart from the well-known fauna of the Cantabrian Zone, other crinoids from the Spanish Devonian are unknown and only fragments have been reported in general works (Carls, 1965). Le Menn (1985) mentioned the species *Pterinocrinus tenuibrachiatus* Le Menn, 1976 in the Mariposas Formation. He also described *Aragocrinus molinoesnsis* Le Menn, 1988, which corresponds to the distal holdfast from an unknown crinoid. Carls and Valenzuela-Ríos (2002) also mentioned the presence of *Seilloucrinus verneuili* (Cailliaud, 1861) and *Asperocrinus minumus* LeMenn, 1976 in the Mariposas Formation based apparently on isolated columnals that have been neither described nor figured. Lastly, Herrera and Villas (2013) figured a rich collection of crinoid columnals from the Mariposas Formation, including *Botryocrinus* sp. and several morphotypes placed in open nomenclature.

In this paper, we describe a new crinoid fauna based on articulated specimens from the Mariposas Formation (Emsian), which crops out in the eastern Iberian Chain. A rich shelly fauna that includes trilobites, corals, mollusks, brachiopods, and crinoidal fragments (Carls, 1965) has been reported previously from this area. Material described here is from large exposures provided by road construction. Five additional taxa are described from the Mariposas Formation, including three new species and two taxa left in open nomenclature. This fills an important gap in the knowledge of crinoids from Spain, and this fauna is compared to other Spanish faunas.

Geological setting

A complete Ordovician to Devonian succession crops out in the vicinity of Fombuena, Luesma, and Santa Cruz de Nogueras (Fig. 1.1), in the eastern Iberian Chain. The complete Devonian thickness is ~4000 m, 95% of which is comprised of siliciclastic rocks; but due to complicated tectonics, a complete Devonian section is lacking. Carls (1965) was a pioneer in describing these Devonian strata in detail, mapping the areas, and providing information on biostratigraphy. German and Spanish disciples of Carls have also worked in the area for the last half century and demonstrated the worldwide importance of Devonian strata around the axial depression of the Cámaras River. The best sequence of Rhenish faunas there is known from the Early Devonian (Carls and Valenzuela-Ríos, 2002).

The section studied herein crops out in a new road cut of the TE-V-1521 road from Santa Cruz de Nogueras to Bádenas villages (Fig. 1.2) where part of the Mariposas Formation is

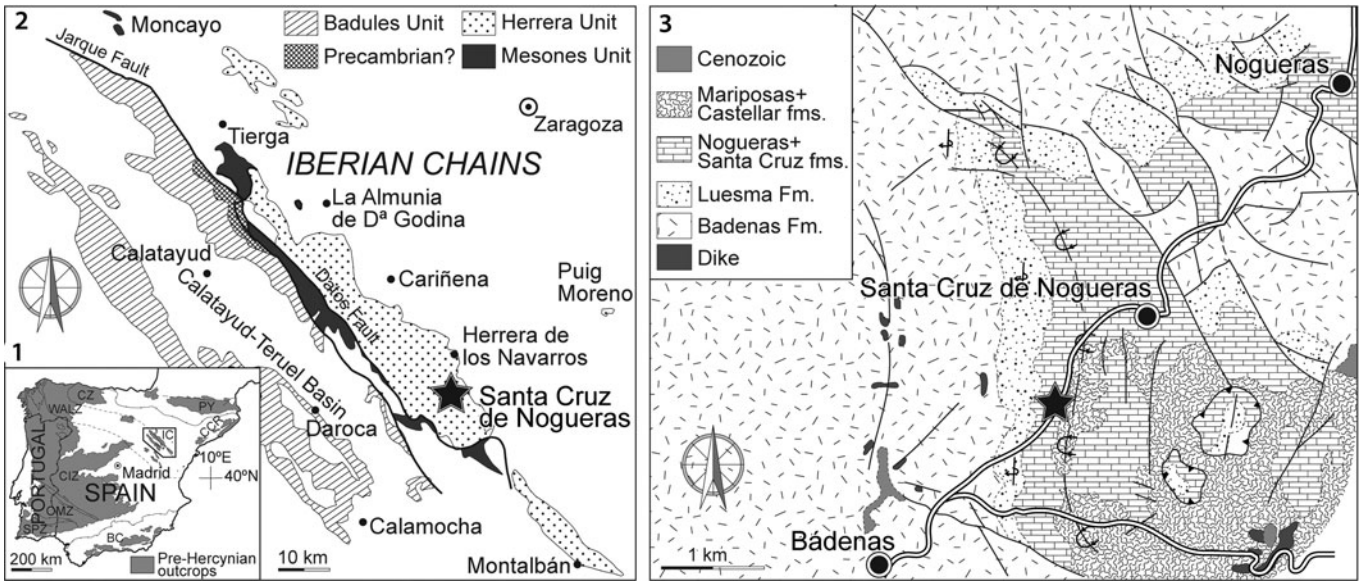

Figure 1. (**1**) General geographic setting of the study area; (**2**) Paleozoic outcrops of the Iberian Chains, indicating the location of the studied area in the Herrera Unit (modified from Gozalo and Liñan, 1988); (**3**) geological map of the Santa Cruz de Nogueras area, with the location of the studied site (modified from Lendínez et al., 1989).

well exposed (Fig. 2). The coordinates of the outcrop are 41° 6′31″N, 1°5′57″W. The Mariposas Formation is one of the most fossiliferous Devonian units in the Iberian Chains. It consists of a 200 m thick interval dominated by shales and carbonates. The faunas change from typical Rhenish facies of shallow water to Hercynian hemipelagic biofacies. The Mariposas Formation is subdivided into two members (d4a and d4b) (Fig. 2).

Carls and Valenzuela- Ríos (2002) provided a synthesis of the Devonian sequence from the Iberian Chains and indicated that the Mariposas Formation starts with an 8 m thick alternation of shelly limestones, bryozoan marls, and shales (submember d4aα), in which the lower boundary of the traditional German Emsian Stage is located (Carls, 1987, 1988). Submember d4aβ is 20 m thick and contains Rhenish brachiopods, trilobites, and endemic conodonts of the genus *Icriodus*. There are rare *Otarion* and proetid trilobites, solitary rugose corals, thamnoporid and micheliniid tabulate corals, tentaculitoids, ostracodes, crinoids, and bivalves. Crinoids described in this paper have been collected from submember d4aβ. According to Villas et al. (2018), the aforementioned interval yielding crinoids is dominated by brachiopods adapted to turbid waters. The low diversity of conodonts "*Polygnathus*" and abundance of "*Icriodus*" in the interbedded limestones indicate a shallow-water environment. The overlying submember (d4aγ) is 15–20 m thick, consists of a shelly crinoidal limestone, and contains a similar fauna to that of previous units, but also includes abundant atrypid brachiopods, some dacryoconarid tentaculitoids, and trilobites (scutellids and *Phacops*).

According to Carls and Valenzuela-Ríos (2002), Rhenish faunas nearly disappear at the beginning of the d4b Member, with only a few trilobites (Asteropyginae) and brachiopods (*Arduspirifer*) present. The classic German Emsian begins 1 m below the pair of limestones beds in the middle of submember d4aβ, where the brachiopod *Arduspirifer prolatestriatus* (Mittmeyer, 1973) marks the classical boundary in Germany (Villas et al., 2018). Thus, the levels containing the crinoids described herein are lower Emsian.

Materials and methods

Repositories and institutional abbreviations.—New material described here is deposited in the Museo de Ciencias Naturales (University of Zaragoza) (MPZ) and the Museo Geominero, Madrid (MGM).

Systematic paleontology

Classification and terminology.—The classification of crinoid higher taxa used here follows Ausich et al. (2015), Cole (2017), Wright (2017), and Wright et al. (2017). Other aspects of suprageneric classification follow Moore and Teichert (1978).

Morphologic terminology follows Ubaghs (1978). The plating of interrays is given in the standard abbreviated form as the number of plates in each range from the proximal-most plate to the last range before the tegmen. In the posterior interray, the primanal is indicated by "P" and the first interradial in regular interrays is indicated by "1." The shorthand notation used to describe the nodal-internodal structure of heteromorphic columns is from Webster (1974). All measurements are in mm; * indicates that the measured feature is either incomplete or crushed. Other abbreviations include: ACH, aboral cup height; ACW, aboral cup width; AH, arm height; BH, basal circlet height; CH, column height; CrH, crown height; RH, radial plate height; RW, radial plate width; TH, tegmen height.

Class Crinoidea Miller, 1821
Infraclass Eucamerata Cole, 2017
Order Diplobathrida Moore and Laudon, 1943
Superfamily Rhodocrinitacea Roemer, 1855
Family Rhodocrinitidae Strimple and Watkins, 1955

Genus *Acanthocrinus* Roemer, 1850

Type species.—*Acanthocrinus longispina* Roemer, 1850, by subsequent designation.

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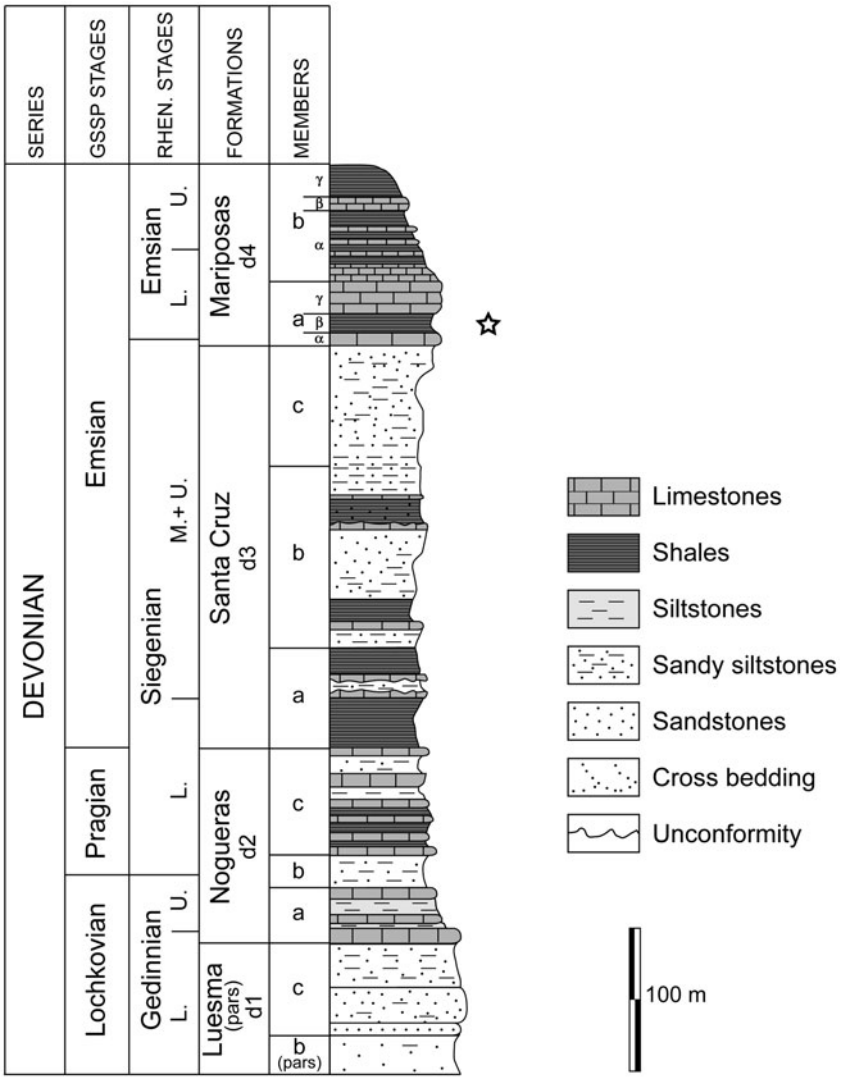

Figure 2. Stratigraphic section of the Lower Devonian of the Iberian Chains in the axial depression of the Cámaras River (simplified from Carls and Valenzuela-Ríos, 2002). Occurrence of crinoids noted.

Other species.—*Acanthocrinus*? *benedettoi* Haude, 2004; *A. brevispina* Roemer, 1850; *A. carlsi* n. sp., *A. faouensis* Le Menn, 1985; *A. gracilior* Jaekel, 1895; *A. gracilior* var. *vermicularis* Schmidt, 1942; *A. heroldi* Schmidt, 1934; *A. jaekeli* Schmidt, 1942; *A. lingenbachensis* Lehmann, 1939; *A. onondaga* Goldring, 1923; *A. rex* Jaekel, 1895; *A. spinosus* (Hall, 1862) non Südkamp, 2007; *A. spinosus* Südkamp, 2007 non Hall, 1862.

Occurrence.—Devonian: Algeria, Argentina, Belgium, France, Germany, Spain, and United States.

Acanthocrinus carlsi new species
Figure 3.4

Holotype.—MPZ2018/513.

Diagnosis.—*Acanthocrinus* with short spines (as known), connection between interradial plating and the tegmen absent, ray ridges absent, anal tube absent (as known), permanently recumbent free arms, nodal columnals with prominent nodes, and a single internodal between nodals in the mesistele.

Occurrence.—Mariposas Formation (Emsian), Iberian Chains, Spain.

Description.—Calyx high vase shape. Calyx plating too poorly preserved to decipher many details. Downward projecting spine with rounded terminus from a more proximal calyx plate (perhaps a radial or basal plate).

Regular interrays not in contact; plating cannot be deciphered.

Free arms presumably 10 from large elliptical arm facets, permanently recumbent (Fig. 3.4), project downward more than twice the height of calyx. Free arms pinnulate, presumably branch (but this is not verified); brachials rounded biserial throughout free arms.

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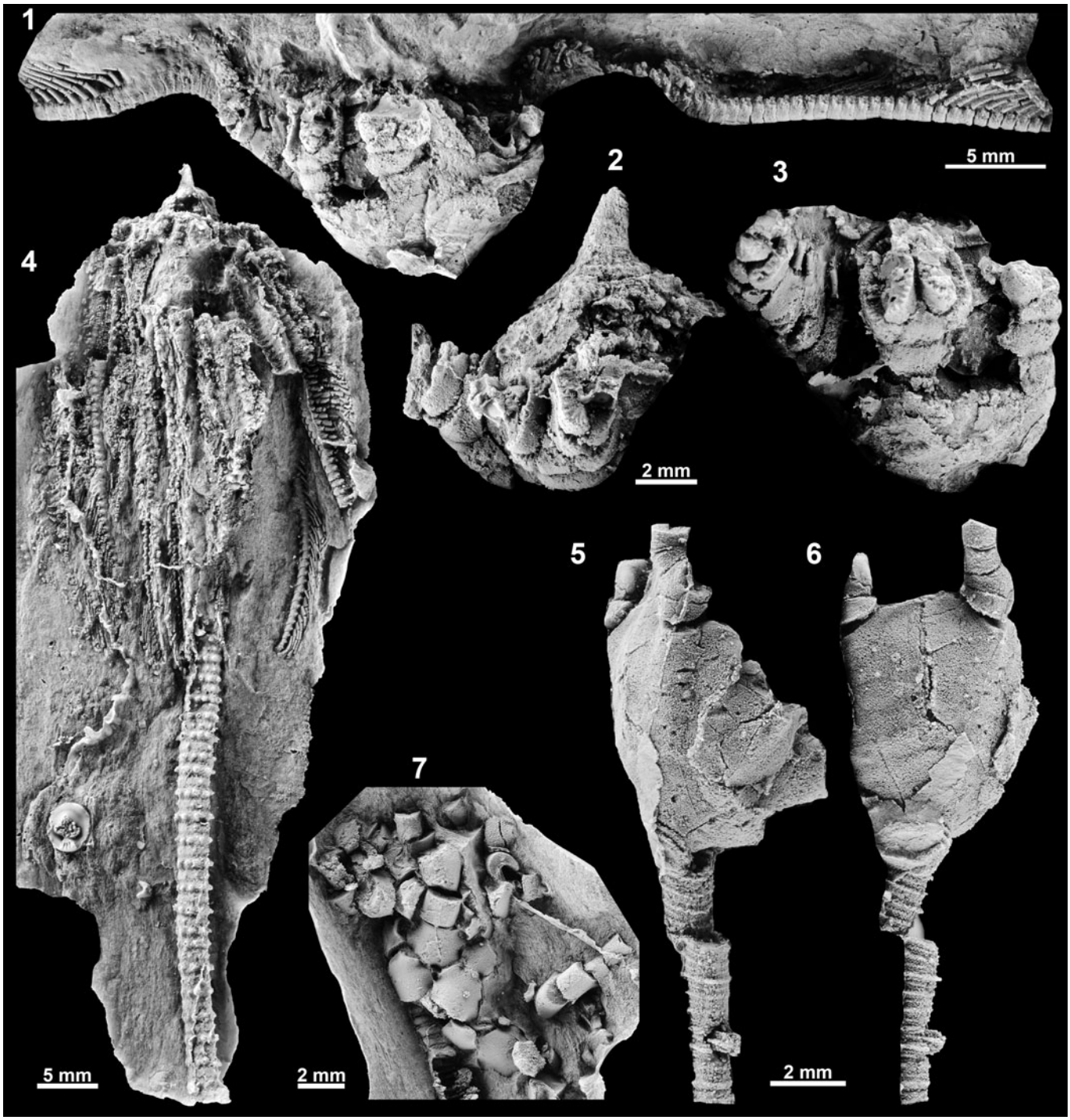

Figure 3. Emsian crinoids from the Mariposas Formation (NE, Spain). (**1–3**). Calyx and arms of Camerata indet.; specimen MPZ2018/518; (**1**) lateral view showing two articulated pinnulate arms; (**2**) lateral view showing a prominent spine on the tegmen; (**3**) lateral view showing arm articulations. (**4**) *Acanthocrinus carsli* n. sp. preserving complete calyx with arms folded down and stem; specimen MPZ2018/513. (**5, 6**) *Platyhexacrinus santacruzensis* n. sp. preserving complete calyx, proximal part of the arms, and stem; specimen MPZ2018/514. (**7**) Eucladid indet.; specimen MPZ2018/519. All specimens are latex casts whitened with ammonium chloride sublimate.

Low inverse cup-shaped tegmen projecting above position of arm openings; width of tegmen 50% of calyx width at position of arm openings; tegmen twice as wide as high. Tegmen plates small, polygonal; position of anal opening unknown.

Column circular, holomeric; heteromorphic N1 construction in medial stem. Distinctive spinose nodals (Fig. 3.4), nodals and internodals sutured along a high syzygial articulation prominent in lateral view. Proximal and distal stem, holdfast, and lumen unknown.

Etymology.—After Peter Carls for his pioneering work in understanding the Devonian of the Iberian Chains.

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Table 1. Species-diagnosis table for *Acanthocrinus*.

Species	Spines	Interradial Plates in Contact with Tegmen	Ray Ridges	Anal Tube	Arms Permanently Recumbant	Nodals with Nodes	Number of Internodals
A.? *benedicti* Haude, 2004	Long, distal part flattened	Absent	Present	Narrow, rises above tegmen surface, with short spines	Present; downward	Absent	"several"
A. brevispina Roemer, 1850	Medium, thck, curved	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
A. faouensis Le Menn, 1985	Spines long, weakly arched	Present	Present	Unknown	Unknown	Absent	4
A. gracilior Jaekel, 1895	Spines long, straight?	Absent	Present	Unknown	Present; outward then downward	Absent	5
A. heroldi Schmidt, 1934	Short?	Present	Present	Unknown	Absent	Absent	at least 3
A. jaekeli Schmidt, 1942	Spines long, straight	Present?	Present	Unknown	Present; outward then downward	Absent	at least 3
A. longispinosa Roemer, 1850	Long	Present?	Present?	Unknown	Unknown	Absent	Unknown
A. longispina Roemer, 1850	Long	Present	Present	Unknown	Present	Absent	3
A. onondaga Goldring, 1923	Short	Absent?	Absent	Unknown	Absent	Absent	Unknown
A. rex Jaekel, 1895	Long	Absent	Present	Unknown	Yes	Absent	7
A. spinosus (Hall, 1862) (non Sudkamp, 2007	Long	Absent	Absent or Present	Absent	Present	Absent	very similar to nodals
A. spinosus Sudkamp, 2007 (non Hall, 1862)	Long, may be divided	Absent?	Absent?	Unknown	Absent	Prsent, Small	15?
A. carlsi n. sp.	Short	Absent	Absent	Absent	Present	Present	1

Measurements.—MPZ2018/513: CrH, 46.0; TH, 3.2; CH, 42.0*.

Remarks.—Despite the relatively poorly preserved condition of the single *Acanthocrinus carlsi* n. sp. specimen from the Mariposas Formation, it has several features that make it distinct from other known species. Short spines (as known), connection between interradial plating and the tegmen absent, ray ridges absent, anal tube absent (as known), permanently recumbent free arms, nodal columnals with prominent nodes, and a single internodal between nodals in the mesistele render this taxon distinctive from other known species. *Acanthocrinus carlsi* n. sp. is compared to other species of *Acanthocrinus* in Table 1.

Order Monobathrida Moore and Laudon, 1943
Superfamily Hexacrinitacea Wachsmuth and Springer, 1885
Family Hexacrinitidae Wachsmuth and Springer, 1885

Genus *Platyhexacrinus* Schmidt, 1913

Type species.—*Platyhexacrinus inornatus* Schmidt, 1913; by subsequent designation.

Other species.—*Platyhexacrinus grandis* Schmidt, 1942; *P. gurievskiensis* Dubatolova, 1964; *P. kegeli* Schmidt, 1931; *P. nollenbachensis* Hauser, 2015; *P. ornatus* (Schmidt, 1913); *P.*? *pisum* Schmidt, 1942; and *Platyhexacrinus santacruzensis* n. sp.

Occurrence.—Devonian of France, Germany, Russia, and Spain.

Remarks.—*Platyhexacrinus* is a relatively poorly known genus, due at least in part to taphonomy. This taxon has very thin aboral cup plates that are poorly sutured. Thus, members of this taxon disarticulated rapidly after death and were easily compressed during compaction, which may be contributing factor to this being a relatively rare crinoid.

Species characters for *Platyhexacrinus* are overall size, aboral cup plate sculpturing, presence or absence of impressed aboral cup plate sutures, relative height of basal circlet, height to width ratio of radial plates, radial facet width, and presence or absence of fixed primibrachials and secundibrachials.

Platyhexacrinus santacruzensis new species
Figures 3.5, 3.6, 4.1

2015 camerate crinoid, Zamora et al., p. 245, fig. 24c, 24d.

Holotype.—MPZ2018/514.

Diagnosis.—Relatively small species of *Platyhexacrinus*, smooth aboral cup plate sculpturing, aboral cup sutures not impressed, basal circlet low, height to width ratio of radial plates ~1.0, radial facet ~33% of distal radial plate width, and fixed primibrachials and secundibrachials absent.

Occurrence.—Mariposas Formation (Emsian), Iberian Chains, Spain.

Description.—Calyx, small in size; only basal and radial plates in calyx that has a low cone shape; smooth plate sculpturing. Basal circlet visible in side view, sides concave, ~33% of aboral cup height, more than three times wider than high (Fig. 3.5). Basal plates five, ~1.4 times wider than high. Radial circlet ~67% of aboral cup height; radial plates presumably five, slightly higher than wide. Radial facets angustary, ~33% of distal radial plate width (Fig. 4.1), horseshoe shaped and protruding laterally.

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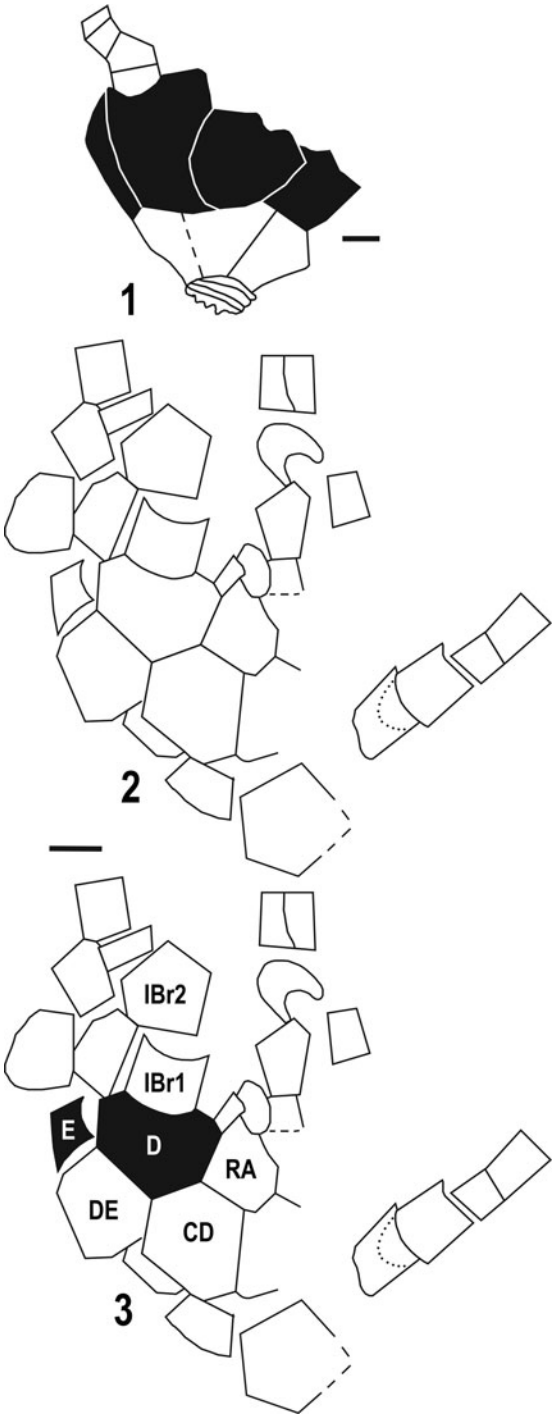

Figure 4. Plate diagrams of Mariposas Formation crinoids. (**1**) Lateral view of *Platyhexacrinus santacruzensis* n. sp. calyx with primibrachials and two secundibrachials preserved in one ray; compare to Figure 3.5; scale bar, 1 mm (MPZ2018/514). (**2, 3**) Eucladid Indeterminate; compare to Figure 3.7 (MPZ2018/519); scale bar, 10 mm; (**2**) plate diagram of mostly disarticulated calyx and arm plates; (**3**) interpretation of plate homologies where possible: black filling, radial plates; E, E radial plate; CD, CD basal plate; D, D radial plate; DE, DE basal plate; IBr1, first primibrachial; IBr2, second primibrachial; RA, radianal plate.

Tegmen plates relatively large, but details unknown. Fixed interradial plates absent (Fig. 3.6), posterior interray unknown.

Free arms five, one arm division as known; first primibrachial free, tetragonal, approximately as high as wide, much smaller than radial plates and somewhat smaller than primaxil; second primibrachial axillary, pentagonal, 1.5 times higher than wide. Second secundibrachial axillary.

Proximal column circular, holomeric, heteromorphic with pattern of N212, nodals and priminternodals with thin, extended epifacet. Secundinternodals moderately convex laterally. Lumen unknown.

Etymology.—Species dedicated to the locality of Santa Cruz de Nogueras where it was found.

Measurements.—MPZ2018/514: CrH, 13.5*; ACH, 5.4; ACW, 6.1*; BH, 2.0; RH, 3.4; RW, 3.2; CH, 9.5*.

Remarks.—Breimer (1962) described several Devonian crinoids from Spain with very few plates fixed into the calyx, including species of *Culicocrinus*?, *Cantharocrinus*, *Oenochoacrinus*, and "*Platycrinus*." *Platyhexacrinus* differs from all of these because the first primibrachial is free and no interradial plates are incorporated into a calyx. The previously described taxa all have one or two fixed brachials and at least one fixed primibrachial.

The small size, smooth sutures that are not impressed, low basal circlet, radial plate height/width of ~1.0, and no fixed primibrachials or secundibrachials distinguish this species of *Platyhexacrinus*. This new species is compared to other species in this genus in Table 2.

Superfamily Platycrinitacea Austin and Austin, 1842
Family Hapalocrinidae Jaekel, 1895

Genus *Culicocrinus* Müller, 1855

Type species.—*Platycrinus nodosus* Müller, 1855, by original designation.

Other species.—*Culicocrinus* breimeri n. sp.; *C. confluentinus* (Müller, 1855); *C.*? *girardeauensis* Brower, 1973; *C. inermis* Jaekel, 1895; *C. inventriosus* Schmidt, 1942; *C. inventriosus intemperans* Schmidt, 1942; *C. nodosus confluentina* (Müller, 1855); *C. nodosus virgo* (Schmidt, 1942); *C. rhenanus* Follmann, 1891; *C. rugosus* de Koninck in Zeiler and Wirtgen, 1855; *C. shotoriensis* Webster et al., 2011; *C. spinatus* Jaekel, 1895; *C. spinosus* Springer, 1926.

Occurrence.—Ordovician, United States; Silurian, United States; Devonian of Germany, Iran, and Spain.

Remarks.—Webster and Webster (2014) list 10 species in *Culicocrinus*, two of which have subspecies. These taxa range in age from the Ordovician to the Pennsylvanian. The Devonian forms are morphologically distinct from the earlier and later forms (*C.*? *girardeauensis*, Ordovician; *C. spinosus*, Silurian; and *C. shotoriensis*, Pennsylvanian). The Devonian forms all have fixed brachials through at least a few secundibrachials. The non-Devonian species lack fixed secundibrachials and are tentatively not regarded as species within *Culicocrinus* for the discussion below. Also, two species listed by Webster and Webster (2014), *C. rhenanus* and *C. rugosus*, are nomina dubia; and *C. confluentinus* is too

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Table 2. Species-diagnosis table for *Platyhexacrinus*.

Platyhexacrinus species	Size	Plate Sculpturing	Basal Circlet	H/W Radial Plate	Radial Facet	Fixed Primibrachials and Secundibrachials
P. grandis Schmidt, 1942	Large	Very fine wrinkles and flat grains; irregular in upper and vertical rows in lower part	Unknown	1.07	30%	No
P. gurivskiensis Dubatoloa, 1964	Unknown	Smooth no impressed sutures	Unknown	1.5	50%	Unknown
**P. inornatus* Schmidt, 1913	Unknown	Smooth no impressed sutures	High, funnel shaped	0.67	30%	No
P. kegeli Schmidt, 1931	Unknown	Fine elongate nodes	High	0.67	Unknown	Yes
P. ornatus Schmidt, 1913	Large	Irregularly arranged spiky warts	Flat base; Low	1	radial facet 20% radial width	No
P.? pisum Schmidt, 1942	Small	Smooth with impressed sutures??	Strongly vaulted, ring-shaped basal cortex; low	0.9	Unknown	No
P. santacruzensis n. sp.	Small	Smooth no impressed sutures	Low	0.96	33%	No

poorly understood to compare to other taxa. Thus, five species are considered for comparison to *Culicocrinus breimeri* n. sp.

Species level characters for Devonian *Culicocrinus* are the following: relative height of the basal circlet, nature of the rim of the basal concavity, nodes on the basal plates, nodes on the radial plates, number and size of interradial plates, and general character of the arms.

Culicocrinus breimeri new species
Figure 5

1962 Hapalocrinidae cf. *Culicocrinus nodosus* (Müller, 1855), Breimer, 1962, p. 122, pl. 11, figs. 1–4.

Holotype.—MPZ2018/515.

Diagnosis.—*Culicocrinus* with relatively high basal circlet, a short rim is present around the periphery of the basal concavity, two circular nodes project outward on the radial plates, more than one small interradial plate in regular interrays, and free arms relatively slender.

Occurrence.—Breimer (1962) figured a single specimen (also figured here) from an unknown locality and indicated that only one specimen was in the collection from Orzonaga (León) from levels near the Coladilla-Santa Lucía Formation boundary. The new material described herein comes from a known horizon (d4aβ) in the Mariposas Formation, so we prefer to choose this known horizon as the type level for *Culicocrinus breimeri* n. sp. These new specimens are from Santa Cruz de Nogueras (Teruel, NE Spain); Mariposas Formation (Emsian), Iberian Chains, Spain.

Description.—Calyx medium globe shape, approximately as high as wide; smooth plate sculpturing other than nodes noted below; plate sutures flush with plate surface.

Basal circlet visible in side view, ~25% of calyx height, pentagonal outline from basal view; basal concavity outlined by short rim (Fig. 5.3). Basal plates three, unequal in size, azygous basal plate in AB interray. Circular nodes in an interradial position around basal circlet (Fig. 5.2, 5.5), which results in one or two circular nodes per plate depending on plate size; nodes project outward.

Radial circlet uninterrupted by interradial plates, ~50% of calyx height; radial plates heptagonal, wider than high; much larger than basal plates; two circular nodes on each radial plate at mid-height, nodes project outward.

Regular interrays in contact with tegmen, not depressed (Fig. 5.2). One small, fixed interradial plate, higher than wide, sutured to narrow upper shoulders of subjacent radial plates; interradial oral surface plates sutured distally to fixed interradial plate of regular interrays.

Posterior interray with small primanal sutured to narrow upper shoulders of radial plates beneath, one small plate sutured to each side of primanal and to other plating distally (not preserved) that leads to anus.

Fixed brachials ~24% of calyx height. Two fixed primibrachials; first primibrachial approximately three times as wide as high; second primibrachial axillary, pentagonal. At least first secundibrachials fixed.

Ten free arms that branch once, pinnulate; brachials round biserial throughout free arms (Fig. 5.7).

Oral surface with exposed ambulacra and presumably moveable ambulacral cover plates (which are not preserved), five primary peristomial cover plates (Fig. 5.1–5.3, 5.6), and a few large interradial plates. Anal opening on posterior side of oral surface.

Proximal stem circular, holomeric; other details unknown.

Etymology.—After Albert Breimer for his outstanding work increasing the knowledge of Spanish Devonian crinoids.

Materials.—Paratypes: MGM2996D, MPZ2018/516 (part and counterpart), and MPZ2018/517.

Measurements.—MPZ2018/515: ACH, 3.6*; ACW, 7.2*; BH, 1.4; RH, 2.0*; RW, 3.1; AH, 13.5; CH, 2.7*.

Remarks.—The specimen illustrated by Breimer (1962, pl. 11, figs. 1–4) is considered conspecific with the new material from the Mariposas Formation, and the description above incorporates the morphology of both Breimer's specimen and new material. This new species is distinct with a relatively high basal circlet, a short rim is present around the periphery of the basal concavity, two circular nodes projecting outward on the radial plates, more than one small interradial plate in regular interrays, and free arms relatively slender. Species of *Culicocrinus* are compared in Table 3.

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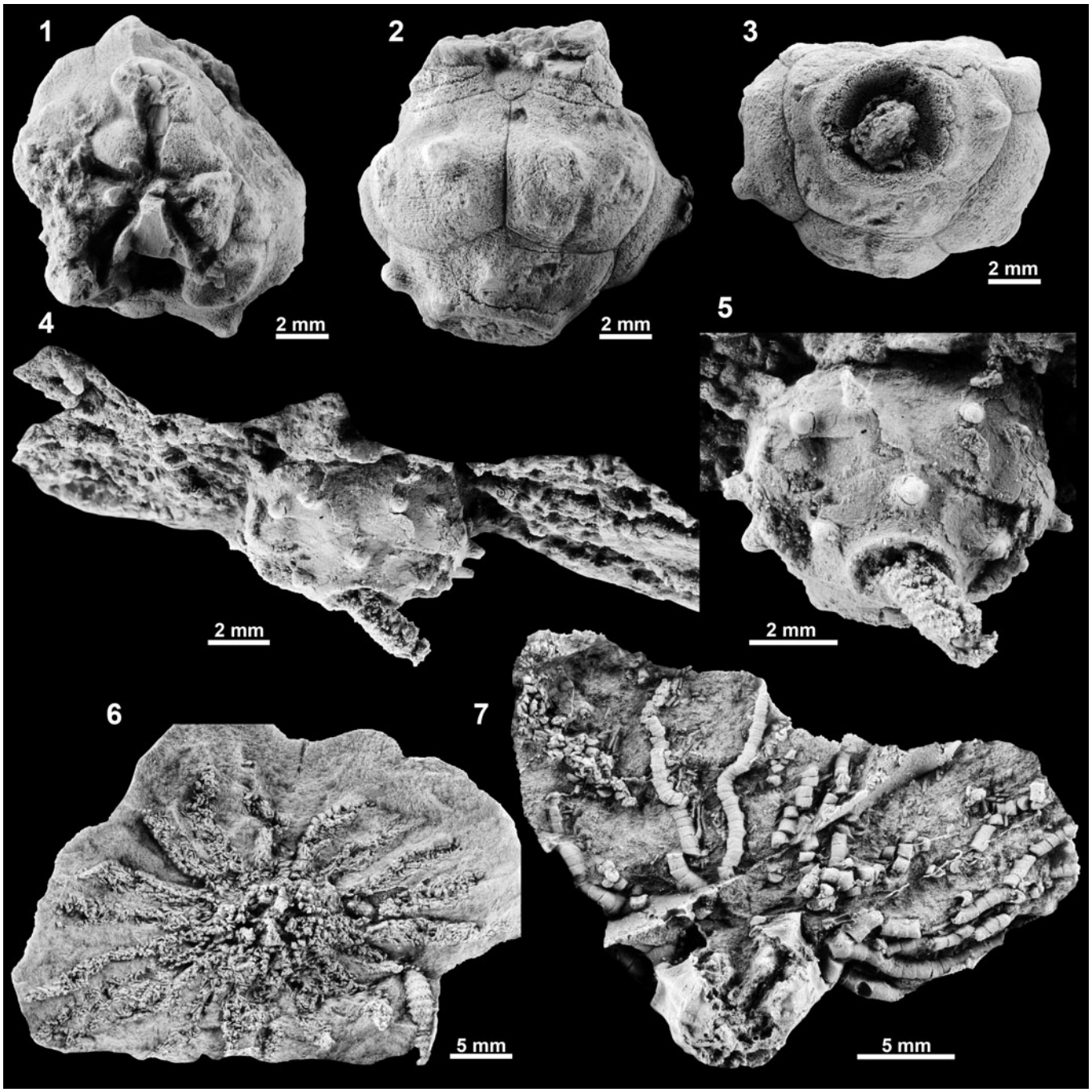

Figure 5. Emsian crinoids from the Coladilla-Santa Lucía formations boundary in the Cantabrian Zone (1–3) and Mariposas Formation (4–7) in the Iberian Chains, North Spain. (**1–3**) Original specimen of *Culicocrinus breimeri* n. sp. figured by Breimer (1962) as Hapalocrinidae cf. *Culicocrinus nodosus*; unknown locality, horizon probably corresponds to the Coladilla-Santa Lucía Formation boundary (according to Breimer, 1962) (MGM2996D). (**4, 5**) *Culicocrinus breimeri* n. sp. from the Mariposas Formation; (**4**) lateral view showing calyx, arms, and proximal stem; (**5**) oblique view of the calyx showing plate boundaries and ornamentation (MPZ2018/515); latex cast whitened with ammonium chloride sublimate; (**6, 7**) *Culicocrinus breimeri* n. sp. MPZ2018/517 and MPZ2018/516.

Camerata indeterminate
Figure 3.1–3.3

Occurrence.—Mariposas Formation (Emsian), Iberian Chains, Spain.

Description.—Calyx small in size; fixed rays protruding with interradial regions depressed. Calyx plate sculpturing smooth. Number and character of aboral cup circlets unknown. One interray exposed (but its orientation is not known), presumably two large interradial plates, arranged 1–1, in contact with tegmen. Tegmen with large plates and one high, central spine (Fig. 3.2).

First secundibrachial distal-most fixed brachial (Fig. 3.2). Free arms presumably 10 and atomous; brachials round chisel biserial; pinnules long, slender (Fig. 3.1).

Column unknown.

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Table 3. Species diagnosis Table for Devonian species of *Culicocrinus.*

Species	Relative Basal Circlet Height	Nature of Rim of Basal Concavity	Nodes on Radial Plates	Fixed Interradial Plates	General Character of Arms
C. inermis Jaekel, 1895	Low	Not distinctive	Elongate nodes	One large	Robust
C. inventriosus Schmidt, 1942	High	Not distinctive	Two circular nodes/spines on each plate projecting downward	One small	Gracile
C. inventriosus intemperans Schmidt, 1942	High	Short basal rim	Two or more circular nodes/spines on each plate projecting downward	One small	Robust
C. nodosus (Müller, 1855)	High	Not distinctive	Two circular nodes on each plate projecting outward	One large	Robust
C. nodosus virgo (Schmidt, 1942)	Low	Broadly convex rim	Two circular nodes/spines on each plate projecting outward and entire middle portion of radial plate expanded outward	One large	Robust
C. spinatus Jaekel, 1895a	Low	Unknown	Two long spines on each plate projecting downward	Unknown	Relatively slender
C. breimeri n. sp.	High	Short basal rim	Two circular nodes on each plate projecting outward	One small	Relatively slender

Material.—This taxon is represented by a single, poorly preserved specimen (MPZ2018/518, part and counterpart).

Remarks.—Although portions of this crinoid are well known, key morphological features, such as the presence or absence of the infrabasal circlet and plating in interradial areas, are not known. Consequently, this camerate crinoid cannot be recognized with certainty as either a monobathrid or diplobathrid camerate and is referred to here as Camerata Indeterminate. Although the central tegmen spine is similar to *Acanthocrinus carlsi* n. sp., the arms are different. The general size and shape, tegmen plating, and fixed rays suggest a monobathrid camerate, but the only Devonian crinoid from Spain and surrounding countries that bears any resemblance to this new specimen is *Macaracrinus*(?) sp. (Breimer, 1962), which is a diplobathrid. Further, *Macaracrinus*(?) sp. has a different tegmen, more fixed brachials, and more plates in interrays. The long, central tegmen spine and protruding fixed rays of Camerata Indeterminate are distinctive characteristics. These and other characters should provide a ready means by which to compare new material, which is needed for a positive identification.

Infraclass Inadunata Wachsmuth and Springer, 1885
Magnaorder Eucladida Wright, 2017
Eucladid indeterminate
Figures 3.7, 4.2, 4.3

Occurrence.—Mariposas Formation (Emsian), Iberian Chains, Spain.

Materials.—MPZ2018/519.

Remarks.—A single incomplete and partially disarticulated eucladid was collected from the Mariposas Formation (Fig. 3.7). Although unidentifiable, it has many distinctive characters. Despite the fact that the specimen is incomplete with plates somewhat askew, the following plates can be identified (Fig. 4.2, 4.3): C and D infrabasal plates; BC, CD, and DE basal plates; D and E radial plates; radianal; and first and second primibrachials in the D ray. In addition other aboral cup, column, and brachials and/or anal sac plates are present.

Key diagnostic characters that are preserved are infrabasal plates visible in lateral view, the radianal is interpreted to be beneath and to the left of the C radial plate, the radianal separates the C and D radial plates, the anal X is interpreted to be directly above the radianal and only partially in the aboral cup, radial facets are peneplenary, primibrachials are rectangular uniserial and broadly convex, the second primibrachial is axillary, and deep pits are present at the triple junction of aboral cup plates. This specimen is superficially similar to *Costalocrinus ibericus* Kammer, 2001 (especially see Breimer, 1962, pl. 15, figs. 9, 10) and *Bactrocrinites robustus* Pidal, 2008. However, it differs from *C. ibericus* in the posterior plate arrangement, as presently understood, and in the relative height and width of the primibrachials. It differs from *B. robustus* by having peneplenary radial facets and the relative height of the infrabasal circlet is unknown on the Mariposas specimen. Until specimens are recovered that reveal the aboral cup shape and arm branching, it is prudent to leave this taxon in open nomenclature.

Devonian Spanish crinoids in time and space

Crinoids are an important component of Devonian faunas in North Spain with isolated columnals a common component in many marine strata, articulated specimens are only present in certain horizons. In order to analyze the occurrence of complete crinoids in Spain, we have updated a list with all occurrences based on previous publications (see Appendix 1). This listing includes all previously known valid crinoid taxa based on preserved crowns (column taxa are excluded) known from Spain. In the present study, only Mariposas crinoids were critically evaluated for generic and specific assignments. A thorough taxonomic re-evaluation of all Devonian crinoids from Spain is needed.

In terms of stratigraphic comparisons, we used the stratigraphic scheme (Fig. 6) of García-Alcalde et al. (2002) that takes into account main areas where complete crinoids have been collected, especially in the Cantabrian Zone (Asturias and León) and the Iberian Chains (herein). Apart from these areas, complete crinoids are limited to the Lochkovian of the Pyrenees where complete crinoids have been described or figured from both Catalan (Haude, 1992) and Aragonesse (Zamora, 2018) regions.

As presently understood, ~124 crinoid taxa (based on crown material) have been named from the Devonian of Spain (Appendix 1). Excluding taxa left in open nomenclature, 93 species have been described. Of these taxa, 76% (71 species) are restricted to Spain. In contrast, only 18% (9 of 51) of the genera are restricted

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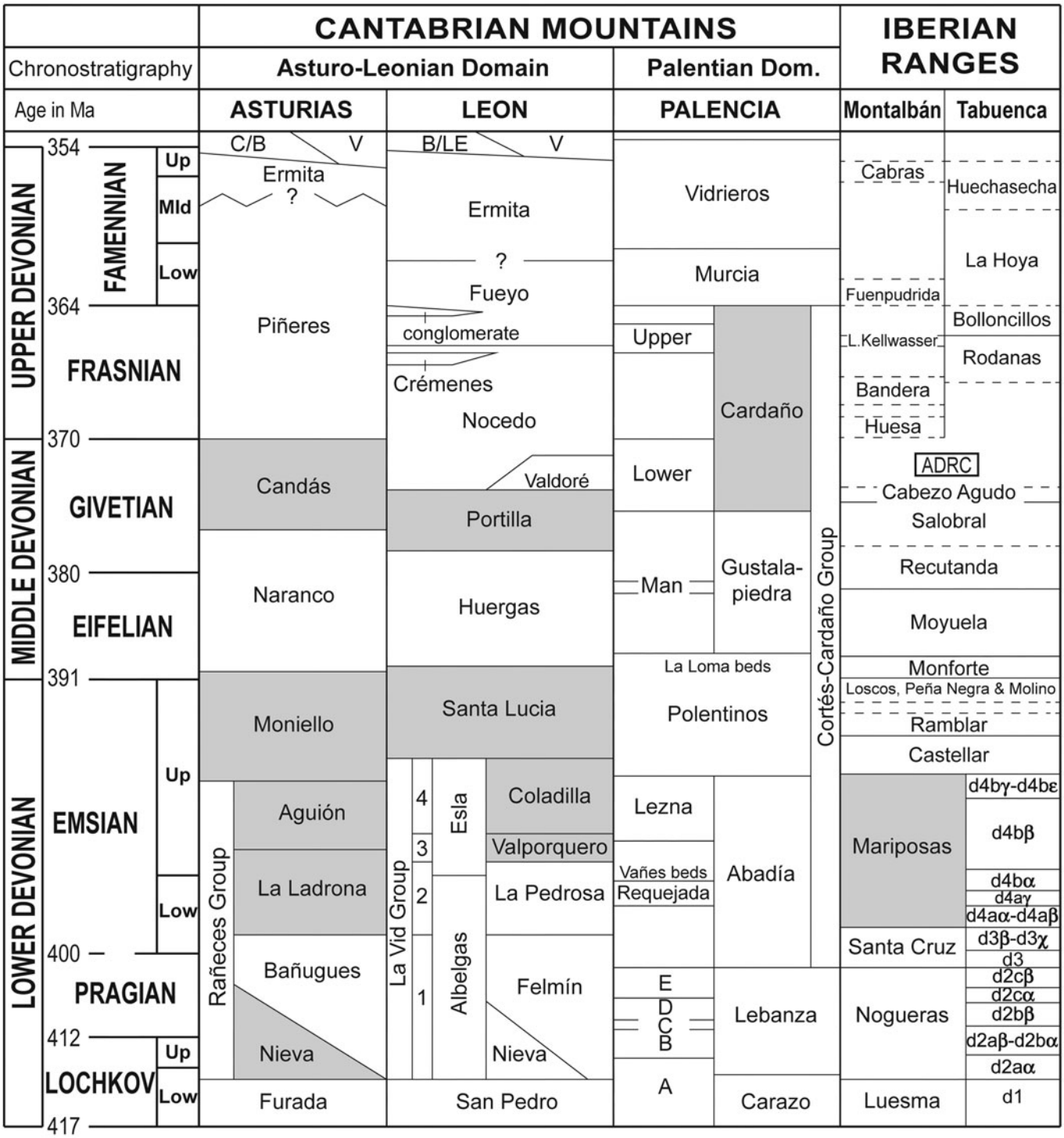

Figure 6. Chronostratigraphic chart of Devonian formations cropping out in the Cantabrian Mountains (Asturias, León, Palencia) and Iberian Ranges (Montalbán, Tabuenca). Formations providing complete crinoids are marked as gray. After García-Alcalde et al. (2002).

to Spain. Many of these taxa with wider geographic distributions are also known from southern Europe, and several are cosmopolitan, being known from Laurentia, across Gondwana, or in both regions. The new species described here are known exclusively from the Mariposas Formation from Spain (with the exception of *C. breimeri* n. sp., which is also known from the Cantabrian Zone), but all Mariposas genera are cosmopolitan.

The stratigraphically oldest complete crinoids from the Devonian in Asturias are from the Nieva Formation (Lochkovian-Pragian) where Hauser and Landeta (2007, 2012) described a crinoid assemblage from Punta de Llampero (Asturias) including an indeterminate flexible (not figured), *Botryocrinus* sp., and *Pisocrinus asturianus* Hauser and Landeta, 2012. Faunas equivalent in age to the Mariposas Formation described

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herein include a low diversity fauna from the lower Emsian that precedes the peak diversity reached during the upper Emsian of the Cantabrian Zone. Compared with Cantabrian crinoids, those from the Iberian Chains are from very shallow marine and turbid environments, and have been preserved in dark shales with few carbonate intercalations. Other important lower Emsian faunas are those from the La Ladrona, Aguión, and Moniello formations. The La Ladrona Formation (Emsian) contains complete crinoids in Asturias. They have been described in the papers of Hauser (2010) and Hauser and Landeta (2012, 2013) and include *Bactrocrinites rauffi* Hauser in Hauser and Landeta, 2012, *Diamenocrinus* sp., *Eutaxocrinus patulus* Schmidt 1942, *Oehlerticrinus anguliferus* (Whidborne, 1897), *Thylacocrinus sitter* Hauser and Landeta, 2013, and *Zenkericrinus asturianus* Hauser in Hauser and Landeta, 2012. All of the species are known exclusively from Spain, as is *Zenkericrinus*, but the remainder of the genera are cosmopolitan.

The Aguión and Moniello formations in Asturias and Valporquero, Coladilla, from the upper part of La Vid Group, and Santa Lucia formations in León record some of the most diversified crinoid assemblages from the Spanish Devonian. The La Vid Group was deposited on a carbonate ramp, and its stratigraphic succession has been tied to two 3rd order transgressive-regressive cycles (Keller and Grötsch, 1990; Keller, 1997). The shales of the Valporquero Formation are thought to record the highstand of the upper 3rd order cycle, and they correspond to one of the richest units in crinoids, especially in the famous locality of Colle and surrounding areas (Breimer, 1962; Zamora et al., 2015). The Aguión crinoid fauna consists of nine species, all of which are known only from Spain.

Crinoids continued to flourish and were abundant in the carbonate platforms from the Emsian Moniello and Santa Lucía formations (Breimer, 1962; Hauser and Landeta, 2007, 2009; Zamora et al., 2015). The Moniello Formation, in the classic locality of Arnao (Asturias), also has a rich diversified crinoid fauna. This peak diversity in crinoids from the Upper Emsian is probably related to several factors that have not been explored in detail and probably include among others the local development of reefs (Arbizu et al., 1995), microbial mounds (Fernández et al., 2006), and different substrata available for crinoid attachment (Zamora et al., 2015). Taphonomic conditions are also favorable for crinoid preservation in this interval with the alternation of high storm-induced energetic events and calm conditions plus high sedimentary rates. The Santa Lucía Formation represents a carbonate shelf with a well-developed lagoon, a reef belt, and an off-reef facies (sensu Hofmann and Keller, 2006), but distribution of crinoids within this model remains to be studied.

Unlike the bryozoans described by Suárez Andrés and Wyse Jackson (2017), the upper Emsian crinoid faunas are dominantly endemic to Spain. Only 27% (3 of 11) of the crinoid species from the Moniello Formation co-occur in Germany (e.g., *Amblacrinus rosaceus* [Roemer, 1844], *Gasterocoma antiqua* Goldfuss, 1839, and *Halocrinus nodosus* [Sandberger and Sandberger, 1856]). None occurs beyond the Rhenish-Bohemian Province of the Old World Realm (see Boucot et al., 1967, 1969; Suárez Andrés and Wyse Jackson, 2017). Similarly, only 7% (2 of 27) of species in the Santa Lucia Formation occur outside Spain (three from Germany and one from Laurentia). In contrast, of the 23 genera in the Moniello and Santa Lucia formations, 17.4% are only known from Spain, 34.7% are restricted to the Rhenish-Bohemian Province, and 47.8% occur in multiple realms and are regarded as cosmopolitan.

The youngest Devonian crinoid occurrences in Spain are from the Givetian Candás and Portilla formations in Asturias and León respectively, and the Givetian–Frasnian Cardaño Formation in Palencia. In Frasnian levels, Breimer (1962) reported a single crinoid, *Lenneocrinus ventanillensis* Breimer, 1962 from the Frasnian portion of the Cardaño Formation (see García Alcalde et al., 1988), and larger faunas are known from both the Candás and Portilla formations. As elsewhere in the Rhenish-Bohemian Province, the Cupressocrinidae are common and diverse. This well-known group has recently been revised by Bohatý (2005, 2009) and Bohatý and Herbig (2010). Givetian crinoid faunas of Spain are substantially more cosmopolitan than older faunas. At the species level, 50% (6 of 12) of Candás Formation species and 38% (3 of 8) of Portilla species are known only from Spain. However, 69% (9 of 13) of genera are cosmopolitan. One other genus is restricted to Spain, and two are known from only the Rhenish-Bohemian Province. Despite the lack of a comprehensive revision of Spanish Devonian crinoids, it is clear that as continental collisions proceeded during the Devonian, Spanish crinoid faunas became progressively more cosmopolitan.

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Appendix 1.

List of Devonian crinoids from Spain. Assignment of species to genera follow Webster and Webster (2014) and the authors that they cite. For publications after those included in Webster and Webster (2014), the generic assignments are listed as published, with the acknowledgement that some taxa may require further study. Taxa based exclusively on columnals and pluricolumnals are excluded.

FRASNIAN

Cardaño Formation; 1 km SW Ventanilla, near Cervera de Pisuerga (Palencia) (García-Alcalde et al., 1988)

Lenneocrinus ventanillensis Breimer, 1962

GIVETIAN

Candás Formation

Codiacrinus globisus Hauser in Hauser and Landeta, 2012
Cupressocrinites crassus Goldfuss, 1831
Cupressocrinites hibrida Hauser in Hauser and Landeta, 2012
Cupressocrinites hieroglyphicus (Schultze, 1866)
Espanocrinus elongatus Hauser in Hauser and Landeta, 2013
Halocrinites schlotheimii Steininger, 1831
Halocrinites sp. aff. *H. townsendi* in (Koenig, 1825)
Haplocrinites boitardi Rouault, 1847
Haplocrinites mespiliformis (Goldfuss, 1831)
Megaradialocrinus elongatus (Goldfuss, 1839)
Megaradialocrinus? *macrotatus* (Austin and Austin, 1845)
Megaradialocrinus tuberculatus (von Koenen, 1886)
Stylocrinus tabulatus depressus (Müller, 1855)
Vasocrinus aff. *turbinatus* Kirk, 1929

Portilla Formation

Ammonicrinus wanneri Springer, 1926
Cupressocrinites spp. in Breimer, 1962
Dolatocrinus cantabricus Hauser in Hauser and Landeta, 2007
Halocrinites inflatus (Schultze, 1866)
Halocrinites sampelayoi (Almela and Revilla, 1950)
Halocrinites townsendi (Koenig, 1825)
Halocrinites sp. aff. *H. townsendi* (Koenig, 1825)
Lemennocrinus truyolsi Pidal, 1984
Myelodactylus spp. in Breimer, 1962
Storthingocrinus cf. *hauhi* Oehlert, 1897
Vasocrinus conicus Hauser in Hauser and Landeta, 2007

Unspecified Formation

Cupressocrinus spp. in Oehlert, 1902

EIFELIAN

Arnao Limestone

Pyxidocrinus? bifrons (Schmidt, 1932)

cultijugatus Biozone

Platyhexacrinus kegeli Schmidt, 1931
Platyhexacrinus? pisum Schmidt, 1942
Storthingocrinus labiatus Schmidt, 1932

Peña Negra Formation

Monstrocrinus aliformis Le Menn, 1990

Unspecified Formation

Griphocrinus ovetensis Breimer, 1962
Halocrinites townsendi (König, 1825)
Orthocrinus planus Schmidt, 1932
Orthocrinus sp. in Breimer, 1962

EMSIAN OR EMSIAN-EIFELIAN BOUNDARY

Santa Lucia Formation

Alejecrinus doyagueae Hauser and Landeta, 2013
Babiacrinites costulatus Hauser in Hauser and Landeta, 2009
Babiacrinites pyramidalis Hauser in Hauser and Landeta, 2007
Bactrocrinites aff. *depressus* (Schultze, 1866)
Bactrocrinites onondagensis Goldring, 1954
Cantharocrinus melladoae Hauser and Landeta, 2012
Cantharocrinus simplex Breimer, 1962
Corocrinus? *grandosensis* Breimer, 1962
Diamenocrinus jouani Oehlert, 1891
Eifelocrinus cantabricus Hauser in Hauser and Landeta, 2007
Espanocrinus barrandei Hauser in Hauser and Landeta, 2012
Eutaxocrinus rhenanus (Roemer, 1851)
Myelodactylus spp. in Breimer, 1962
Oenochoacrinus galeatus Hauser in Hauser and Landeta, 2007
Oenochoacrinus pileatus Breimer, 1962
Orthocrinus elongatus Breimer, 1962
Orthocrinus sp. aff. *primaevus* in Le Menn, 1980
Orthocrinus robustus Mellado in Arenal, 1950
Pithocrinus abbreviatus Hauser in Hauser and Landeta, 2013
Pithocrinus ovatus Breimer, 1962
Pithocrinus aff. *P. ovatus* Breimer, 1962
Pithocrinus spinosus Breimer, 1962
Pithocrinus waliszewskii (Oehlert, 1897)
Platyhexacrinus kegeli Schmidt, 1932 in Hauser, 2015
Pyxidocrinus collensis Breimer, 1962
Sphaerocrinus wolfgangschmidti Hauser and Landeta, 2007
Storthingocrinus aff. *haughi* Oehlert, 1897
Vasocrinus breimeri Hauser in Hauser and Landeta, 2007
Verneuilicrinus ibericus (Kammer, 2001)

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Emsian-Eifelian Boundary Beds

Gasterocoma antiqua Goldfuss, 1839

Unspecified Formation

Gennaeocrinus sp. cf. *G. nyssa* (Hall, 1862)
Macarocrinus? sp. in Breimer, 1962

EMSIAN

Aguión Formation

Espanocrinus lemonei Webster, 1976
Gasterocoma xivaresensis Hauser in Hauser and Landeta, 2007
Oenochoacrinus princeps Breimer, 1962
Periechocrinus baylii (de Verneuil, 1850)
Pterinocrinus decembrachiatus Breimer, 1962
Stamnocrinus intrastigmatus (Schmidt, 1932)
Stamnocrinus sp. 1 in Breimer, 1962
Vasocrinus fernandolandetai Hauser in Hauser and Landeta, 2007
Verneuilicrinus landetai Hauser in Hauser and Landeta, 2013

Coladilla Formation

Bactrocrinites robustus Pidal, 2008

La Vid Group

Bactrocrinites sp. in Breimer, 1962
Cantharocrinus minor Breimer, 1962
Eutaxocrinus collantesi Hauser in Hauser and Landeta, 2007
Lasiocrinus? sp. in Breimer, 1962
Oenochoacrinus scaber Breimer, 1962
Pradocrinus baylii de Verneuil, 1850
Pterinocrinus tenuibrachiatus Le Menn, 1976
Pyxidocrinus collensis Breimer, 1962
Pyxidocrinus latus Breimer, 1962
Situlacrinus costatus Breimer, 1962
Trybliocrinus collensis Hauser in Hauser and Landeta, 2007
Verneuilicrinus consolidatus (Schmidt, 1942)
Verneuilicrinus ibericus (Kammer, 2001)
Verneuilicrinus thymos (Kammer, 2001)

La Ladrona Formation

Bactrocrinites rauffi Hauser in Hauser and Landeta, 2012
Diamenocrinus sp. in Hauser and Landeta, 2013
Eutaxocrinus patulus Schmidt 1942
Oehlerticrinus anguliferus (Whidborne, 1897)
Thylacocrinus sitteri Hauser and Landeta, 2013
Zenkericrinus asturianus Hauser in Hauser and Landeta, 2012

Mariposas Formation

Acanthocrinus carlsi n. sp. Ausich and Zamora, present study
Culicocrinus breimeri n. sp. Ausich and Zamora, present study
Platyhexacrinus santacruzensis n. sp. Ausich and Zamora, present study
Pterinocrinus tenuibrachiatus Le Menn, 1976
Camerata Indeterminate in Ausich and Zamora, present study
Eucladida Indeterminate in Ausich and Zamora, present study

Moniello Formation (mostly Emsian)

Amblacrinus rosaceous (Roemer, 1844)
Cantharocrinus aff. *minor* in Breimer, 1962
Codiacrinus sp. aff. *C. granulatus* Schultze, 1866
Espanocrinus arnaoiensis Hauser, 2008
Eutaxocrinus asturianus Hauser in Hauser and Landeta, 2007
Gasterocoma antiqua Goldfuss, 1839
Hallocrinus nodosus (Sandberger and Sandberger, 1856)
Moniellocrinus alcaldei Pidal, 1984
Oenochoacrinus galeatus Hauser and Landeta, 2007
Orthocrinus planus Schmidt, 1932 in Hauser and Landeta, 2009
Pithocrinus knorri Hauser and Landeta, 2012
?*Platyhexacrinus* sp. in Hauser in Hauser and Landeta, 2007
Robustocrinites scaber Schultze, 1866
Sphaerocrinus wolfgangschmidti Hauser in Hauser and Landeta, 2007

Unspecified Formation

Codiacrinus spp. in Breimer, 1962
Diamenocrinus spp. in Breimer, 1962
Gennaeocrinus sp. cf. *G. nyssa* (Hall, 1862)
Halocrinites sp. cf. *C. schlotheimi* (Steininger, 1831)
Hapalocrinidae cf. *Culicocrinus nodosus* (Müller, 1855)
Orthocrinus sp. (nov.?) in Breimer, 1962
Pterinocrinus diensti Schmidt, 1934

PRAGIAN

Nieva Formation (Rañeces Group)

Botryocrinus llamperensis Hauser in Hauser and Landeta, 2012
Pisocrinus asturianus Hauser and Landeta, 2012

LOCKHOVIAN

?Late Silurian, Early Devonian, Pridoli–Lochkovian (probably Lochkovian).

Camarocrinus n. sp.? 1 in Haude, 1992
Camarocrinus n. sp.? 2 in Haude, 1992

UNKNOWN HORIZON IN SPAIN

Orthocrinus sp. cf. *O. elongatus* in Breimer, 1962
Pleurocrinus sp. (ex. gr. *coplowensis* Wright, 1938) in Breimer, 1962 [Devonian or Mississippian]

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Pyxidocrinus sanmigueli (Astre, 1925) [glacial drift; Silurian or Devonian]
Pyxidocrinus sp. in Ruhrmann, 1971
Scyphocrinus sp. ind. in Waagen and Jahn, 1899 [Pridoli or Lockhovian]
Sphaerocrinus sp. indet. in Schmidt, 1942
Stamnocrinus sp. 2 in Breimer, 1962
Storthingocrinus haugi Oehlert, 1897
Trybliocrinus flatheanus (Geinitz, 1867)
Vasocrinus sp. cf. *V. sculptus* Lyon, 1857
Vasocrinus stellaris (Schultze, 1866)
Vasocrinus turbinatus Kirk, 1929
Vasocrinus aff. *V. turbinatus* Kirk, 1929

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