

# Filling the Silurian gap of solutan echinoderms with the description of new species of *Dehmicystis* from Spain

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Solutans were among the most enigmatic pre-radial and asymmetric echinoderms. A new species *Dehmicystis ariasi* sp. nov. is described from the upper part of the Llagarinos Formation, lower Ludlow (Silurian) of Northwest Spain. This is the first solutan formally described from Iberia and the first from the Silurian worldwide. *Dehmicystis* was previously known based on a small number of poorly preserved specimens from the Emsian, Lower Devonian Hunsrück Slate of Germany. New observations based on the newly studied material suggest that *Dehmicystis* displayed a feeding appendage facing towards the substrate, and the periproct on the opposite face of the theca. Comparisons with other solutans and new data suggest that *Dehmicystis* was a detritus feeder that moved over the substrate capturing organic particles from the sediment with a single feeding arm.

Key words: Echinodermata, Soluta, pre-radial, asymmetric, Rhuddanian, Silurian, Spain.

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## Introduction

Solutans are one of the most enigmatic, exclusively Paleozoic, group of fossil echinoderms whose phylogenetic position is controversial. They had a single ambulacrum and lacked the typical five-fold symmetry of modern echinoderms. Due to their bizarre morphology, the taxonomic position of the group has changed over time since they were first described in the mid-19th century (Noailles et al. 2014 and references therein). They were originally considered as a group of pelmatozoans related with diploporans, eocrinoids, and stylophorans (Bather 1899). Jaekel (1901) considered them as a group of carpoids within pelmatozoans, and grouped them with the asymmetric rhipidocystid eocrinoids. Gill and Caster (1960) were the first to remove rhipidocystids (that they assigned to the subclass Homostelea) from the “order” Soluta providing a better definition of the group. With the publication of the *Treatise on Invertebrate Paleontology*, Caster (1968) recognized the status of solutans (then included within homoiosteleans) (see further information about the early history of solutans in Lefebvre et al. 2012 and Noailles et al. 2014).

Recent contributions consider solutans as a separate class of echinoderms (Lefebvre et al. 2012; Noailles et al. 2014; Nohejlová and Lefebvre 2022), with major disagreements over whether they represent preradial echinoderms before the development of the five-fold symmetry (Smith 2005, 2008; Zamora and Rahman 2014; Rozhnov 2022) or as a distinct group of blastozoans (David et al. 2000; Sprinkle and Guensburg 2004; Noailles et al. 2014).

Solutans ranged from the middle Drumian (Cambrian) to the Emsian (Lower Devonian) (Lefebvre and Lerosey-Aubril 2018). Diversity rapidly increased in the Cambrian Series 3, dropped by the Furongian and started to increase again by the Ordovician (Zamora et al. 2013; Lefebvre and Lerosey-Aubril 2018). No solutan taxa have been described so far from Silurian strata, suggesting that this class was very likely severely impacted by the Hirnantian mass-extinction (Domínguez et al. 2002; Nohejlová and Lefebvre 2022). However, here we fill the Silurian gap of solutans with the description of *Dehmicystis ariasi* sp. nov. from the ?Gorstian (lower Ludlow, Silurian) of Northwest Spain. This is the first formally described solutan from Iberia, although the Upper Ordovician from Central Spain and Iberian Chains has also provided incomplete specimens

of *Dendrocystites* (Gil Cid et al. 1996; Zamora et al. 2014). This unquestionable record of a Silurian solutan has only been preceded by possible remains of the group in the Wenlock of Wales, which however, have not yet been described (Lefebvre in Nohejlová and Lefebvre 2022: 524). The new material from Spain also helps elucidating the posture of *Dehmicystis* with respect to the substrate, and provides evidence of feeding behavior in flattened solutans that have the feeding appendage and the periproct on opposite thecal surfaces.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains have been registered in ZooBank: <http://zoobank.org/urn:lsid:zoobank.org:pub:FE359270-26C4-419A-AA05-6F68C88A3173>.

*Institutional abbreviations.*—MGM, Museo Geominero, Instituto Geológico y Minero de España-CSIC, Madrid, Spain; SMF, Naturmuseum Senckenberg, Germany.

## Geological setting

Upper Silurian strata from the NW of the Iberian Peninsula crop out in the boundary between the West Asturian-Leonese and the Central Iberian zones of the Iberian Massif (Robardet and Gutiérrez-Marco 2002), where they have provided a diverse shelly fauna with Bohemian affinities including trilobites, crinoids and bivalves (Rábano et al. 1993; Gutiérrez-Marco et al. 2001). Echinoderms are rare and only consist of a few remains of primitive planktonic scyphocrinitid crinoids, being restricted to the Siluro-Devonian formations of the Courel-Peñalba and Sil synclines in the northern Central Iberian Zone (Gutiérrez-Marco et al. 2001). According to the map of Apalategui Isasa et al. (1981), the single specimen of *Dehmicystis ariasi* sp. nov. described here comes from a Silurian outcrop located in the northern flank of the Sil Syncline near its eastern termination, right below the so-called “cuarcitas

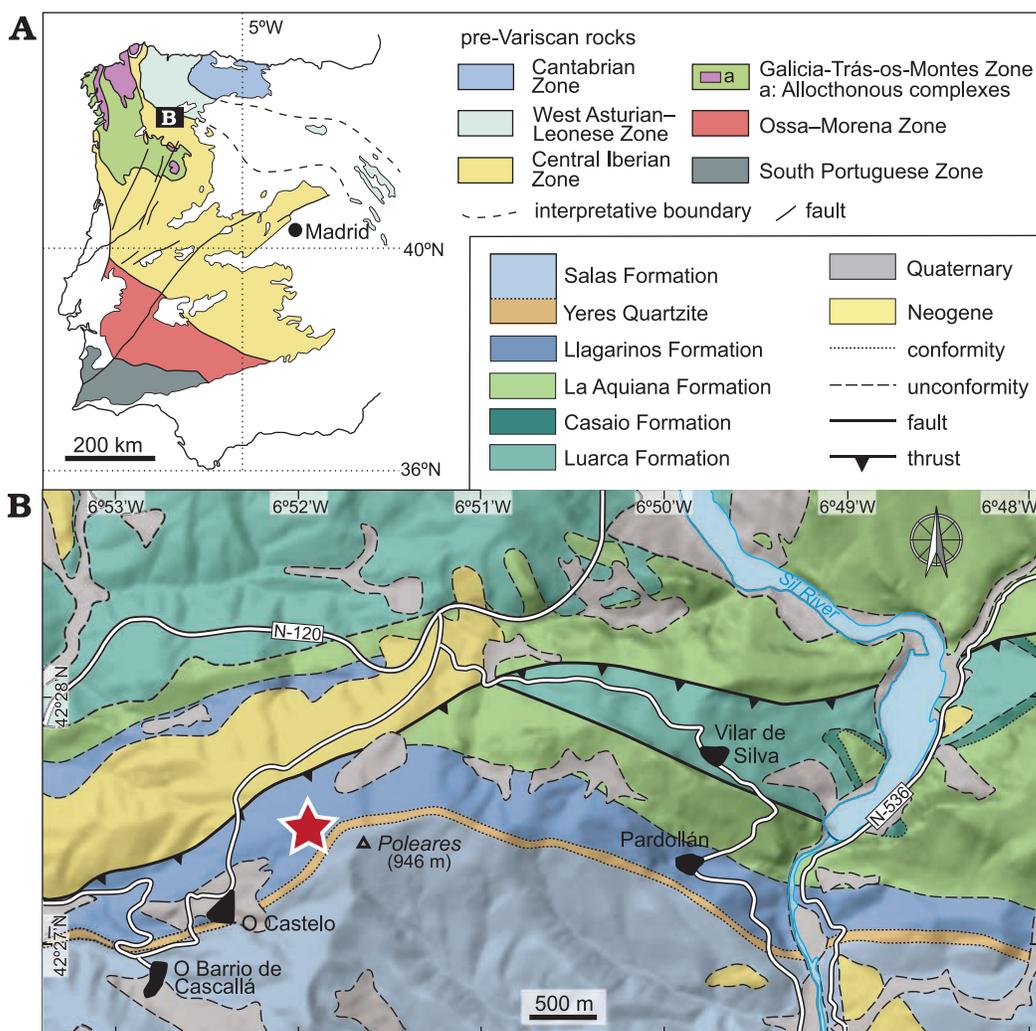


Fig. 1. Localization of the study area in the northern part of the Central Iberian Zone, Spain. **A.** Sketch of the Iberian Massif showing the different structural and palaeogeographic zones with Neoproterozoic and Palaeozoic rocks. **B.** Schematic geological map, showing the position of the fossil locality (star) yielding the studied specimen. Base map modified from Villar Alonso et al. (2008) and González Menéndez et al. (2008), with Silurian subdivision adapted from Apalategui Isasa et al. (1981) and Abril Hurtado et al. (1982).

azules” (“blue quartzites” = Yeres Quartzite of Zeitz and Nollau 1984). Corresponding beds, containing crinoids, were interpreted by Apalategui Isasa et al. (1981: 190) as probably belonging to the Silurian–Devonian transition, but according to a modern stratigraphical reappraisal for the Silurian of this syncline (Gutiérrez-Marco and Rábano 1997; Gutiérrez-Marco et al. 2001) they can be correlated with Ludlow strata, developed in a slightly chloritoid shaly facies, intercalated at the upper part of the Llagarinos Formation. The latter unit consists of ca. 150–180 m of graptolite black shale ranging from the *Spirograptus guerichi* to the *Neodiversograptus nilssoni* graptolite zones (Telychian [upper Llandovery] to Gorstian [lower Ludlow]; Gutiérrez-Marco et al. 2001 and references therein). In the periclinal termination of the Sil Syncline, the base of the Llagarinos Formation is transgressive over diverse Ordovician formations such as the La Aquiana Limestone (upper Katian) in the northern flank, or the Losadilla Sandstone (Hirnantian) in the southern flank (Rodríguez Fernández et al. 2021). Additionally, the base of the Llagarinos Formation records an earlier development in the core of the adjacent Truchas Syncline, where it starts in the Rhuddanian *Parakidograptus acuminatus* Zone (Gutiérrez-Marco and Robardet 1991). Graptolites recorded close to the top of the Llagarinos Formation belong to the lower Gorstian (lower Ludlow) *Neodiversograptus nilssoni* Graptolite Zone, as for instance occur in the Yeres section placed 8 km east-southeast of the present locality (Gutiérrez-Marco and Rábano 1997). Consequently, an early Gorstian (sensu lato) (early Ludlow) may be the most probable age for the studied solutan due to its similar stratigraphic position with regard to the graptolite strata recorded below the Yeres Quartzite from this second nearby section. The position of the fossil locality of the studied specimen is indicated in Fig. 1, and this is situated ca. 960 m northeast of the chapel of Santo Tirso in O Castelo, a village situated to the west of the municipality of Rubiá, province of Ourense (Galicia Region, NW Spain). The point is also 340 m west of the peak of the Poleares hill (946 m high: also known as “cave of La Zorra” in older papers), and lies within an area cleared for a forest repopulation recently destroyed by fire, at the coordinates 42°27'22.5"N, 6°51'57.1"W.

## Systematic palaeontology

Phylum Echinodermata Bruguière, 1791 (ex Klein, 1734)

Class Soluta Jaekel, 1901

*Remarks.*—Soluta is herein considered as a class of echinoderms following Noailles et al. (2014). Previous workers such as David et al. (2000) suggested they possess a feeding appendage in the form of a brachiote, whereas others like Smith (2005) thought they had a true arm. We consider solutans as distinct from any other blastozoan group because of

the lack of radial symmetry, distinct oral area and absence of brachioles, and treat them as a plesiomorphic group of early pre-radial echinoderms according with Smith (2005, 2008). Antero-posterior orientation follows Caster (1968) with the homoiostele at the posterior pole. Rahman and Lintz (2012) in the description of *Dehmicystis* considered the thecal surface bearing the ambulacrum (and associated mouth) as the oral surface, with the opposite face as the ab-oral surface (as suggested by Kolata et al. 1977). This does not necessarily imply direct homologies with other echinoderms. Descriptive terminology follows a recent review by Noailles et al. (2014).

Order Dendrocystitida Noailles, Lefebvre, and Kašička, 2014

Family Dendrocystitidae Bassler, 1938

Genus *Dehmicystis* Caster, 1968

*Type species:* *Dendrocystites (Dendrocystoides?) globulus* Dehm, 1934, Lower Devonian of western Germany (Fig. 2).

*Emended diagnosis.*—Solutan with a rounded flattened theca composed of polygonal plates. Medium-size feeding appendage on one of the thecal surfaces, with the hydro-pore and gonopore on same surface but separated one from each other. Periproct on the opposite face of the theca than the feeding appendage, consisting of a terminal anal pyramid, right to the homoiostele insertion. Large tetramerous proxistele and long dististele composed of paired ossicles.

*Remarks.*—From all characters listed by Rahman and Lintz (2012) for the genus *Dehmicystis* the most important is the presence of a feeding appendage (arm) and anus “on the same face of the theca” (Rahman and Lintz 2012: 62). The position of the anal pyramid in *Dehmicystis* is problematic due in part to the poorly preservation of the material and also because the limited number of specimens available for study. Rahman and Lintz (2012) considered that both structures are on the same face of the theca based on a new studied specimen (Fig. 2B: individual 1). This contradicts the position of the anus in the holotype (Fig. 2A) which appears in the right side and opposite to the face where the feeding appendage is located. Specimens from Germany are extremely flattened and distorted resulting in the superimposition of both faces of the theca. Rahman and Lintz (2012) proposed three hypotheses explaining such position of the anus. The first of them considers this was a result of preservation, in which thecal plates have been displaced to partly reveal the opposing thecal surface where the anus is located, so that it appears to be on the opposite side of the theca. The second as a result of a “situs inversus” where structures located on one side of the theca are transposed to the opposite side, presumably as a result of developmental abnormalities. Finally, they choose a favored scenario in which flattening trajectories during burial affected the position of the anus. Our new material from Spain is less flattened than German specimens because different preservation in a coarser rock. The single

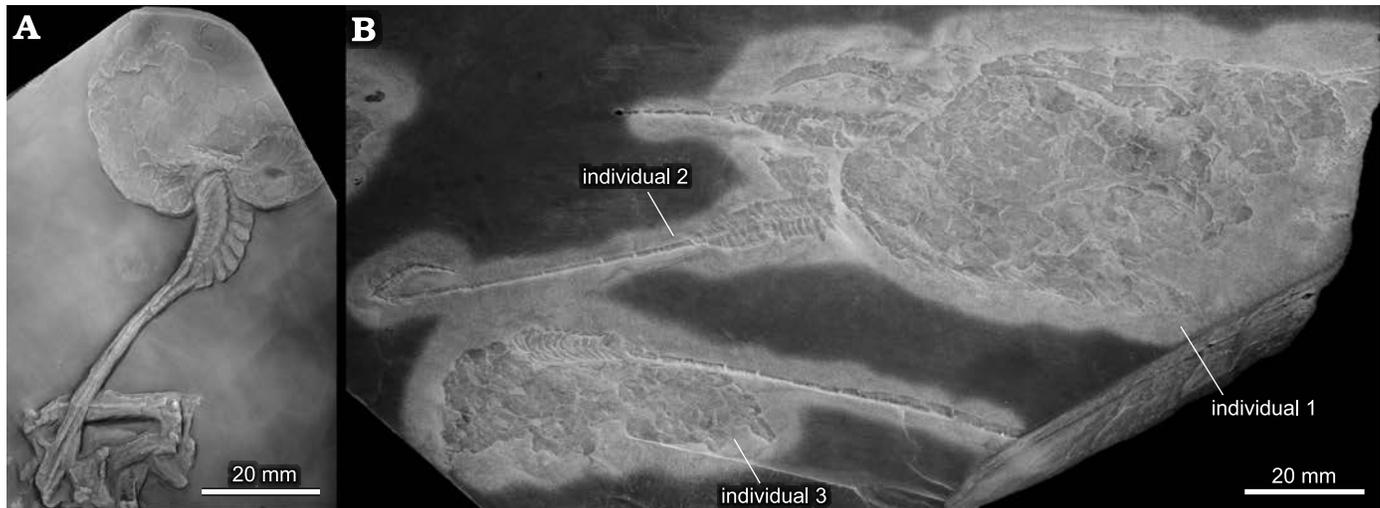


Fig. 2. Solutan echinoderm *Dehmicystis globulus* (Dehm, 1934) from the the Lower Devonian Hunsrück Slate, Germany. **A.** Holotype (SMF-HS 432), almost complete specimen showing the theca and posterior appendage. Note anus in on right side. **B.** SMF-HS 969, slab containing three individuals. Note that individual 1 has the anus on “left” position. Repository number assigned to a replica of the newly prepared slab. Photographs courtesy of Ulrich Jansen.

specimen shows the arm and anus in the same face (Fig. 3A), but close observations of the anal pyramid (Fig. 3A<sub>4</sub>) suggest that it is preserved in a different plane than the feeding appendage. This supports the first scenario suggested by Rahman and Lintz (2012) in which some plates have been displaced revealing the opposite side of the theca where the anus was located. We thus consider that in *Dehmicystis* the arm and anus are on opposite faces. Other solutans (i.e., *Dendrocystites* Barrande, 1887, *Coleicarpus* Daley, 1996 and *Maennilia* Rozhnov and Jefferies, 1996) also have the arm and anus on opposite extremities; or have a terminal arm and the anus on one of the integuments (*Girvanicystis*) (Noailles et al. 2014). An undescribed Ordovician species from Hope Shale Formation in Shropshire shows the arm and stele on the same thecal face, and the anus on opposite face. A similar situation occurs in “Solutan indet., gen. et sp. nov.,” from the Middle Ordovician of Bohemia (Lefebvre et al. 2012). For contrast *Dehmicystis* has a terminal homoiosteale, offset arm on one of the integuments and anus on the opposite side, right to the homoiosteale insertion. Kolata et al. (1977) also consider that *Belemnocystites wetherbyi* Miller and Gurley, 1894, had the arm located some distance away from the margin. *Minervaecystis* (see Ubaghs 1970), *Pahvanticystis* (see Lefebvre and Lerosey-Aubril 2018) and *Plasiacystis* (see Lefebvre et al. 2012) also have an offset position of the arm.

### *Dehmicystis ariasi* sp. nov.

Figs. 3, 4.

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*Etymology*: Dedicated to Francisco Arias Ferrero (Ponferrada, Spain) for collecting the only specimen known and making it available for study.

*Holotype*: MGM-208S-a (part) and MGM-208S-b (counterpart).

*Type locality*: 340 m west of Poleares high (946 m), about 960 m north-east of O Castelo village in the Rubiá municipality, Ourense Province, Galicia, NW Spain. GPS coordinates: 42°27'22.5" N, 6°51'57.1" W.

*Type horizon*: Shale bed with a slight chloritoid content in the upper part of the Llagarinos Formation. Bed of a probably Gorstian (early Ludlow) age by lateral correlation with a nearby locality.

*Material*.—Holotype only.

*Diagnosis*.—A species of *Dehmicystis* with a globular theca, proxistele equal in length to the theca. Undifferentiated mesistele.

*Description*.—Thecal shape rounded, large (45 mm in length, 30 mm in width), nearly bilaterally symmetric with the left side more developed than the right. Theca widening posteriorly with an invagination for the insertion of the homoiosteale. Narrow peripheral ring as a result of compression rather than originally biological. Plates very thin, superimposed integuments (taphonomic), polygonal and relatively large. Boundaries between plates are poorly preserved. Feeding appendage off the apex, on an integument with attachment to the theca on left side; relatively large with wider rectangular basal plates (flooring plates) and thinner, cover plates. Feeding appendage thinning distally, with food groove oriented to the substrate (see interpretation below). Small gonopore on a circular tiny plate, associated with some rugose plates interpreted as hydro-pore. Both separated one another. Periproct large, on the opposite side of the theca, close to the appendage insertion but on the right position. Proxistele very large, consisting of eleven tetramerous rings, two on each side. Posterior side of each ring with a depressed side for the articulation of adjacent rows distally. Distal stele only preserved proximally, composed of two dimeres. Theca slightly longer than the proxistele.

*Remarks*.—Comparison with the type species *Dehmicystis globulus* (Dehm, 1934) from Germany (Fig. 2), poses several

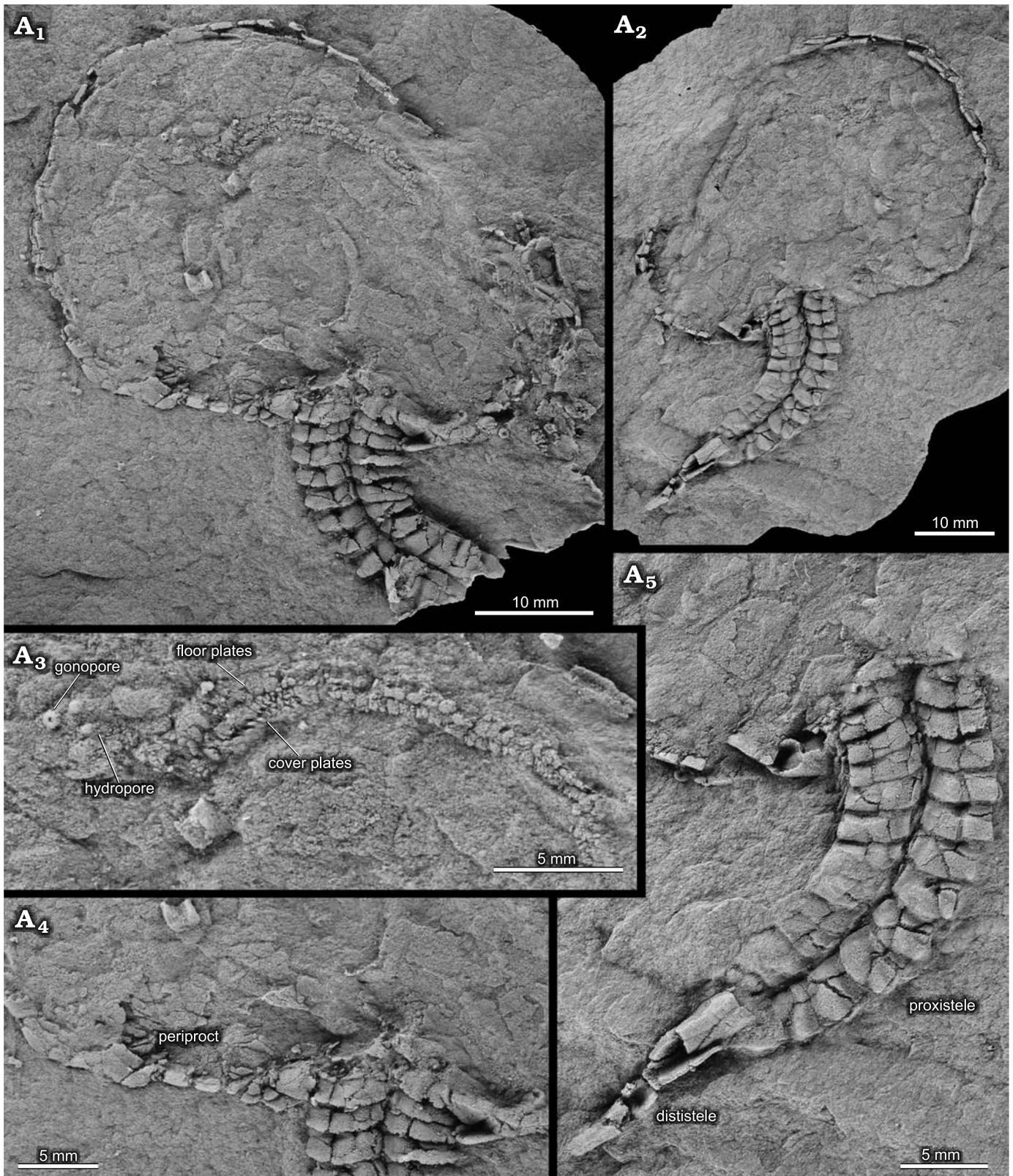


Fig. 3. Solutan echinoderm *Dehmicystis ariasi* sp. nov. from the Llagarinos Formation, Ludlow, Silurian, northern Central Iberian Zone, Spain. A. MGM-208S. A<sub>1</sub>, complete specimen in dorsal aspect preserving proxistele and feeding appendage above the body. A<sub>2</sub>, counterpart of same specimen. A<sub>3</sub>, detail of feeding appendage consisting on biserial floor plates and cover plates. Gonopore on single plate, and a possible hydropore close to the feeding appendage attachment. A<sub>4</sub>, detail of the periproct on right position. Note that the periproct is visible from the inside and was located on dorsal right part of the theca. A<sub>5</sub>, detail of the appendage preserving the complete proxistele and proximal dististele. Photographs are from latex casts whitened with ammonium chloride sublimated.

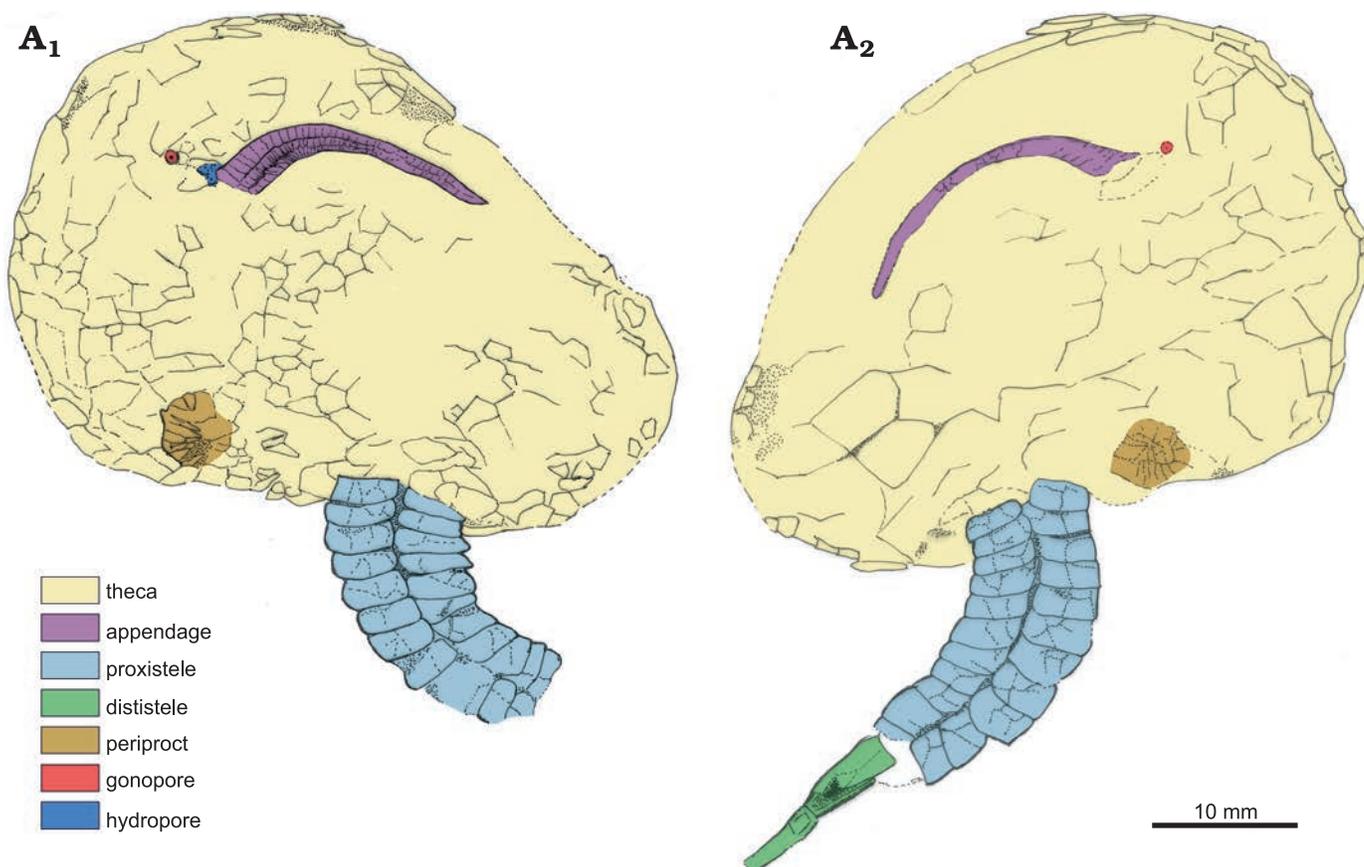


Fig. 4. Camera lucida drawings of solutan echinoderm *Dehmicystis ariasi* sp. nov. from the Llagarinos Formation, Ludlow, Silurian, northern Central Iberian Zone, Spain; with interpretation of main anatomical parts.

problems; specially because German specimens are flattened and tectonically distorted, and also because none of the known specimens is totally complete (Fig. 2). Holotype and individual 1 from Rahman and Linz (2012) have the anterior part of the theca incomplete, individual 2 preserves only the homoiostele and individual 3 preserves only the homoiostele and posterior part of the theca. Rahman and Linz (2012) indicated that the dimensions of the holotype are  $70 \times 67$  mm, but based on new observations, this is unlikely (see Table 1). The length of the holotype is unknown because incomplete preservation of the anterior part and its width is about 40 mm. So dimensions of the holotype are comparable to *D. ariasi*. The other individuals seem relatively larger. Shape of the theca between both species seems different, being more elongate in the German taxon, but this

difference can be also due to the strong tectonic distortion affecting the Hunsrück material. Another important difference is the relation between thecal and proxistele lengths. Spanish material seems to have a longer proxistele which is almost equal than the length of the theca. For contrast *D. globulus* has a shorter proxistele. Mesistele is well preserved in the individual 2 of Rahman and Linz (2012), but it is absent in the Spanish material, where transition from the proxistele to the dististele is more abrupt. Further comparison with the type species is not possible due to incomplete preservation of material from both Spain and Germany, and different preservation styles being German specimens more compressed.

*Stratigraphic and geographic range.*—Type horizon and locality only.

Table 1. Comparative measures (in mm) from *Dehmicystis ariasi* sp. nov. and *Dehmicystis globulus* (Dehm, 1934). L, length, W, width; (i), incomplete measure.

Specimen	Repository number	Thecal L	Thecal W	Proxistele L	N° segments proxistele
<i>Dehmicystis ariasi</i> sp. nov. (holotype)	MGM-208S	45	30	20	11
<i>Dehmicystis globulus</i> (holotype)	SMF-HS 432	30 (i)	40	15	?10–11
<i>Dehmicystis globulus</i> (individual 1)		70 (i)	40	25	17
<i>Dehmicystis globulus</i> (individual 2)	SMF-HS 969	?	?	20	15
<i>Dehmicystis globulus</i> (individual 3)		?	50	18	12

## Concluding remarks

The earliest solutans in the Cambrian lived either permanently attached (i.e., *Coleicarpus*) (Ubaghs and Robison 1988; Daley 1996; Zamora et al. 2017) or were free living on muddy substrates (i.e., *Castericystis*, *Pahvanticystis*) (Ubaghs and Robison 1985; Lefebvre and Lerosey-Aubril 2018). In these earliest solutans (with the exception of *Pahvanticystis*), thecal faces are undifferentiated and the feeding appendage is positioned at the adoral pole of the theca on one of the margins, with the periproct on the opposite side, close to the homoiostele insertion (Ubaghs and Robison 1985). This is also the case for most Ordovician solutans like *Dendrocystites* and *Girvanicystis* (Noailles et al. 2014; Nohejlová and Lefebvre 2022); however, at least in *Girvanicystis* the periproct is positioned on one of the thecal faces (Daley 1992). In the case of *Coleicarpus*, which was permanently fixed on a hard substrate, the most likely interpretation is that it was a suspension feeder (Daley 1996), like some blastozoans. Most free living solutans were probably detritus feeders (Daley 1992; Noailles et al. 2014 and references therein) living on the sediment-water interface, as were other analogous early echinoderms like *Dibrachicystis purujoensis* (Zamora and Smith 2012) and pleurocystitids (Gorzela and Zamora 2016). The situation is more complicated in solutes that have the periproct on one thecal surface and the feeding appendage away from the margin, on the opposite surface. Examples include “Solutan indet., gen. et sp. nov.”, from the Middle Ordovician of Bohemia (Lefebvre et al. 2012), an undescribed solutan from the Ordovician Hope Shale Formation in Shropshire, UK (SZ personal observation, 2004), *Belemnocystites* (Kolata et al. 1977) and species of *Dehmicystis*. Undescribed solutan from Hope Shale Formation is critic in such respect. Its theca is delimited by a narrow marginal frame and comprises two morphologically distinct surfaces: one is almost flat and hosts the insertions of the two appendages (free ambulacrum and homoiostele), whereas the opposite thecal surface is domed (convex) and bears the periproct (Bertrand Lefebvre, personal communication 2023). Comparison with some other free living, epibenthic echinoderms (e.g., cinctans, pleurocystitids, edrioasteroids) suggests the flat surface was in contact with the substrate, whereas the convex one was facing upwards; this is also supported by the insertion of the stele in the flat surface, in the same face than the feeding arm. Rahman and Lintz (2012) interpreted *Dehmicystis* as having the feeding appendage and periproct on same surface based on very flattened specimens, but the specimen described herein and comparison with other solutans suggest that *Dehmicystis* is better interpreted as having feeding appendage and periproct on opposite faces (see discussion above). If correctly interpreted, *Dehmicystis* probably laid on the substrate with the periproct on the upper surface and the feeding appendage directed to the substrate. Under such interpretation *Dehmicystis* was probably a detritus feeder capturing organic particles from the muddy substrate.

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