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Lower Devonian crinoids from the Basque Massifs (Western Pyrenees, Northeast Spain)

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Articles

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Abstract

Two new exquisitely preserved crinoids *Eifelocrinus baztani* n. sp. and *Gastrocrinus canteri* n. sp. are described from the late Emsian (Lower Devonian) Western Pyrenees in Northern Spain. Specimens were collected in the Cinco Villas Massif, which is considered part of the Basque Massifs. The material is preserved in finely laminated mudstones from the "Arizakun Limestone" associated with a rich invertebrate fauna. In terms of the paleobiogeography *Eifelocrinus* and *Gastrocrinus* were first reported from the Devonian of Germany, but the former is also known from the Cantabrian Zone. *Gastrocrinus aldudensis* has been described from the Aladudes Massif, in France, but this species is considered a nomen dubium herein.

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Non-technical Summary

The Devonian of the Basque Massifs in Western Pyrenees is a poorly known remote area in the boundary between Spain and France. Devonian invertebrate faunas have been known since the sixties, but they have received little attention. Herein, we describe two new crinoid species *Eifelocrinus baztani* n. sp. and *Gastrocrinus canteri* n. sp. from the late Emsian (Early Devonian, ca. 400 million years ago) of this area. The specimens are exquisitely preserved in association with a rich invertebrate fauna of trilobites, mollusks, bryozoans, and brachiopods. *Eifelocrinus* and *Gastrocrinus* are present in the classic Hunsrück Slate Lagerstätte from Germany reinforcing the connection of faunas between Spain and Germany during the Lower Devonian.

Introduction

Articulated Devonian crinoids from Spain are well known from the Cantabrian Zone, the Iberian Chains, and the central part of the Pyrenees (see summary in Ausich and Zamora, 2019) but unreported from other areas. The Devonian from the west Pyrenees in the Basque area (mainly located in Navarra Country) is one of the most unexplored areas with Devonian rocks from Spain. The Basque Massifs (including Cinco Villas, Aldudes, and Oroz-Betelu = Quinto Real) (Fig. 1) are made of Paleozoic rocks from the Ordovician to the Permian including thick Devonian successions (DeFelipe et al., 2018). Juch and Schäfer (1974) studied the Devonian of the Cinco Villas Massif, proposed a stratigraphic framework with thick Lower and Upper Devonian siliciclastic rocks, and reported indeterminate crinoids in a faunal list from the "Arizakun Limestone" that was considered upper Emsian. Exploration of the "Arizakun Limestone" in this area has resulted in the discovery of new outcrops with a rich invertebrate fauna of echinoderms, mollusks, trilobites, and brachiopods that confirm the presence of important faunas (see below). The echinoderm fauna is rich in mitrate stylophorans and crinoids that appear fully articulated. Among the later *Eifelocrinus baztani* new species and *Gastrocrinus canteri* new species are here described based on beautifully articulated specimens.

Eifelocrinus Wanner, 1916, and *Gastrocrinus* Jaekel, 1895, are primarily known from the Emsian of Germany, with exceptions being *Eifelocrinus cantabricus* Hauser in Hauser and Landeta, 2007 (Emsian or Emsian–Eifelian boundary, Spain) and *Gastrocrinus* sp. and *Gastrocrinus aldudensis* Le Maitre and Heddebaut, 1962 (Early Devonian, France) (see Webster and Webster, 2014). *Eifelocrinus cantabricus* is from the Santa Lucia Formation of northern Spain and is known from a single specimen composed of an aboral cup with several articulated primibrachials and several articulated columnals attached. *Gastrocrinus* sp. is based on a single anal sac from Mayenne (NW, France) (Le Menn, 1985) and *Gastrocrinus aldudensis* is known from another anal sac from the Aldudes Massif (South France) (Le Maitre and Heddebaut, 1962).

The new crinoids reported here, *Eifelocrinus baztani* n. sp. and *Gastrocrinus canteri* n. sp., extend the occurrence of these genera into the Western Pyrenees of Spain. Both *Eifelocrinus* and *Gastrocrinus* occur in the classic Hunsrück Slate Lagerstätte (Emsian of Germany), which is famous for exceptional fossil preservation (e.g., Bartels, et al., 1998). Perhaps counterintuitively,

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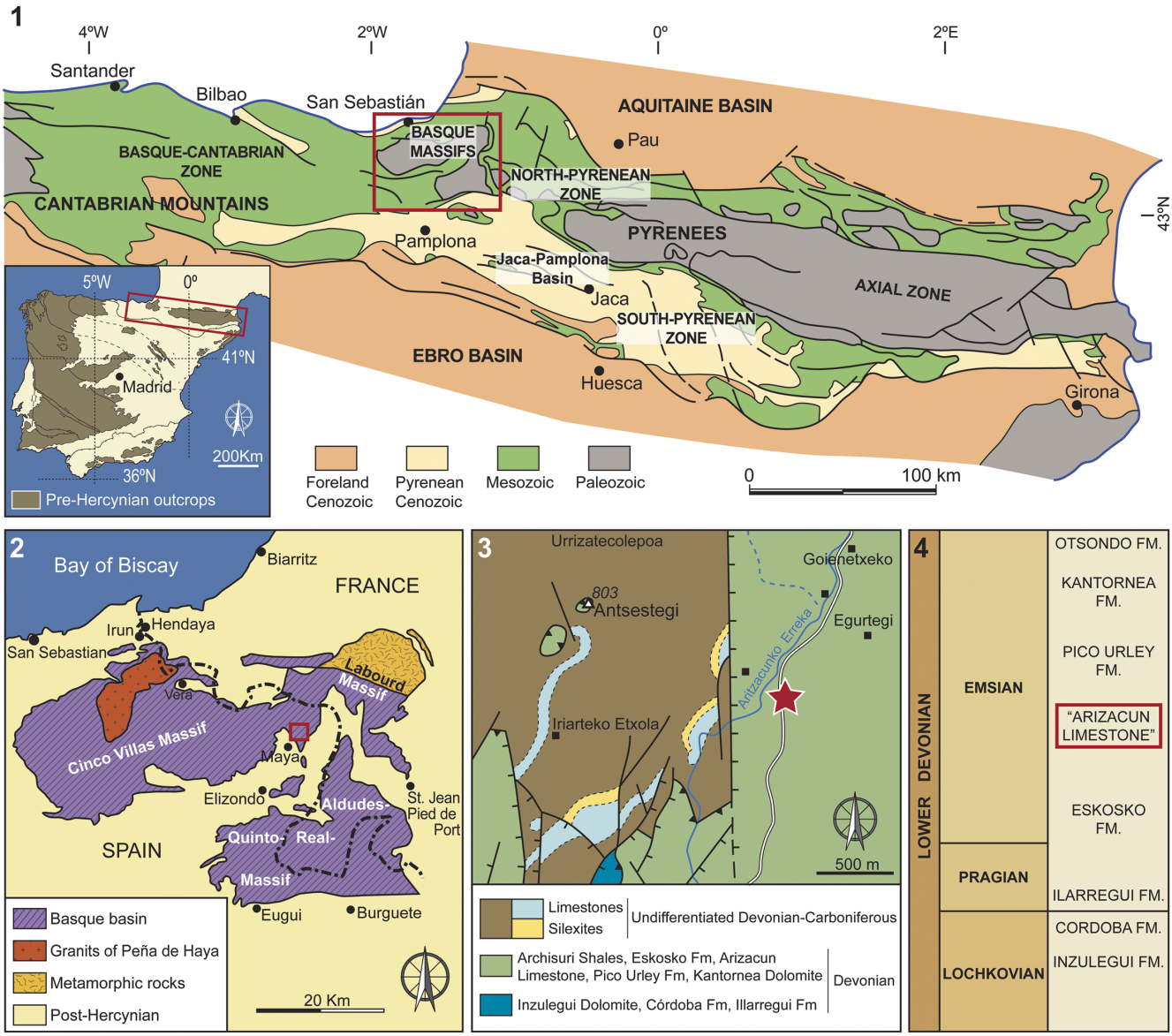


Figure 1. (**1**) Location of the Basque Massifs area in NE Spain (after Teixell, 1998, and DeFelipe et al., 2018). (**2**) Geographic and geologic setting of the Basque Massifs with location of the studied area in the Cinco Villas massif, in North Maya (modified from Juch and Schäfer, 1974). (**3**) Geologic map of the Devonian and Carboniferous of the study area; red star indicates the sampled locality (modified from Juch et al., 1972). (**4**) Stratigraphy of the Devonian in the studied area; crinoids are from the "Arizacun Limestone" (after Sanz-López, 2004).

the moldic preservation of *E. baztani* n. sp. and *G. canteri* n. sp. significantly expands our understanding of the morphology of these genera (Fig. 2.3–2.5).

Location and stratigraphy

The Basque Massifs in the Western Pyrenees include several small massifs including Cinco Villas, Aldudes, and Oroz-Betelu = Quinto Real, with Paleozoic rocks. Heddebaut (1970) and Juch and Schäfer (1974) studied the Devonian from the Cinco-Villas Massif located in the westernmost part of the Basque area (Fig. 1.2). They provided the first stratigraphic framework and faunal lists from the fossiliferous formations. The Emsian in this area is divided into five lithostratigraphic units with the age based on conodonts and brachiopods (Juch and Schäfer, 1974; see Sanz-López, 2004, for a synthesis). In ascending stratigraphic order the units are: the Eskosko Formation, "Arizacun Limestone", Pico Urley Formation, Kantornea Formation, and Otxondo Formation.

All the material described in the present paper comes from the "Arizacun Limestone", which is a 50- to 200-meter-thick unit comprised mostly of dolostones with interbedded mudstones. The formation crops out in the sides of a small path that connects the small village of Maya with France to the northeast by crossing the mountains, in the Baztan valley (Navarra). Coordinates to the place are 43°14′31.4″N, 1°26′26.4″W. The invertebrate fauna is rich and was listed by Carls (in Juch et al., 1972) and García Alcalde (personal communication, September 2019). The outcrops are fully covered with vegetation, but access to some parts of the section allowed sampling of the mudstones interbedded with the dolostones characteristic of the "Arizacun Limestone". The invertebrate fauna recognized includes the coral *Pleurodyctium problematicum* Goldfuss, 1829, trilobites (Homalonotidae

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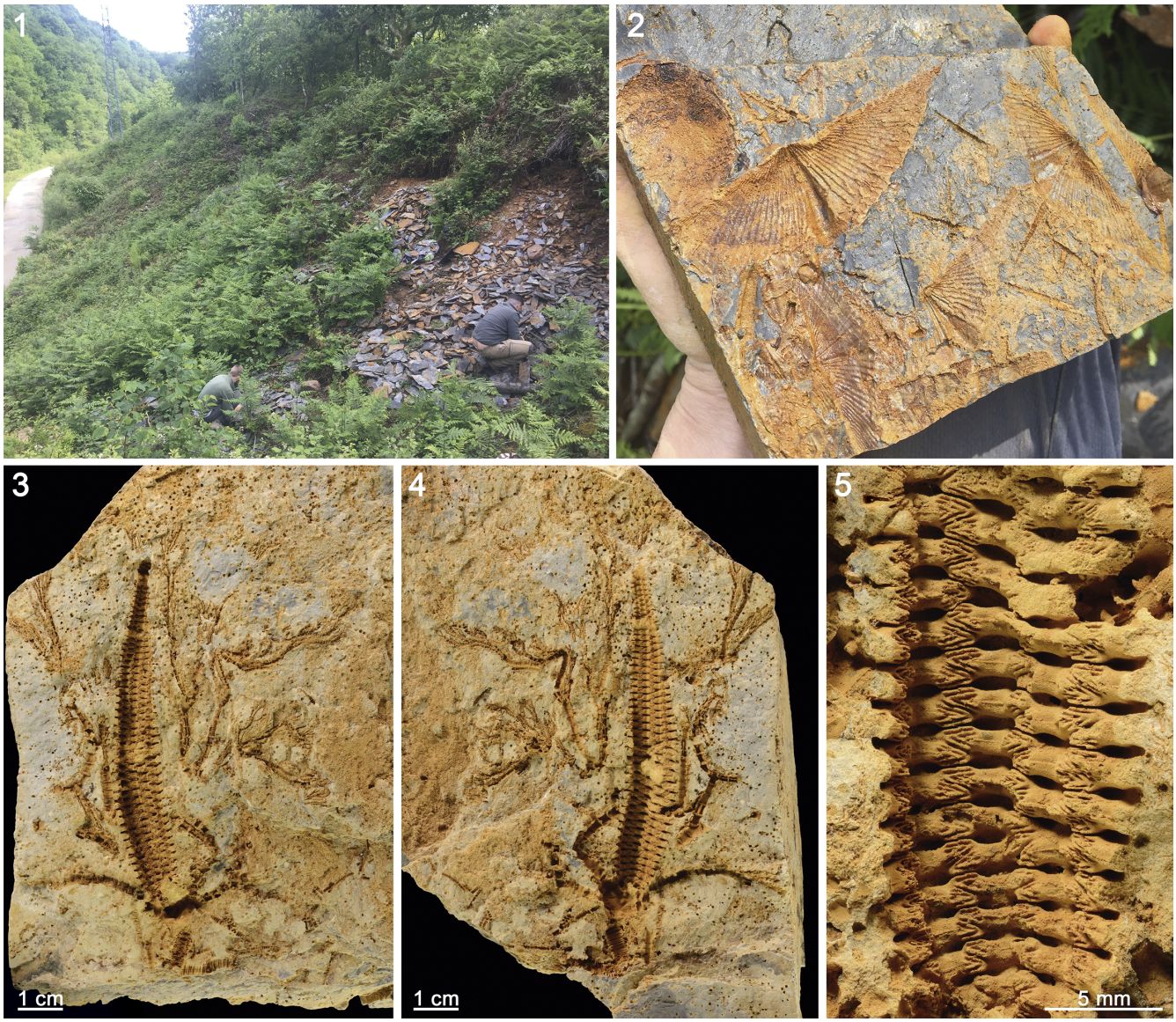


Figure 2. (**1**) Field photograph of outcrops that yielded the crinoids described here. (**2**) Moldic preservation of brachiopods (*Euryspirifer pellicoi*) and tentaculitids. (**3–5**) *Gastrocrinus canteri* n. sp. crown, MGM-3426D, holotype, part, counterpart, and detail of the anal sac.

indet., *Asteropyge* (*Kaiserops*?) cf. *A.* (*K.*?) *diadema* Richter, 1909, Bryozoa indet., Ostracoda indet., indeterminate bivalves, tentaculitids, echinoderms (crinoids and mitrate stylophorans), and the brachiopods *Euryspirifer pellicoi* (Verneuil and d'Archiac, 1845), *Leptostrophiella explanata* (Sowerby, 1842), *Plicathyris ezquerrai* (Verneuil and d'Archiac, 1845), *Schizophoria beaumonti* (Verneuil, 1850), *Plebejochonetes* sp., and Fascistropheodonta indet. (Fig. 2.2). These faunas are indicative of the upper Emsian (Juch et al., 1972).

Material and methods

Fossil crinoids in the studied area are preserved articulated with complete calyxes, arms, and part of the stem. In some instances, disarticulated columnals are rare. Fossils are concentrated in certain layers, with other layers apparently unfossiliferous. When present, shelly faunas are abundant and well preserved. Tentaculitids are common and have a high degree of orientation in some cases indicating unidirectional currents. All the invertebrates are preserved as natural molds. Horizontal trace fossils are abundant in certain levels.

Specimens were casted with latex prior to photography and whitened with ammonium chloride sublimate (Figs. 3–5). All measurements are in mm; * indicates a measurement was incomplete.

Repository and institutional abbreviation. Specimens are deposited in the Museo Geominero, Instituto Geológico y Minero de España-CSIC, Madrid, Spain under acronym MGM.

Systematic paleontology

The superfamilial classification used here follows Wright et al. (2017) and Wright (2017). Family-level classifications follow Moore and Teichert (1978). Morphologic terminology follows Webster (1974), Ubaghs (1978), Ausich et al. (2020), Ausich (2021), Donovan (2021), and Ausich and Donovan (2023).

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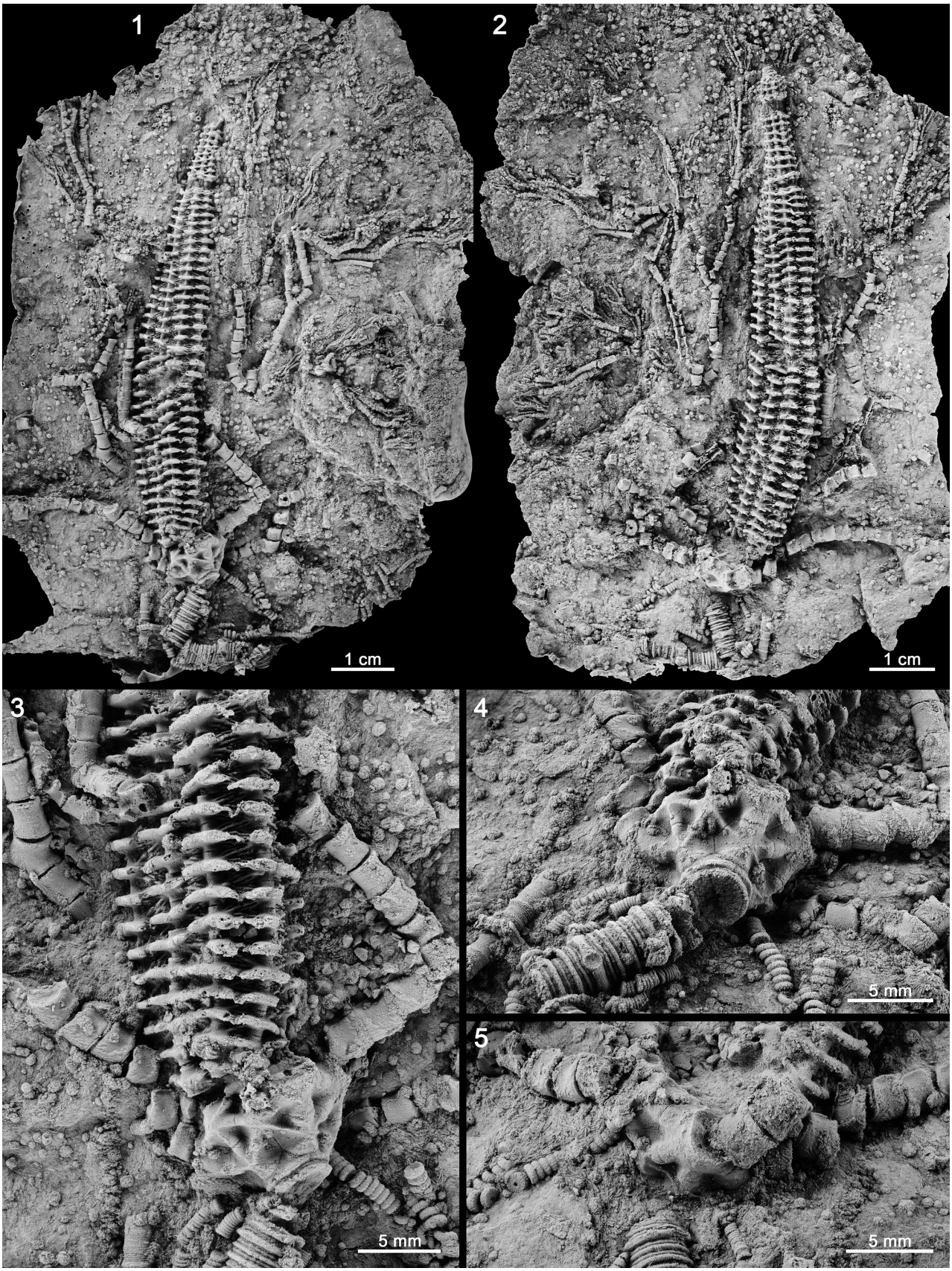


Figure 3. *Gastrocrinus canteri* n. sp. crown, holotype, MGM-3426D. (**1**) Part, note distal arm branching. (**2**) Counterpart. (**3**) Enlargement of aboral cup and proximal anal sac, note subcircular radial facet with axial canal and strong articular ridge, part. (**4**) Oblique view of proximal column and aboral cup, CD interray, note radice scars on nodal plates, part. (**5**) Radial plate with proximal brachials attached, note the radial facet, counterpart. All specimens are latex casts whitened with ammonium chloride sublimate.

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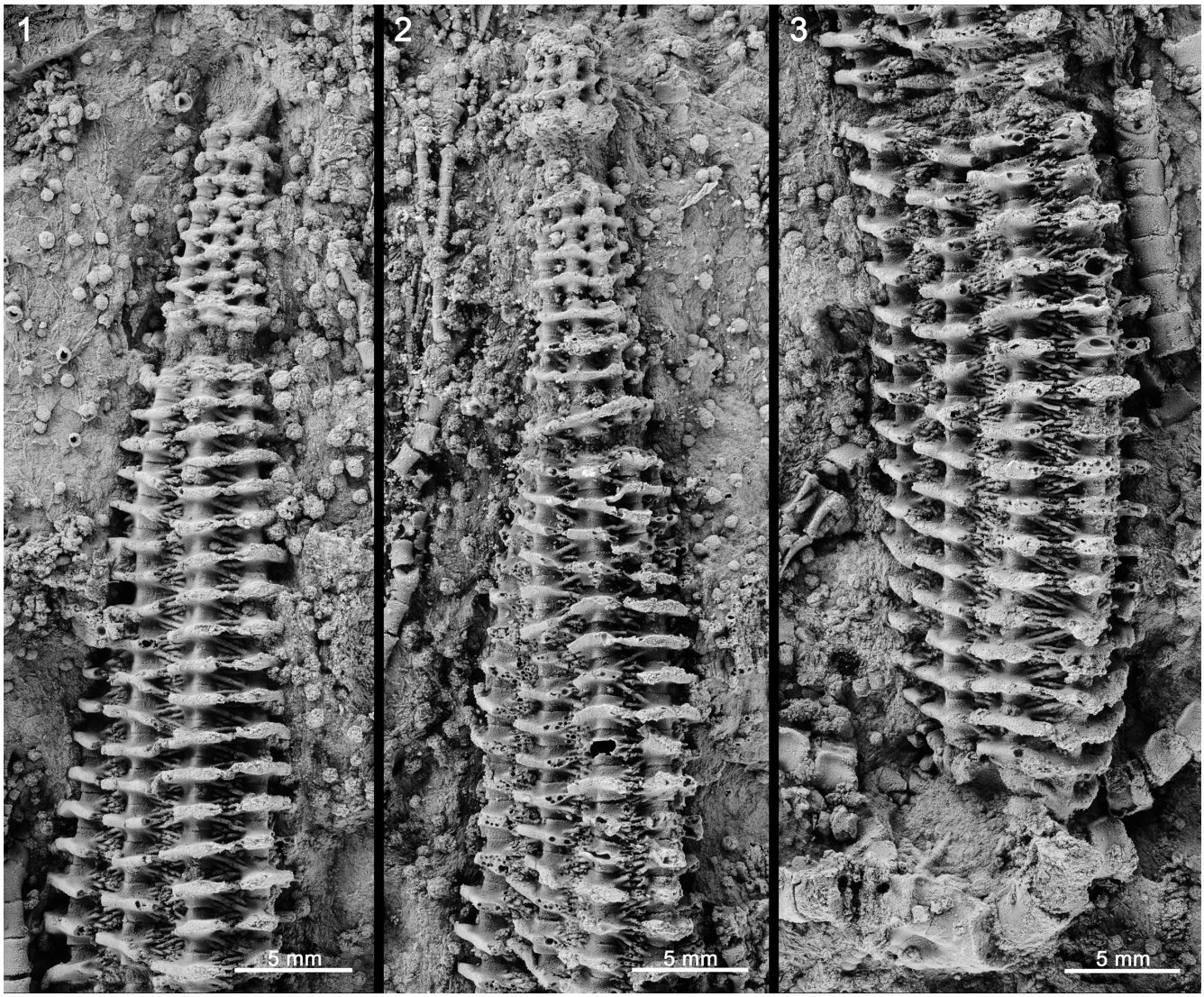


Figure 4. *Gastrocrinus canteri* n. sp., holotype MGM-3426D, note the plicate nature of the anal sac ridges and lack of pores into the interior of the anal sac (except where broken), compare to Figure 2.5. (**1**) Enlargement of distal and medial anal sac, part. (**2**) Enlargement of distal and medial anal sac, counterpart. (**3**) Enlargement of proximal and medial anal sac, counterpart. All specimens are latex casts whitened with ammonium chloride sublimate.

Class **Crinoidea** Miller, 1821
Subclass **Pentacrinoidea** Jaekel, 1918
Infraclass **Inadunata** Wachsmuth and Springer, 1885
Parvclass **Cladida** Moore and Laudon, 1943
Magorder **Eucladida** Wright, 2017
Family **Botryocrinidae** Wachsmuth and Springer, 1886
Genus ***Gastrocrinus*** Jaekel, 1895

Type species. *Poteriocrinus patulus* Müller, 1859; monotypy.

Included species. *Gastrocrinus brancai* Schmidt, 1914; *G. canteri* Zamora and Ausich n. sp.; *G. dahmeri* Schmidt, 1942; *G. drevermanni* Schmidt, 1914; *G. eupelmatus* (Schmidt, 1915); *G. follmanni* Schmidt, 1914; *G. giganteus* Schmidt, 1934; *G. leunisseni* Franke, 2012; *G. patulus* (Müller, 1859); and *G. rugosus* Schmidt, 1914.

Gastrocrinus canteri new species
Figures 2.3–2.5, 3–5; Table 1

Types. The holotype, MGM-3426D, is a complete specimen lacking the distal stem and preserving both part and counterpart. The paratype, MGM-3430D, is also a nearly complete specimen but the calyx is crushed.

Other material. MGM-2427D, MGM-2428D (part and counterpart), MGM-3429D (part and counterpart), MGM-3431D, MGM-3432D (part and counterpart), and MGM-3433D (part and counterpart).

Diagnosis. *Gastrocrinus* with a low cone-shaped aboral cup; prominent development of plicated aboral cup plates, anal sac prominent, ~10 times higher than aboral cup height; ~24 anal sac plates in first 2 cm of height; horizontal or slightly angled ridges are the dominant anal sac ridges, arms robust.

Occurrence. "Arizacun Limestone" (Baztan Valley, Navarra, NE Spain).

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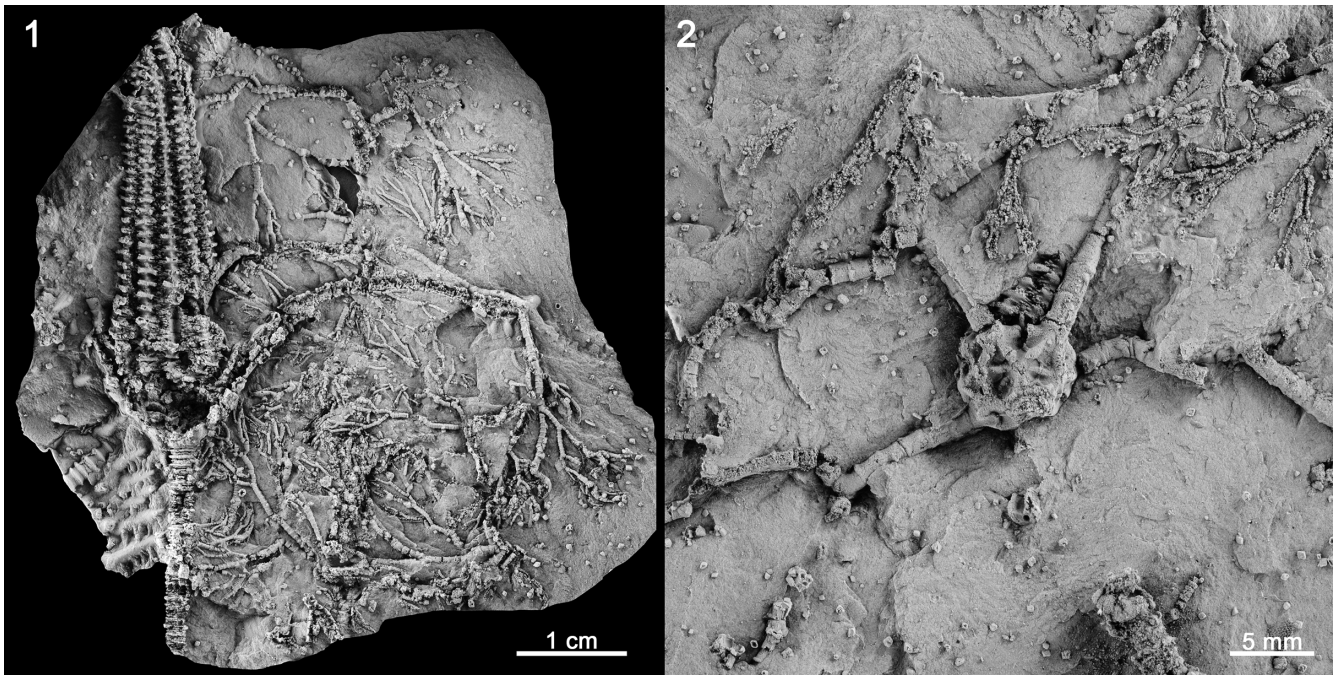


Figure 5. *Gastrocrinus canteri* n. sp. (**1**) Crown with crushed calyx, note dense distal arm branching, paratype, MGM-3430D. (**2**) Calyx with partial proximal anal sac and arms, specimen, MGM-3427D. All specimens are latex casts whitened with ammonium chloride sublimate.

Description. Crown small in size (Figs. 2, 3.1, 5). Aboral cup low cone-shaped (height/width ~0.57); plates with prominent ridges as part of plate plications connecting to like plications on adjacent plates; and deep, triangular depressions at plate triple junctions (Fig. 3.4). Infrabasal circlet ~20% of aboral cup height. Infrabasal plates presumably five, visible in lateral view, ~2.0 times wider than high. Basal circlet ~30% of aboral cup height. Basal plates presumably five, hexagonal or heptagonal, as high as wide (Fig. 3.3); BC basal plate mostly beneath C radial plate; CD basal plate sutured above to D radial plate, anal X, and radianal (not in sutural contact with C radial plate) (Fig. 3.4). Radial circlet height ~50% of aboral cup height. Radial plates five, pentagonal, height/width ratio ~0.89. Radial facets peneplenary, subcircular, strongly declivate (Fig. 3.5), occupies ~77% of distal radial plate width; axial canal penetrates through center of radial facets and a prominent articular ridge across width of facet and on either side of axial canal (Fig. 3.3).

Three posterior plates in aboral cup. Radianal smaller than radial plates pentagonal, sutured beneath to upper shoulders of BC and CD basal plates; sutured laterally to anal X and C radial plate, and sutured above to right sac plate (Fig. 3.4). Anal X plate sutured beneath with D radial plate, CD basal plate, and radianal; above sutured to anal sac plates and right sac plate. Right sac plate partially in aboral cup, sutured below to the radianal and above to anal sac plates. Anal sac very high (~10 times higher than aboral cup height), gradually tapering cone (Fig. 3.1, 3.2), composed of ~8 columns of highly plicate plates (Fig. 4.1–4.3). Anal sac plates strongly convex laterally. Plates of adjacent columns alternate (Fig. 4.2). Perpendicular to the anal sac height a thick longitudinal ridge connects to similar ridges on plates of the adjoining columns of anal sac plates. Small ridges radiate from the side of anal sac column plates and also connect to similar ridges on adjoining column anal sac plates (Fig. 4) forming "rhomb-like" endothecal structures.

Arms poorly preserved, nonpinnulate, irregularly dichotomous branching in proximal arm with at least 4 major branches per ray (probably more) (Fig. 3.1, 3.2). Distal arms very narrow, branch many times with poor isotomy (Fig. 5). Brachials rectilinear uniserial proximally. Number of primibrachials more than 10. Primibrachials as high as wide, secundibrachials and above higher than wide, widest part of brachial plates at suture with adjacent plates, sides of brachials convex.

Proximal column holomeric, heteromorphic, and circular. Proximal column with nodal-internodal pattern N3231323; more internodals distally. Nodals with radices, much wider and higher than internodals; expanded, protruding radice facet (Fig. 3.4).

Etymology. The species name refers to Antonio García Cantero who collected this crinoid. He also helped during field work.

Measurements. MGM-3426D holotype: aboral cup height, 6.5 mm; aboral cup width, 9.5 mm; anal sac height, 57.0* mm. MGM-3430D, paratype: crown height, 105.0* mm; aboral cup height, 7.0* mm; aboral cup width, 18.0* mm; anal sac height, 57.0* mm.

Remarks. The large anal sac, cone-shaped aboral cup, subcircular peneplenary radial facets, arrangement of CD interray plates, sparsely branched proximal and medial arms, and densely branched distal arms align this new species with *Gastrocrinus*. Previously, *Gastrocrinus* was primarily known from the Emsian Hunsrückshiefer in Germany, although it has also been reported from other Emsian units in Germany and from Algeria and France (Webster and Webster, 2014). *Gastrocrinus aldudensis* from the close Aldudes Massif in France (Fig. 1.2) is only known from an isolated anal sac, so comparison to other species is not possible. Herein, we consider *G. aldudensis* a nomen dubium, and this specimen should be referred to as *Gastrocrinus* sp. Several Devonian crinoid faunas have been described from Spain (e.g., Breimer, 1962;

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Table 1. Characters that differentiate species of *Gastrocrinus*

Gastrocrinus species	Age/Locality	Aboral Cup Shape	Development of Aboral Cup Plate Plications	Anal Sac Size	Anal Sac Height	Number of Anal Sac Plates in First 2 cm	Dominant Ridges: Vertical or Horizontal	Attitude of Primary Horizontal Ridge	Arm Size
G. brancai Schmidt, 1914	Emsian Germany	Low cone	Moderate?	Slender	~14 times higher than aboral cup	~22	Vertical	Horizontal	Slender
G. dahmeri Schmidt, 1942	Emsian Germany	Very low cone	Moderate?	Prominent	~10 times higher than aboral cup	20	Horizontal	Horizontal	Robust
G. drevermanni Schmidt, 1914	Emsian? Germany	Unknown	Absent?	Prominent	Unknown	Unknown	Vertical	Horizontal or slightly angled	Robust
G. euplematus (Schmidt, 1915) [defined primarily on column characters]	Emsian Germany	Low cone	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
G. follmanni Schmidt, 1914	Emsian Germany	Low bowl	Prominent	Prominent	Unknown	14	Horizontal	Horizontal or slightly angled	Robust
G. giganteus Schmidt, 1934	Emsian Germany	Very low cone	Moderate	Prominent	~20 times higher than aboral cup	10 to 11	Horizontal	Horizontal or slightly angled	Robust
G. leunisseni Franke, 2012	Emsian Germany	Very low cone	Moderate	Prominent	~13 times higher than aboral cup	~25	Vertical and horizontal subequal	Horizontal or slightly angled	Robust
**G. patulus* (Muller, 1859)	Emsian Germany, Algeria	Very low cone	Prominent	Prominent	Unknown	10 to 13	Vertical and horizontal subequal	Horizontal or slightly angled	Robust
G. rugosus Schmidt, 1934	Emsian Germany	Unknown	Slight	Prominent	Unknown	Unknown	Vertical and horizontal subequal	Angled	Unknown
G. canteri n. sp.	Emsian Spain	Low Cone	Prominent	Prominent	10 times higher than aboral cup	24	Horizontal	Horizontal or slightly angled	Robust

Hauser and Landeta, 2007; Hauser, 2012; see a summary in Ausich and Zamora, 2019), but *G. canteri* n. sp. is the first report of this genus from Spain.

Characters that differentiate species of *Gastrocrinus* are aboral cup shape, degree of development of plications of the aboral cup plates, relative size of the anal sac, anal sac height, number of plates in the first 2 cm of the anal sac, ridges on anal sac plates are dominant, the attitude of the primary horizontal ridges on anal sac plates, and relative arm size. *Gastrocrinus canteri* n. sp. is most similar to *G. brancai* and *G. follimanni*. *Gastrocrinus brancai* has a low cone-shaped aboral cup; moderate development of plicated aboral cup plates; slender anal sac, ~14 times higher than aboral cup height; ~22 anal sac plates in the first 2 cm of anal sac height; vertical ridges are the dominant anal sac ridges; additional horizontal ridges on anal sac plates, and slender arms. *Gastrocrinus follmanni* has a low bowl-shaped aboral cup; moderate development of plicated aboral cup plates; anal sac prominent, height relative to aboral cup unknown, ~14 anal sac plates in the first 2 cm of anal sac height; horizontal ridges are the dominant anal sac ridges additional ridges on anal sac oriented horizontal or slightly angled; and robust arms. In contrast, *G. canteri* n. sp. has a low cone-shaped aboral cup; prominent development of plicated aboral cup plates; anal sac prominent, ~10 times higher than aboral cup; ~24 anal sac plates in the first 2 cm of anal sac height; horizontal ridges are the dominant anal sac ridges, oriented horizontally or slightly oblique; and robust arms. All species assigned to *Gastrocrinus* are compared in Table 1.

The anal sac of *Gastrocrinus* has endothecal "rhomb-like" structures formed by the small plications at the lateral margins of two adjacent anal sac plates. Where broken, it is evident that the smaller and perhaps larger plications of these endothecal structures were open to the interior of the aboral cup, but there is no evidence that these endothecal structures directly connected the interior of the specimen to open sea water. Hence, these "rhomb-like" structures are similar to those of the anal sac in several other eucladids (e.g., *Aesiocrinus* Miller and Gurley, 1890; see Lane, 1975).

The distinctive arms of *Gastrocrinus* are quite unusual. The proximal two-thirds of the arms have widely spaced, poor isotomy branching, whereas the distal third of the arms are densely branched with poor isotomy. The result is a very open filtration fan in the lower portion of the arms and very dense branching in the upper third.

Family **Mastigocrinidae** Jaekel, 1918
Genus ***Eifelocrinus*** Wanner, 1916

Type species. *Ptilocrinus dohmi* Wanner, 1916; original designation.

Included species. *Eifelocrinus baztani* Zamora and Ausich n. sp.; *E. bifurcatus* Haarmann, 1920; *E. cantabricus* Hauser *in* Hauser and Landeta, 2007); *E. dohmi* (Wanner, 1916); *E. hefteri* Schmidt, 1942; *E. pennula* Schmidt, 1942; *E. pulvinatus* Schmidt, 1942; and *E. rhenanus* Jaekel, 1918.

Eifelocrinus baztani new species
Figure 6;Table 2

Type. The holotype, MGM-3435D, is a complete specimen (one part only) preserving the cup, arms, and stem.

Other material. MGM-3434D is a partial specimen.

Diagnosis. *Eifelocrinus* with a high cone-shaped aboral cup, robust primary ramules, and gracile and long secondary ramules.

Occurrence. "Arizacun Limestone" (Baztan Valley, Navarra, NE Spain).

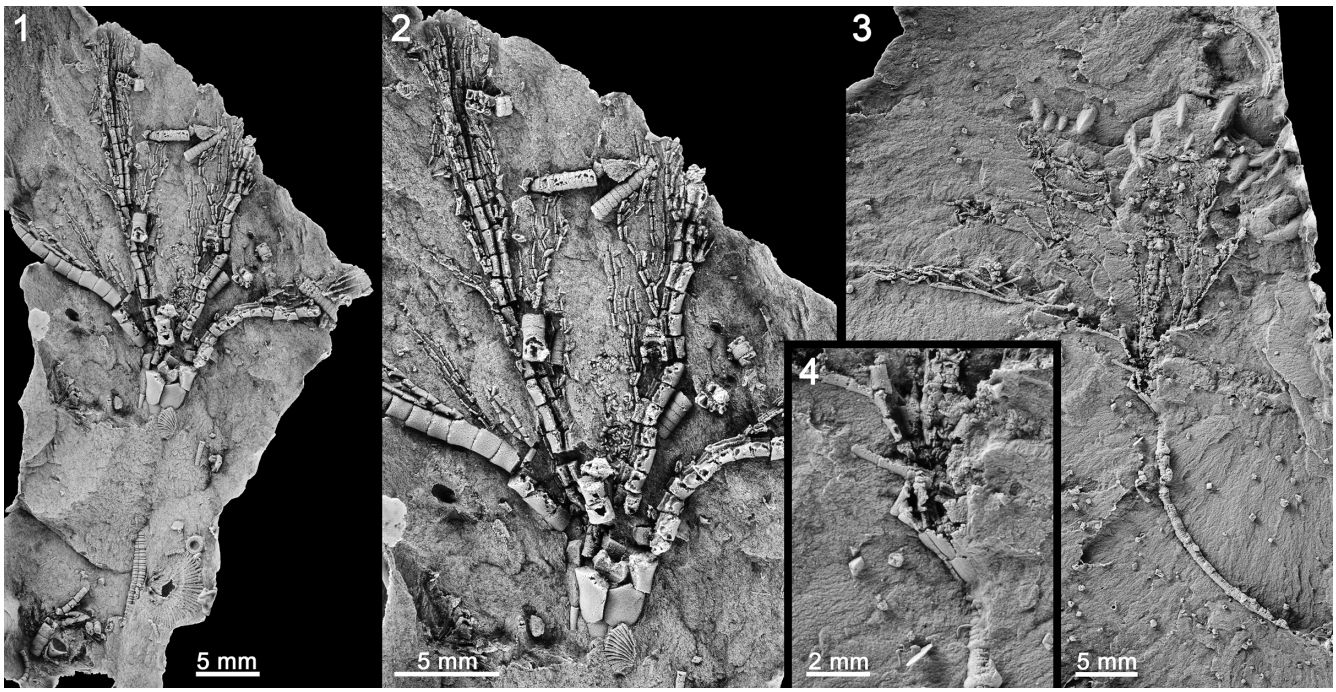


Figure 6. Incomplete crowns of *Eifelocrinus baztani* n. sp. (**1**) Crown and part of column, holotype MGM-3435D, (**2**) enlargement of aboral cup and proximal anal sac. ?*Eifelocrinus baztani* n. sp. (**3**) Crown, arms, and column, MGM-3434D, (**4**) enlargement of aboral cup of specimen illustrated in (**3**). All specimens are latex casts whitened with ammonium chloride sublimate.

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Table 2. Characters that differentiate species of *Eifelocrinus*

Eifelocrinus species	Age/Locality	Aboral Cup Shape	Primary Ramules	Secondary Ramules
E. bifurcatus Haarmann, 1920	Emisan Germany	Medium bowl	Gracile	Gracile, long
E. catabricus Hauser in Hauser and Landeta, 2007	Emsian-Eifelian Spain	Medium cone	Unknown?	Unknown?
E. dohmi (Wanner, 1916)	Emsian Germany	Medium cone	Gracile	Gracile, long
E. hefteri Schmidt, 1942	Emsian Germany	Medium cone	Gracile	Robust, long
E. pennula Schmidt, 1942	Emsian Germany	Medium cone	Gracile	Gracile, short
E. pulvinatus Schmidt, 1942	Emsian Germany	Unknown	Robust	Robust, long
E. rhenanus Jaekel, 1918	Emsian Germany	Very low cone	Unknown?	Unknown?
E. baztani n. sp.	Emsian Spain	High cone	Robust	Gracile, long

Description. Crown small in size. Aboral cup plates broadly convex with smooth plate sculpturing (Fig. 6.2). Aboral cup high bowl-shaped. Infrabasal plate circlet ~28% of aboral cup height; infrabasal plates presumably five, higher than wide, visible in lateral view. Basal plate circlet ~39% of aboral cup height (Fig. 6.4); basal plates presumably five, hexagonal, higher than wide (height/width ratio ~1.3). Radial plate circlet ~33% of aboral cup height; radial plates presumably five, approximately as high as wide, pentagonal. Radial facets subcircular to ellipsoidal, peneplenary (~90% of radial plate width), gently declivate, deep adoral groove, a linear articular ridge along the width of the facet below adoral groove.

Posterior plates of aboral cup not preserved.

Five arms; with ramulate branching (Fig. 6.1–6.3). First ramule branches from ~4th primibrachial, subsequent branches at irregular intervals. Individual primary ramules bear ramules approximately every other ramular with secondary ramules always branching on the adaxial side of primary ramules. Brachials and ramulars rectilinear uniserial, higher than wide, sides straight.

Middle column may be pentameric, pentalobate, heteromorphic (Fig. 6.1, 6.4). Nodal-internodal pattern N-1.

Etymology. The name *baztani* refers to the Baztan valley in the Basque massifs where the material has been collected.

Measurements. MGM-3435D, holotype: Crown height, 30.4* mm; aboral cup height, 5.4* mm; aboral cup width, 4.4* mm; basal plate height, 2.4* mm; basal plate width, 1.9* mm; radial plate height, 2.2 mm; radial plate width 2.2* mm.

Remarks. Eifelocrinus is a distinctive eucladid with variously shaped aboral cups, five arms with primary ramules that have secondary ramules branching only on the adaxial side of the first-order ramules, and a pentalobate column. Based on these defining characters MGM-3435D can be confidently assigned to *Eifelocrinus*, despite the fact that the aboral cup is poorly preserved and the posterior interray is not known.

A second specimen (MGM-3434D) (Fig. 6.3, 6.4) is tentatively assigned to *E. baztani* n. sp. The aboral cup of this second specimen is nearly one-half the size of the *E. baztani* n. sp. holotype. The aboral cup is also partially disarticulated, the arms are much thinner and poorly preserved, it has a long length of column, and an anal sac preserved. The aboral cup is very similar to that of *E. baztani* n. sp., but the thin arms are too poorly preserved to discern whether the arm branching pattern is that of *Eifelocrinus*. The anal sac of MGM-3434D is cylindrical, narrow, and high but shorter than the arms (Fig. 6.3). It probably consists of 4–5 columns of small, convex plates. A long portion of the column is preserved with pentalobate proximal columnals and circular columnals in the middle portion of the column.

Seven species of *Eifelocrinus* have been described previously, all but one were described from the Emsian of Germany (Webster and Webster, 2014). The single exception is *E. cantabricus*, which was described from the Emsian Santa Lucia Formation (Ausich and Zamora, 2019) in northern Spain (see Hauser in Hauser and Landeta, 2007). The holotype and only known specimen of *E. cantabricus* is an aboral cup with a few proximal primibrachials and proximal column. The height of the arms on this specimen is insufficient to preserve the characteristic ramule branching of *Eifelocrinus*.

Characters that differentiate species of *Eifelocrinus* are the aboral cup shape, character of the primary ramules, and character of the secondary ramules. *Eifelocrinus baztani* n. sp. is most similar to *E. dohmi* and *E. pulviatus*. *Eifelocrinus dohmi* has a medium cone-shaped aboral cup, gracile primary ramules and gracile and long secondary ramules. *Eifelocrinus pulviatus* has gracile primary ramules and robust and gracile and long secondary ramules (the shape of the aboral cup is not known). In contrast, *E. baztani* n. sp. has a high cone-shaped aboral cup, robust primary ramules, and gracile and long secondary ramules.

Discussion and concluding remarks

Devonian crinoids from Spain are well documented from the Cantabrian Zone (Breimer, 1962), Iberian Chains (Ausich and Zamora, 2019), and central Pyrenees (Haude, 1992). With the description of *E. baztani* n. sp. and *G. canteri* n. sp., we expand the distribution of complete articulated crinoids to the western Pyrenees. Both genera also have been described from the Lower Devonian of Germany. *Gastrocrinus* is also present in the Devonian of France. These data reinforce the observations from other authors on the similarities of echinoderm faunas between the Iberian Peninsula and France (Le Menn, 1985) and Germany (Smith et al., 2013) during the Lower Devonian.

A striking character of *G. canteri* n. sp. is the deeply plicated plates on the anal sac. Although not common, similar structures occur in other eucladids, including *Botryocrinus* Angelin, 1878 (middle Silurian–Middle Devonian, Europe and North America), *Proctothylacocrinus* Kier, 1952 (Middle Devonian, North America), *Gilmocrinus* Laudon, 1933 (Lower Mississippian, North America), and *Aesiocrinus* Miller and Gurley, 1890 (Lower Pennsylvanian, North America). The structure on *Aesiocrinus* is quite different than that on *Gastrocrinus*, but one of the functions proposed by Lane (1975) for the plicated plates and canals was

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respiration. Although untestable, this is a reasonable interpretation for *Gastrocrinus*.

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Competing interests. The authors declare none.

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