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► **To cite this version:**

Bertrand Lefebvre, Aude Cincotta, Pierre Guériaux, Sebastian Schöder, Sébastien Olive, et al.. First report on the occurrence of the echinoderm classes Soluta and Stylophora in a new Lower Devonian (Pragian) Konservat-Lagerstätte from southern Belgium. *Geologica Belgica*, 2025, 28 (3-4), pp.93-106. <10.20341/gb.2025.008>. <hal-05361777>

HAL Id: hal-05361777

<https://hal.science/hal-05361777v1>

Submitted on 12 Nov 2025

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First report on the occurrence of the echinoderm classes *Soluta* and *Stylophora* in a new Lower Devonian (Pragian) Konservat-Lagerstätte from southern Belgium

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ABSTRACT

In the Neufchâteau–Eifel Synclinorium (southern Belgium), remnants of the spoil heap of the disused and now flooded underground Sainte-Barbe Quarry (Warmifontaine) yielded an invertebrate Pragian assemblage occurring in the dark monotonous slates of the La Roche Formation (Martelange Member). This locality is considered as a new Belgian Konservat-Lagerstätte (fossil conservation deposit) due to the presence of both biomineralised and soft-bodied organisms. Two specimens from the Sainte-Barbe Quarry Biota are described and assigned to two distinct classes of extinct echinoderms. The first one corresponds to an almost complete, flattened and distorted dendrocystitid solutan, which is tentatively identified as *Dehmicystis?* sp., based on similarities with *D. globulus* from the Hunsrück Slate (Emsian) of Germany. The second echinoderm specimen is a well-preserved, flattened, fully articulated and almost complete mitrate stylophoran, morphologically close to *Mitrocystites? styloideus*-like peltocystidans from the Lower and Middle Devonian of Germany. Taphonomic attributes of the two echinoderms from Warmifontaine (e.g. both fully articulated; mitrate with its aulacophore preserved in feeding position) suggest they were probably killed and entombed by obrution deposits in an otherwise quiet and deep setting. Other echinoderms (asteroids, crinoids, blastoids, cyclocystoids, ophiuroids) reported from the Lower Devonian of Belgium are also briefly discussed and illustrated (e.g. holotypes).

KEYWORDS

Echinodermata,
fossil conservation
deposit,
Neufchâteau–Eifel
Synclinorium,
solutans,
stylophorans

Article history

Received 04.03.2025, accepted in revised form 02.07.2025, available online 12.11.2025.



1. Introduction

Relatively similar morphologies were acquired independently and convergently in at least three groups of epibenthic, free-living (unattached) Palaeozoic echinoderms (pleurocystitids, solutans, and stylophorans), very likely as adaptations to a comparable ‘homalozoan’ mode of life on soft substrates (Parsley, 1972; Lefebvre, 2007; Parsley & Sumrall, 2007). These three groups are characterised by a reduced number of ambulacra (one or two), a flattened, more or less bilaterally symmetrical theca, and the possession of few, if any, respiratory structures (e.g. rhombs). Unsurprisingly, pleurocystitids, solutans and stylophorans are often co-occurring in the same assemblages, and their fossil records are very similar.

All three groups underwent a significant increase in diversity and palaeobiogeographic distribution during the Ordovician, with an acme in the Sandbian–Katian interval (Sprinkle & Guensburg, 2004; Lefebvre et al., 2013). Pleurocystitids, solutans and stylophorans were strongly affected by the Late Ordovician Mass Extinction (LOME) in the Hirnantian. Rare occurrences of Silurian stylophorans have been documented in Australia (Gill & Caster, 1960; Philip, 1981; Caster, 1983; Ruta, 1997; Ruta & Jell, 1999a, b), Canada (Lefebvre & Ausich, 2021), Mongolia (Rozhnov, 1990), Sweden (Lindström, 1888; Regnéll, 1945, 1960; Reich et al., 2007), and the United Kingdom (de Koninck, 1869; Jefferies & Lewis, 1978). The Silurian record of pleurocystitids is totally cryptic, while solutans are only known by two occurrences: in Spain (Zamora & Gutiérrez-Marco, 2023) and in the United Kingdom (Nohejlová & Lefebvre, 2022). In contrast, all three

groups are characterised by a second (lower) peak of diversity in the Early Devonian (McIntosh & Macurda, 1979). In particular, pleurocystitids, solutans and stylophorans are co-occurring in the Lower Devonian of Australia (Humevale Formation; Gill & Caster, 1960; Jell, 1983), Germany (Hunsrück Slate; Dehm, 1932, 1934), and the USA (Bois d’Arc Formation; Parsley & Sumrall, 2007).

The aim of this paper is to report the first occurrence of two of these groups (solutans and stylophorans) in the Lower Devonian (Pragian) of southern Belgium, and to discuss their palaeobiogeographic affinities.

2. Geological setting

The two studied specimens were collected in June 2021 (RBINS a14020) and 2022 (RBINS a14021) at Warmifontaine (Fig. 1), a small village of the commune of Neufchâteau that is established on the northern flank of the Neufchâteau–Eifel Synclinorium (Asselberghs, 1946). This major tectonic unit belongs to the Ardenne Allochthon that was overthrust on the Brabant Parautochthon during the Variscan orogeny (e.g. Belanger et al., 2012). The echinoderms were found on the remnants of the spoil heap of the disused and now flooded underground Sainte-Barbe Quarry situated in the centre of the village (e.g. Asselberghs, 1924; Watteyne, 2016); consequently, no information about their precise position in the lithological column is available. The residual spoil heap, which was particularly huge in the past (see Watteyne, 2016, fig. 193), was converted over the last decade into slate chippings for garden, and the chances of making new discoveries will become slim in

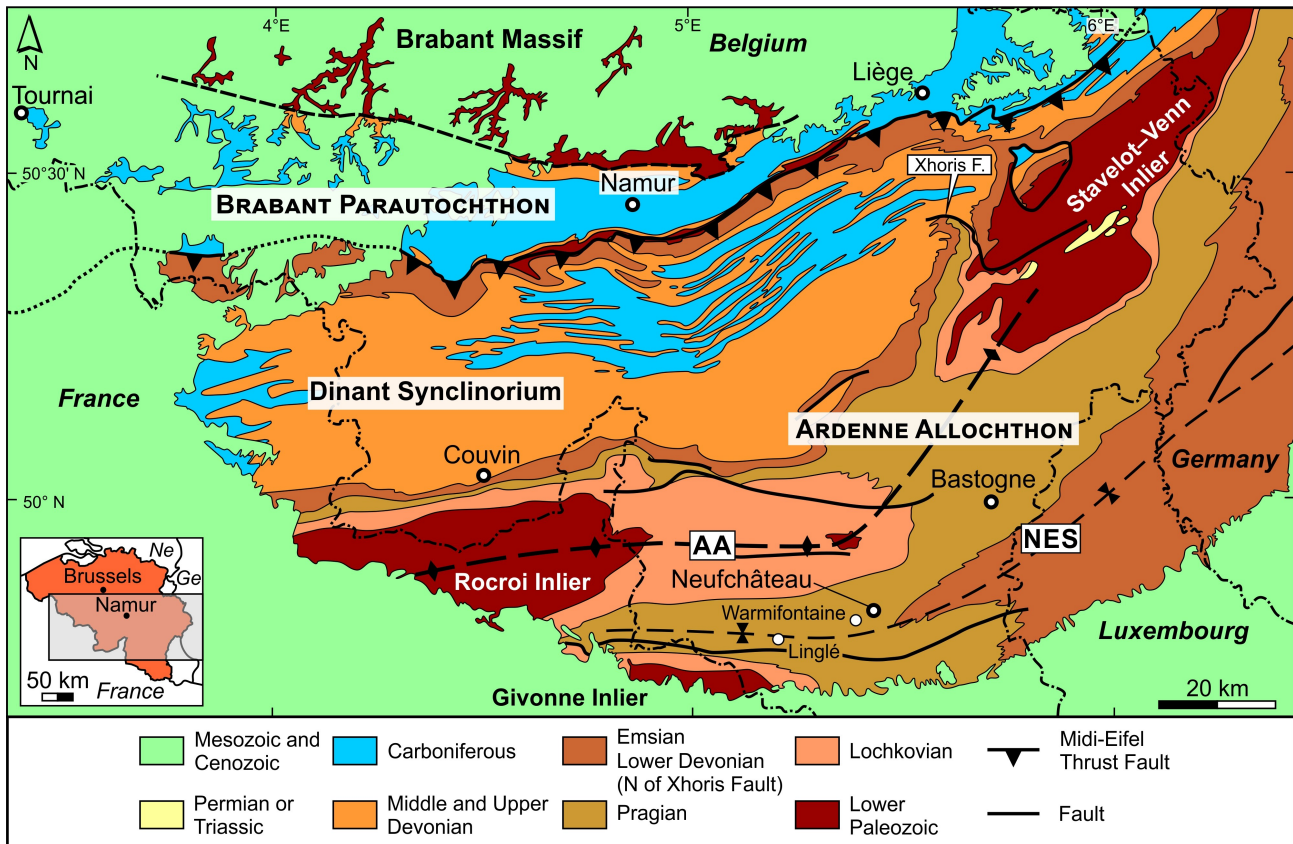


Figure 1. Simplified geological map of southern Belgium (modified from de Béthune, 1954 and Candela & Mottequin, 2022) with the location of the village of Warmifontaine (Sainte-Barbe Quarry) and the hamlet of Linglé (Mortehan). Abbreviations: AA, Ardenne Anticlinorium; F., Fault; NES, Neufchâteau–Eifel Synclinorium. Abbreviations in the insert: Ge, Germany; Ne, the Netherlands.

the future. According to Ghysel (2022), the Sainte-Barbe Quarry intensively exploited the dark grey to black, monotonous slates of the local Martelange Member of the La Roche Formation (Fig. 2) until the early 2000s. This basal member is distinguished from the rest of the La Roche Formation (see description in Denayer & Mottequin, 2024) by the absence of sandy laminae and sandstone beds (e.g. Ghysel, 2022), which allowed the production of high-quality slates at Warmifontaine as reflected by the awards obtained at the Liège (1905) and Brussels International expositions (1910) (Watteyne, 2016). The thickness of the Martelange Member is comprised between 100 and 150 m in its type area (Ghysel, 2023) on the Belgian–Luxembourg border, but that of the La Roche Formation is highly variable from the southern margin of the Dinant Synclinorium up to the Neufchâteau–Eifel Synclinorium (see Denayer & Mottequin, 2024) (Fig. 1): from 215 m south of Couvin (Stainier, 1994) to more than 800 m in the Ardenne Anticlinorium (Dejonghe & Hance, 2001), whereas Ghysel (2022) estimated its minimal thickness at 700 m (300 m for the Martelange Member) in the western part of the Neufchâteau–Eifel Synclinorium (Fig. 1). The La Roche Formation (Fig. 2) is mostly Pragian (Siegenian) in age, but it is probable that its upper part, in the Couvin area, is early Emsian in age based on the presence of the conodont *Caudicriodus celtibericus* (Bultynck et al., 2000). Macrofossils are rare and poorly diverse within the Martelange Member (Fig. 2) as shown by the few available faunal lists (Dewalque, 1891; Maillieux, 1940; Asselberghs, 1946) that were based notably on the collections of the Royal Belgian Institute of Natural Sciences and of the Liège University. All these old collections essentially include solitary rugose corals, bivalves, orthoconic cephalopods and trilobites as is the case of those recently discovered at the Centre Grégoire Fournier of the Maredsous Abbey (Fig. 3), where Mottequin (2021) also pointed out the existence of an enigmatic fossil from Warmifontaine, which was considered as a putative early chordate by Olive et al. (2022). The specimens are compressed, a characteristic inherent to fossils preserved in slate, and sometimes elongated, due to the tectonic strains they have undergone. Despite our local requests, we were unable to find any other Warmifontaine collections assembled by amateur geologists of the Neufchâteau area.

Recent fieldwork at Warmifontaine in 2021 and 2022 yielded hundreds of fossils that are generally poorly preserved and quite difficult to identify, but some of which have preserved soft parts (Cincotta et al., 2022, 2023). Besides the two echinoderms, the fauna includes arthropods, molluscs, corals, unidentified fossils and specimens probably similar to that mentioned by Mottequin (2021) and Olive et al. (2022). However, the fossils recently collected on the spoil heap of the Sainte-Barbe Quarry are markedly different from those present in the old aforementioned collections, by their preservation and their taxonomic identification. Either they come from a horizon that was not exploited during the first decades of slate mining, or that was a strong collection bias in the past.

The high degree of disarticulation of the fossils and the scarcity of large specimens indicate that they would have been transported over an unknown distance, but it is not excluded that some were buried in situ, notably the echinoderms described in this paper, as is the case of the fossils of the Lower Devonian Hunsrück Slate deposits of Germany (Brett & Seilacher, 1991; Bartels et al., 1998; Sutcliffe et al., 1999). The Belgian locality constitutes a new Lower Devonian Konservat-Lagerstätte (fossil conservation deposit sensu Shields, 1998), with the preservation of both biomineralised and soft-bodied organisms. However, further studies are required for identifying problematic taxa that would shed more light on the biodiversity of this new fossil locality.

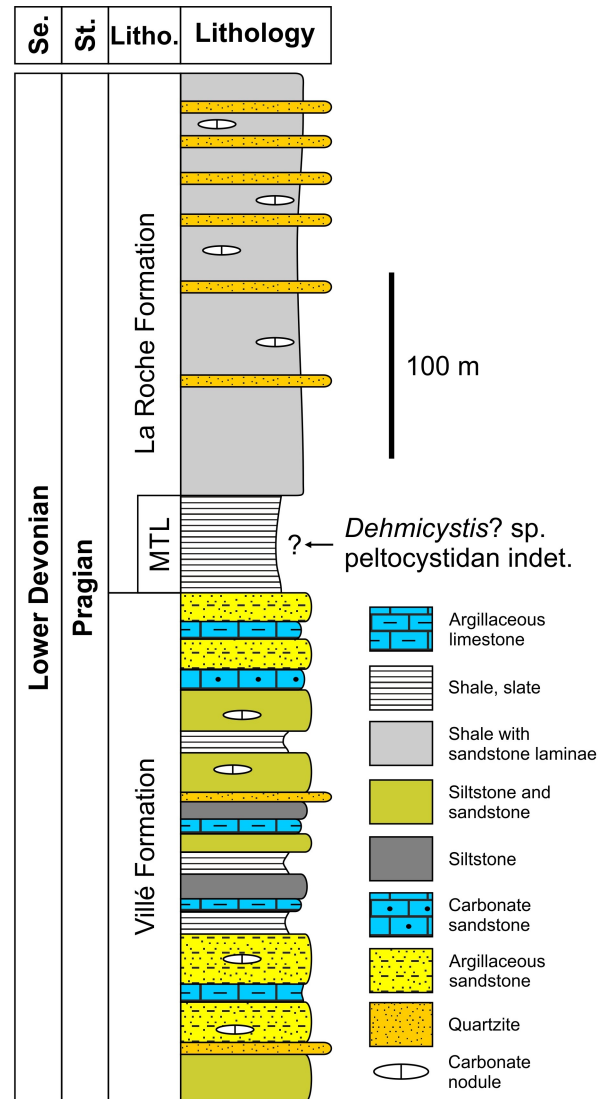


Figure 2. Schematic lithological column of the Pragian lithostratigraphic units (pars) encountered in the western part of the Neufchâteau–Eifel Synclinorium (modified from Ghysel, 2022). The range of the two studied echinoderms within the lower part of the La Roche Formation is unknown. Abbreviations: Litho., Lithostratigraphy; MTL, Martelange Member; Se., Series; St., Stage.

3. Material and methodology

The two echinoderm specimens from Warmifontaine are deposited at the Royal Belgian Institute of Natural Sciences, Brussels (prefixed RBINS). The other specimens illustrated here are deposited at the Liège University (prefixed PA.ULg), the Centre Grégoire Fournier of the Maredsous Abbey (prefixed CGF), and the Naturhistorisches Museum Mainz (prefixed NHMMZ PWL).

The specimens from Warmifontaine and Morthan (RBINS) and Bundenbach (NHMMZ PWL) were photographed using a Nikon D850 digital camera, equipped with a 70mm f/2.8 Sigma macro lens and a Canon EOS 750D digital camera, equipped with a Canon EF 100mm f/2.8L macro IS USM macro lens, respectively. The other echinoderms were coated with ammonium chloride and photographed using an Olympus OM-D E-M10 Mark II digital camera, equipped with an Olympus M.Zuiko Digital ED 60 mm macro lens, with the exception of the single blastoid (PAULg) selected for scanning electron

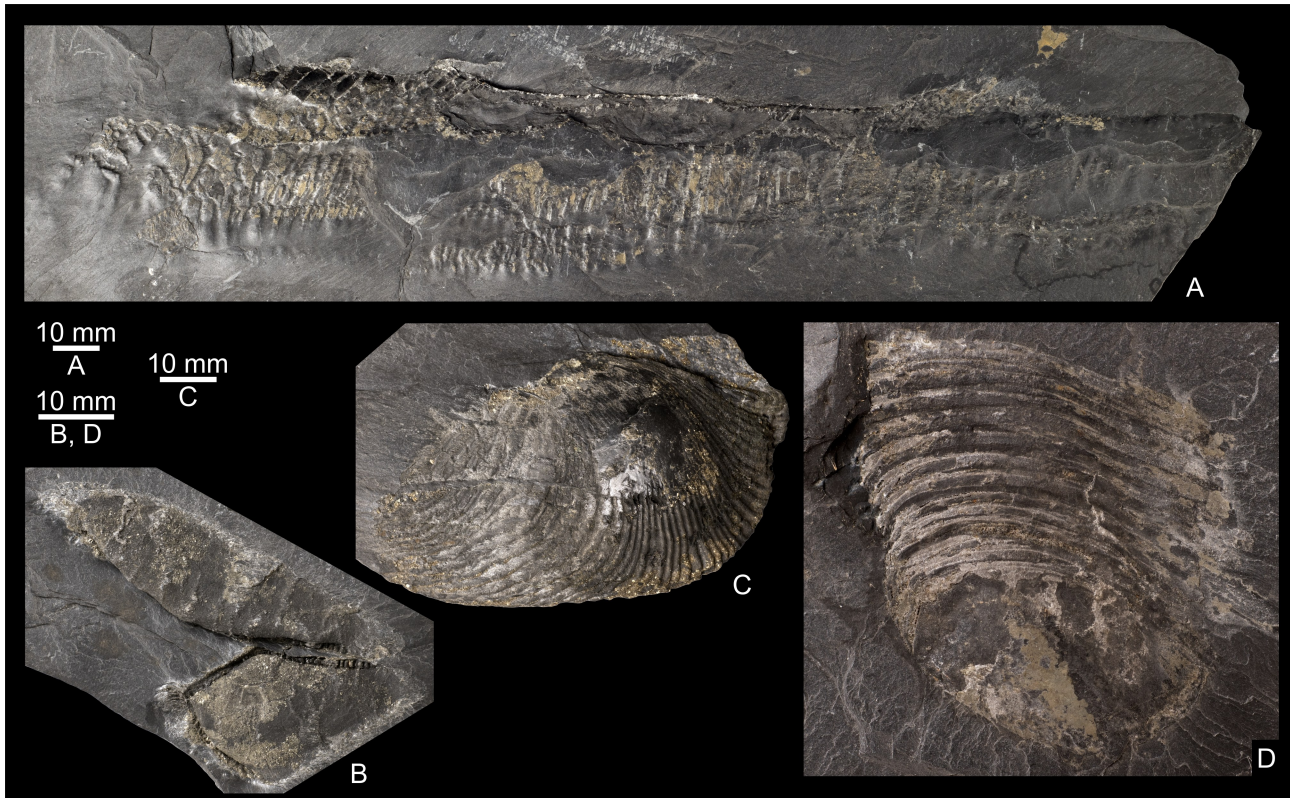


Figure 3. Pyritised and distorted invertebrates from the Sainte-Barbe Quarry at Warmifontaine, La Roche Formation (Martelange Member), Pragian. **A.** Orthoconic cephalopod (identified as *Kionoceras rhysum* in Maillieux, 1940), RBINS a14160. **B.** Bivalve, CGF II. 232. **C.** Bivalve (identified as *Puella cf. elegantissima* in Maillieux, 1940), RBINS a14161. **D.** Homalonotid trilobite in dorsal view (pygidium and thorax), CGF II. 69.

microscopy that was uncoated and imaged with an ESEM FEI Quanta 200, under low vacuum.

The morphology of one of the specimens (RBINS a14021) was further documented using synchrotron-based micro-X-ray fluorescence (μ XRF) major-to-trace elemental and laboratory-based X-ray microcomputed tomography (μ CT).

μ XRF was performed at the PUMA beamline of the SOLEIL synchrotron source (France) (Schöder et al., 2024), using a monochromatic beam of 18.5 keV, selected for excitation of K-lines from phosphorus to zirconium and L-lines from cadmium to uranium. The incoming X-ray beam was focused using Kirkpatrick-Baez mirrors down to a spot size of $\sim 7 \times 5 \mu\text{m}^2$ ($H \times V$, full width at half maximum). The specimen was mounted on a scanner stage allowing 150 mm and 100 mm movements (in horizontal and vertical directions respectively) with micrometre accuracy, and orientated at 30° to the incident beam, producing an effective beam size of $\sim 8 \times 5 \mu\text{m}^2$ ($H \times V$) on the specimen. XRF was collected using a SiriusSD silicon drift detector (SGX Sensortech Ltd, 80 mm^2 active area) oriented at 90° to the incident beam, in the horizontal plane. Two-dimensional spectral images, i.e. images for which each pixel is characterized by a full XRF spectrum, were collected on the fly over the specimen at a $100 \mu\text{m}$ lateral resolution with a 40 ms dwell time (effective counting time was 90% of the dwell time). We present herein a false-colour RGB overlay of the distributions of Fe (red), Pb (green), and Ni (blue), reconstructed from integrated intensities in spectral regions of interest (peaks) using the PyMCA data-analysis freeware (Solé et al., 2007). Elemental distributions are presented using a logarithmic colour scale that goes from dark to light, corresponding respectively to lower and higher concentrations.

μ CT was carried out at the RBINS, using a RX EasyTom instrument (RX Solutions, Chavanod, France; www.rx-solutions.com). The tube power, voltage, and current were 30

W, 150 kV, and $200 \mu\text{A}$, respectively, with a 0.4 mm copper filter. The scan parameters included a frame rate of 4.9, an average of four frames per image, a horizontal shift of 2, and a vertical stack of 4, capturing 2880 individual radiographs per 360° rotation, in middle spot mode, and an isotropic voxel size of $48.86 \mu\text{m}$. The resulting 16-bit TIFF stack was inspected in 2D and 3D with Dragonfly ORS software (from Object Research Systems Inc, Montreal, Canada). Since the slab containing the specimen was not unidimensional, beam hardening was mitigated by scanning it alongside three other Sainte-Barbe slabs of similar dimensions.

4. Systematic palaeontology

Phylum Echinodermata Klein, 1778

Subphylum Blastozoa Sprinkle, 1973

Remarks. The feeding appendages of solutans and stylophorans are considered here as free (erect) ambulacral structures, i.e. brachioles (see e.g. Haugh & Bell, 1980; Lefebvre, 2022; Guensburg et al., 2023). The possession of brachioles represents the defining apomorphy of blastozoans (Sprinkle, 1973; David et al., 2000; Nardin et al., 2017). Solutans and stylophorans are therefore interpreted here as two distinct clades belonging to this subphylum (Mooi et al., 2024).

Class Soluta Jaekel, 1901

Order Dendrocystitida Noailles et al., 2014

Family Dendrocystitidae Bassler, 1938

Genus *Dehmicystis* Caster, 1967

Type species. *Dendrocystites (Dendrocystoides?) globulus* Dehm, 1934 from the Lower Devonian (lower Emsian) of Germany.

Remarks. The possession of large, well-defined suranal plates ('sugar loaf' plates) strongly supports the assignment of *Dehmicystis* to the family Dendrocystitidae (Dehm, 1934; Caster, 1967; Noailles et al., 2014; Zamora & Gutiérrez-Marco, 2023). However, several aspects of its morphology remain poorly known, due to the limited number of available specimens and tectonic distortion (Dehm, 1934; Rahman & Lintz, 2012). The type species, *D. globulus*, was originally described from the Hunsrück Slate (Emsian) of Rhineland-Palatinate, Germany, based on its holotype and only known specimen (Dehm, 1934; Caster, 1967). More recently, three additional individuals, all located on a same slab, were documented (Rahman & Lintz, 2012). All other figured specimens assigned to *D. globulus* correspond to peltocystidan mitrates (see below). *Dehmicystis* was recently also reported from the Silurian (Ludlow Series) Llagarinos Formation of the Central Iberian Zone, Spain (Zamora & Gutiérrez-Marco, 2023), therefore considerably extending its stratigraphic range and palaeobiogeographic distribution. The holotype and only known specimen of the Spanish *Dehmicystis* (*D. ariasi*) is particularly well-preserved and makes it possible to document several poorly known morphological features of the genus (Zamora & Gutiérrez-Marco, 2023). For example, the brachiole is not inserted in apical position, but more posteriorly, on the lower (plano-concave) thecal surface. Moreover, the periproct is not located in lateral position, at the posterior extremity of the anal lobe, but displaced on the upper (plano-convex) thecal surface (Zamora & Gutiérrez-Marco, 2023).

Dehmicystis? sp.

(Fig. 4A–B)

Material. RBINS a14020, part and counterpart.

Description. Part and counterpart of strongly flattened organism consisting of two distinct parts: elongate, pear-shaped 'body' (~6.0 cm long, up to 2.5 cm wide), and ~8.8 cm long, narrow (~0.1–0.15 cm wide), segmented 'appendage' (Fig. 4A–B).

Body outline nearly bilaterally symmetrical, with two opposite, unequal, rounded extremities, and elongate, gently convex lateral sides. Lateral edges of body apparently slightly thickened, into narrow (0.2–0.25 cm wide) 'marginal' frame, best visible on counterpart (Fig. 4B). Body consisting of numerous, small, polygonal, smooth, poorly distinct elements (plates). Next to appendage insertion, more or less circular structure consisting of a ~1.0 cm wide ring, enclosing few, large plates (Fig. 4A). At opposite, narrowest extremity of body (apex), short segmented(?) extension (~1.0 cm long, 0.3 cm wide) protruding next to appendage (Fig. 4A–B).

Appendage inserted in poorly distinct, segmented(?) area at largest body extremity (opposite the apex), and forming long, slender structure extending along the entire length of the body, and ~3.0 cm beyond the apex (Fig. 4A–B). Appendage distally curved, with shorter (~3.0 cm long), straight, distal-most portion forming an angle of ~45° with long (~5.0 cm), straight to sinuous, more proximal part. Proximal-most portion of appendage very short, straight, possibly broken. Appendage consisting of numerous elongate segments, some of them, apparently slightly displaced. Distinct longitudinal groove along the whole length of appendage (Fig. 4A–B).

Remarks. The identification of specimen RBINS a14020 is particularly difficult, because of the strong flattening and tectonic distortion affecting it. However, the preservation of several morphological features, such as a bipartite organisation, with a 'body' composed of numerous plates and a very long and

narrow appendage consisting of articulated segments, makes it possible to rule out its assignment to most metazoan phyla, with the exception of echinoderms. Within this phylum, affinities with most Devonian groups can be excluded (e.g. asterozoans, blastoids, crinoids, echinoids, edrioasteroids, holothurians, ophiocystioids) because of major differences in general organisation. The morphology of RBINS a14020 is only compatible with a limited number of echinoderm clades: pleurocystitids, stylophorans, and solutans.

RBINS a14020 shares with pleurocystitids the possession of a bipartite body, consisting of a multi-element stem inserted into a flattened, elongate, nearly bilaterally symmetrical theca. However, a detailed comparison with the morphology of Devonian pleurocystitids (e.g. *Henicocystis*, *Regulaecystis*, *Turgidacystis*) makes it possible to identify several important differences. For example, the stem of pleurocystitids is made of numerous, relatively short, ring-shaped elements (columnals), forming a wide, regularly tapering structure (Dehm, 1932, 1934; Jell, 1983; Parsley & Sumrall, 2007). In marked contrast, the appendage of RBINS a14020 is a narrow, elongate structure, remaining of the same width all along its length, and made of one (possibly two, if the longitudinal groove corresponds to plate sutures) series of elongate elements (Fig. 4A–B). In Devonian pleurocystitids, the upper thecal surface consists of a limited number of stout, usually ornamented (with strong ridges) plates, while the opposite (lower) thecal side comprises a large, polyplated anal area (Dehm, 1932, 1934; Jell, 1983; Parsley & Sumrall, 2007). The theca of RBINS a14020 does not show any evidence of contrasted plate patterns between its two opposite faces, both apparently made exclusively of small, polygonal, non-ornamented elements (Fig. 4A–B).

As is the case in RBINS a14020, the long feeding appendage of mitrate stylophorans (aulacophore) is frequently preserved in recurved position over the body (theca). In mitrates, this preferential taphonomic posture is generally interpreted as resulting from a post-mortem contraction (Ruta & Bartels, 1998; Lefebvre, 2003; Lefebvre & Ausich, 2021). In such preserved mitrates, portions of the particularly long distal aulacophore can also extend far beyond the posterior extremity of the theca (see e.g. Ubaghs, 1979). However, distal portions of mitrate aulacophores are not bent (or hooked), as this is the case in RBINS a14020. Another intriguing aspect of this specimen is that its appendage is visible all along its length in both the part and the counterpart, i.e. even when it extends below the theca (Fig. 4A–B). This implies that the body wall was made of very thin elements. This interpretation is in good accordance with the occurrence of thickened lateral edges (Fig. 4B). The apparent marginal frame is probably taphonomic in origin, and results from the flattening of a globose, polyplated theca made of numerous small plates (see comparable examples in e.g. Dupichaud et al., 2023a; Zamora & Gutiérrez-Marco, 2023). Such a body organisation departs from the situation in Devonian mitrates, all characterised by a theca made of a limited number of thick plates (see e.g. Ruta & Bartels, 1998; Ruta, 1999; Lefebvre & Ausich, 2021). There is no known example of a mitrate stylophoran with its recurved aulacophore leaving an imprint on the opposite (lower) surface of the theca (see e.g. Dehm, 1932, 1934; Gill & Caster, 1960; Jefferies & Lewis, 1978; Ubaghs, 1979; Ruta & Bartels, 1998; Ruta & Jell, 1999a, b; Lefebvre & Ausich, 2021).

Devonian solutans share with RBINS a14020 the possession of a very long, stem-like appendage (homoiosteale), inserted in a more or less globose theca made of numerous, unorganised plates (see e.g. Dehm, 1934; Gill & Caster, 1960; Caster, 1967; Parsley & Sumrall, 2007; Rahman & Lintz, 2012; Zamora & Gutiérrez-Marco, 2023). Similarly to the situation in RBINS a14020, solutans can be preserved with their homoiosteale

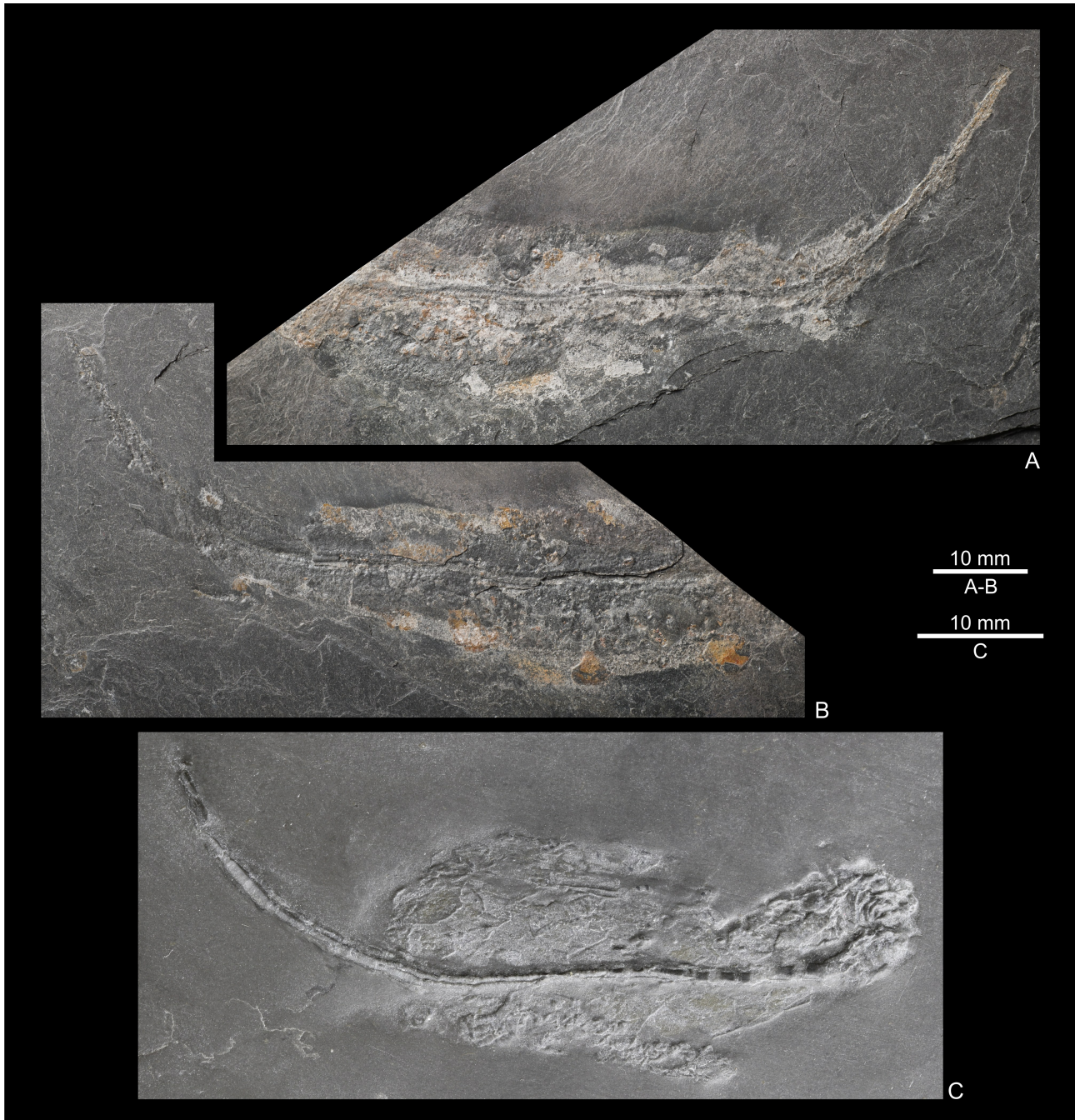


Figure 4. A–B. *Dehmicystis?* sp., RBINS a14020, part and counterpart; Warmifontaine, spoil heap of the Sainte-Barbe Quarry, La Roche Formation (Martelange Member), Pragian. C. *Dehmicystis globulus* (Dehm, 1934), NHMMZ PWL 2000/90-LS; pit near Bundenbach (Germany), Kaub Formation (Emsian).

recurved over the theca (Fig. 4C; see also individual 3 in Rahman & Lintz, 2012, figs 4, 7). In solutans, the homoiostele is made of two parts: a long and narrow distal portion (dististele), and a wider, shorter proximal region, made of telescopic rings (proxistele) (Caster, 1967; Ubaghs, 1981; Noailles et al., 2014). This organisation is compatible with the situation in RBINS a14020, with a narrow, elongate appendage corresponding to the dististele, and the wider, segmented region at its proximal extremity, to the proxistele (Fig. 4A). Comparison with the solutan homoiostele also suggests that the longitudinal groove running over the length of the appendage in the Warmifontaine specimen could correspond to the suture between the two sets of upper and lower series of ossicles forming the dististele (Fig. 4A–B). Moreover, as in RBINS a14020, the distal extremity of the homoiostele is frequently

bent or hooked in solutans (see e.g. Rozhnov & Jefferies, 1996; Noailles et al., 2014; Dupichaud et al., 2023b). If the interpretation of RBINS a14020 as a solutan is correct, the short, segmented (?) structure protruding next to its dististele, beyond the apex of the theca, could then very likely correspond to the poorly preserved distal extremity of its unique brachiole (Fig. 4A–B). Finally, if this interpretation is correct, the large, rounded structure near the homoiostele insertion of RBINS a14020 could then represent the periproct, and the large associated skeletal elements, ‘sugar loaf’ anal plates. In solutans, large suranal plates are an apomorphy of the family Dendrocystitidae (Noailles et al., 2014). Consequently, although poorly preserved, strongly flattened and distorted, all available morphological features observed in RBINS a14020 are compatible with its assignment to dendrocystitid solutans.

Comparison of RBINS a14020 with the three Siluro–Devonian solutan genera known so far suggests closer affinities with *Dehmicystis* and *Rutroclypeus*, both characterised by large rounded thecae made of numerous small plates (Dehm, 1934; Gill & Caster, 1960; Caster, 1967; Rahman & Lintz, 2012), than with *Claritacarpus*, possessing a more quadrangular theca, consisting of few, large elements (Parsley & Sumrall, 2007). *Rutroclypeus* differs from both *Dehmicystis* and the Warmifontaine solutan by the possession of ornamented thecal plates (all of them bearing a small central tubercle) and the more lateral position of its periproct, at the posterior extremity of the anal lobe (Gill & Caster, 1960; Jell & Holloway, 1982). Consequently, RBINS a14020 is tentatively assigned to *Dehmicystis*. Its morphology is too poorly known and tectonically distorted to suggest an identification at species level.

Occurrence. Warmifontaine, disused underground Sainte-Barbe Quarry; La Roche Formation (Martelange Member), Pragian (Fig. 2).

Class Stylophora Gill & Caster, 1960

Order Mitrata Jaekel, 1918

Suborder Peltocystida Jefferies, 1973

Remarks. Peltocystidan mitrates are the most long-ranging clade of stylophorans, with representatives known at least from the Tremadocian (Early Ordovician) to the Bashkirian (Early Pennsylvanian). They are characterised by the possession of a single posterior spine (glossal) and two particularly large adorals on the upper thecal surface. Although peltocystidans were highly diverse and palaeogeographically widespread during the Ordovician, their younger record is particularly cryptic (Lefebvre, 2007; Lefebvre & Ausich, 2021). They are so far undocumented in the Silurian, and are known from a handful of later occurrences: in the Lower and Middle Devonian of Germany (Haude, 1983; Südkamp, 2017) and the Carboniferous (Pennsylvanian) of Oklahoma (Kolata et al., 1991; Domínguez et al., 2002). Another occurrence of post-Ordovician peltocystidans is reported here from the Lower Devonian (Pragian) of southern Belgium.

The stratigraphic range of the family Kirkocystidae was recently tentatively extended to the Early Devonian by Südkamp (2017), so as to include all specimens from the Hunsrück Slate (lower Emsian) of Rhineland-Palatinate (Germany) regularly mentioned as *Mitrocystites? styloideus* (see e.g. Dehm, 1934; Bartels & Brassel, 1990; Bartels et al., 1998; Rahman & Lintz, 2012), *Dehmicystis globulus* (Bartels & Brassel, 1990, fig. 162; Bartels et al., 1998, fig. 139), or homalozoans indet. (Bartels et al., 1998, fig. 140). The family Kirkocystidae traditionally comprises the two Ordovician genera *Anatifopsis* and *Balanocystites* (Lefebvre, 1999; Lee et al., 2004, 2006). Both taxa are characterised by the possession of two particularly extensive, subequal adorals, forming together the whole upper thecal surface and the lateral edges of the lower side. The lower thecal surface comprises five marginals and, posteriorly, a relatively wide left infracentral area (Jefferies, 1981; Lefebvre, 1999, 2001; Lee et al., 2004, 2006). Marginals are more or less overlapped by adorals, some of them, completely. The anal opening is slit-like and located along the posterior margin of a wide infracentral element modified into a rounded anal plate. A single elongate spine (glossal) is articulated to the posterior extremity of the marginal frame, right of the anal opening. The aulacophore of kirkocystids is characterised by particularly spinose stylocone and ossicles.

Within peltocystidan mitrates, kirkocystids differ from peltocystids mainly by the possession of more extensive adorals,

a single infracentral area (instead of two), and of a well-defined rounded anal plate on the lower thecal surface (instead of a transverse slit-like orifice located within the supracentral area) (Lefebvre, 1999, 2001; Lee et al., 2006; Lefebvre & Botting, 2007). Jaekelocarpids differ from kirkocystids mainly by the loss of the left infracentral area, and the modification of the anal plate into a large element inserted medially in between the posterior extremities of two less extensive adorals, restricted to the upper thecal surface (Kolata et al., 1991; Domínguez et al., 2002).

Südkamp (2017) considered that Hunsrück peltocystidans show all apomorphies of the family Kirkocystidae (e.g. large adorals extending to and overlapping part of the lower thecal surface, single posterior spine, rounded anal plate, large left infracentral area, spinose aulacophore) and, therefore, he assigned them to the Ordovician genus *Anatifopsis*. However, the detailed morphology of *Mitrocystites? styloideus* and slightly younger peltocystidans from the Middle Devonian of Rhenish Massif (Germany) figured by Haude (1983, fig. 3) remains imperfectly known. In particular, the precise extension of their adorals and exact number of thecal plates are not documented so far. Moreover, Devonian peltocystidans from Germany seem to be characterised by an unusually ornamented stylocone bearing a strongly spinose transverse crest on its lower surface (Dehm, 1934; Haude, 1983). Therefore, their precise taxonomic assignment to any peltocystidan family (Jaekelocarpidae or Kirkocystidae) would require a detailed investigation of their morphology, which is beyond the scope of this paper.

Peltocystidan indet.

(Figs 5, 6)

Material. RBINS a14021, part and counterpart.

Description. Flattened fossil consisting of two distinct parts (Figs 5, 6): broad heart-shaped body, almost as long as wide (~2.4 cm) and, articulated to it, elongate, straight appendage (~3.8 cm long and 0.4–0.5 cm wide).

Pentagonal, slightly asymmetrical body outline, with deep, median V-shaped concavity along ‘proximal’ margin at appendage insertion (Fig. 5). Lateral margins unequal in length: one nearly straight, the other longer and strongly bent. Lateral sides converging to relatively short, truncated, oblique distal extremity. Very faint, gently curved longitudinal median line extending from distal tip of body to opposite extremity (at appendage insertion), and dividing body into two subequal halves (Fig. 5). Narrow, slightly thickened U-shaped ‘collerette’ framing more or less regularly curved lateral and distal body margins, and distally delimiting faint, more or less rounded area (Fig. 6A). Two other lines, subequal in length, extending from median part of each lateral side, converging proximally, and forming together faint V-shaped structure directed towards appendage insertion (Fig. 6). No other structure or limit clearly visible on body.

Proximal-most portion of appendage relatively short and wide, inserted into deep, concave body cavity (Figs 5, 6). Distal-most portion very long, almost straight, composed of numerous (at least 20) well-defined segments, all of relatively comparable width, but decreasing in length distally (Fig. 6B). Each segment made of well-defined, massive central element and, at least in distal part of appendage, two smaller V-shaped plates (one of the left, one of the right) articulated to lateral margins of each central element (Fig. 6B–C).

Remarks. Specimen RBINS a14021 is better preserved and less tectonically distorted than RBINS a14020 (*Dehmicystis? sp.*, see

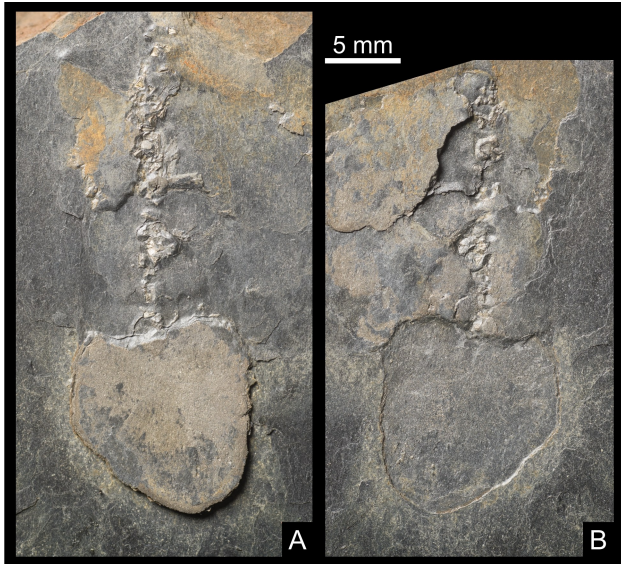


Figure 5. A–B. Peltocystidan indet., RBINS a14021, part and counterpart; Warmifontaine, spoil heap of the Sainte-Barbe Quarry, La Roche Formation (Martelange Member), Pragian.

above). Its identification is therefore more straightforward. The bipartite organisation of this specimen, with a long, delicate, segmented appendage inserted into a more massive, asymmetrical and flattened body strongly supports echinoderm affinities and, more precisely, its assignment to either pleurocystitids, solutans, or stylophorans. In the distal part of the appendage, the occurrence of two series of small V-shaped

plates articulated on both sides (left and right) of large central ossicles is incompatible with the identification of this appendage as a stem-like structure (pleurocystitid stem, solutan homoiosteole). Stem-like appendages are cylindrical, closed structures made of tightly sutured elements (David et al., 2000; Lefebvre et al., 2019). On the other hand, the organisation of the distal appendage of RBINS a14021 is typical of ambulacral structures in echinoderms and, more precisely, the stylophoran aulacophore (Lefebvre et al., 2019, 2022). In this context, the large central ossicles can be identified as uniserial ossicles, and the smaller articulated elements as left and right series of ambulacral cover plates. This identification makes it possible to identify which views of RBINS a14021 are exposed in lower (Figs 5A, 6) and upper aspects (Fig. 5B).

Within stylophorans, only three clades of mitrates survived the LOME and eventually diversified in the Early Devonian: anomalocystitids, paranacystids, and peltocystidans (Lefebvre, 2007; Lefebvre & Ausich, 2021). Devonian anomalocystitids and paranacystids share the same basic (mitrocystitidan) organisation for their lower thecal surface, with two central elements surrounded by several, relatively large marginal plates (Lefebvre, 1999, 2001). The lower thecal side of RBINS a14021 does not show any evidence of such a plate pattern. In contrast, it is very likely that the faint longitudinal line extending from the distal extremity of the theca to the aulacophore insertion corresponds to the imprint of the suture between two very large adorals (on the opposite, upper surface), therefore clearly suggesting peltocystidan affinities. This identification is supported by the pentagonal thecal outlines of RBINS a14021, identical to those of Devonian peltocystidans from the Hunsrück Slate (see e.g. Bartels et al., 1998, fig. 139). At the distal extremity of the lower thecal surface, the occurrence of a

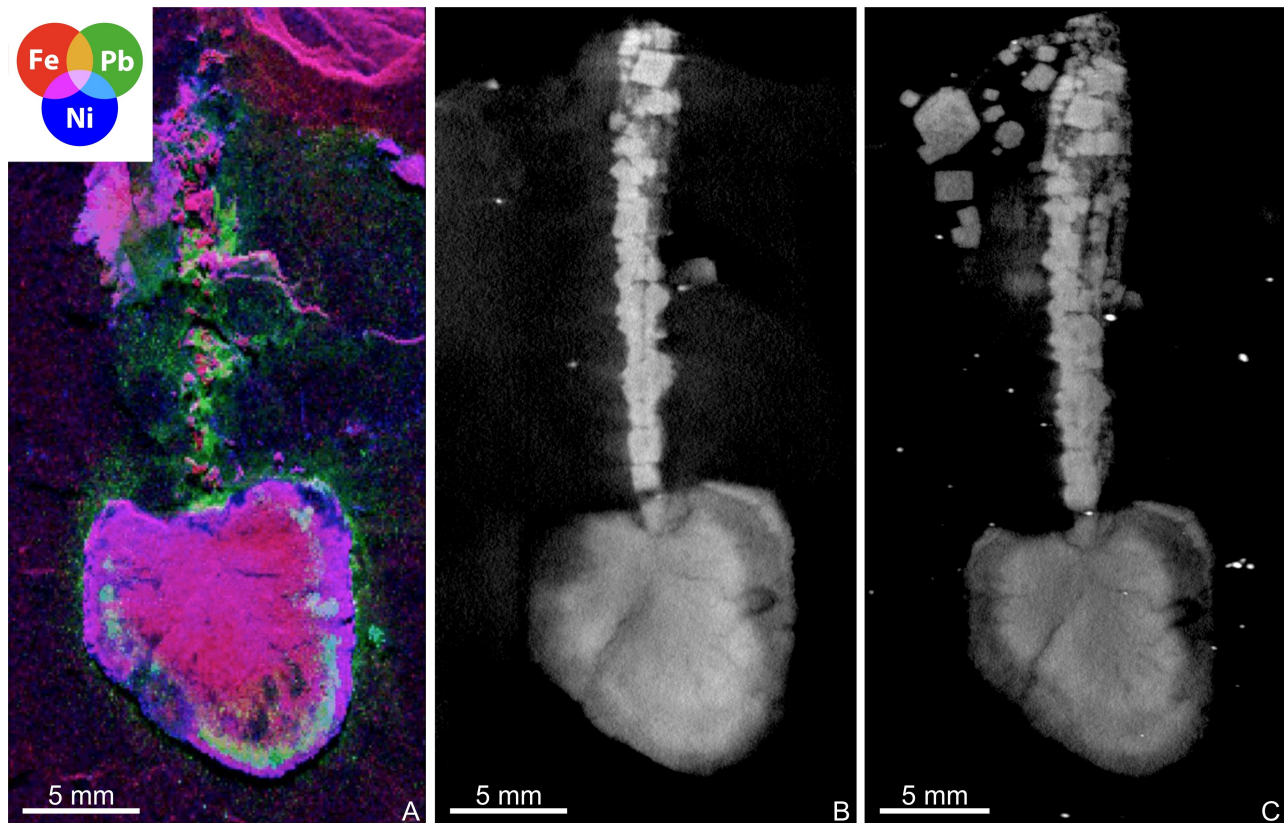


Figure 6. A–C. Peltocystidan indet., RBINS a14021; Warmifontaine, spoil heap of the Sainte-Barbe Quarry, La Roche Formation (Martelange Member), Pragian. **A.** μ XRF overlay of iron (red), lead (green) and nickel (blue) distributions. **B.** Tomogram parallel to the slate surface. **C.** Maximum intensity projection of 46 tomograms parallel to the slate surface.

rounded element, morphologically identical to the anal plate of *Mitrocystites? styloideus*, further supports the assignment of RBINS a14021 to this family. Comparison with other peltocystidans suggests that the faint V-shaped structure on the lower thecal surface of the Warmifontaine specimen very likely corresponds to the strong, U- to V-shaped ridge occurring in some taxa (e.g. *Anatifopsis trapeziiformis*, *Jaekelocarpus oklahomaensis*; see Haude, 1983; Kolata et al., 1991; Lefebvre, 1999; Lee et al., 2004). No posterior spine (glossal) is present in RBINS a14021, but this plate is seldom preserved in Devonian peltocystidans (see e.g. Dehm, 1934; Haude, 1983; Bartels & Brassel, 1990; Bartels et al., 1998; but see Südkamp, 2017). Consequently, all available morphological features displayed by RBINS a14021 support its identification as a stylophoran (aulacophore with two series of cover plates articulated to uniserial ossicles) and more precisely as a peltocystidan mitrate (large adorals, rounded anal plate). The morphology of the Warmifontaine specimen seems to be very close to that of *Mitrocystites? styloideus* from the Hunsrück Slate, which was tentatively placed within the genus *Anatifopsis* by Südkamp (2017). However, a precise taxonomic assignment of the Warmifontaine mitrate remains difficult in the absence of a proper (re)description of the more abundant and better preserved peltocystidans from the Devonian of Germany, including *Mitrocystites? styloideus*.

RBINS a14021 is preserved with its aulacophore in extended position (Figs 5, 6). This posture is unusual in mitrates: they are generally preserved with their aulacophore flexed and recurved above the upper thecal surface (Parsley, 1991; Ruta & Bartels, 1998; Lefebvre, 2003; Lefebvre & Ausich, 2021). This posture is interpreted as resulting from the post-mortem contraction of the appendage (Dehm, 1932; Ruta & Bartels, 1998; Lefebvre, 2003; Lefebvre & Ausich, 2021; Lefebvre et al., 2022; Saleh et al., 2023). The preservation of the aulacophore in extended position, generally interpreted as corresponding to its life (feeding) posture, implies that the organism was very likely buried alive by a sudden influx of sediments (Parsley & Gutiérrez-Marco, 2005; Lefebvre & Botting, 2007; Lefebvre & Ausich, 2021; Lefebvre et al., 2022; Saleh et al., 2023).

Occurrence. Warmifontaine, disused underground Sainte-Barbe Quarry; La Roche Formation (Martelange Member), Pragian.

5. Discussion

Uppermost Silurian (Pridoli) and Lower Devonian invertebrate faunas from the Ardenne Allochthon are strongly similar to those from the contemporaneous siliciclastic succession of the nearby Rhenish Massif (Germany), but it has to be said that palaeontologists essentially paid attention to the brachiopods during the last decades (see references in Mottequin, 2019 and Mottequin & Jansen, 2025). These benthic organisms proliferated in the ‘Rhenish’ (rhenotypic) facies (e.g. Erben, 1962; Jansen, 2016), which would represent shallow-marine, nearshore palaeoenvironments with turbulent, turbid water and essentially coarse siliciclastic sedimentation in contrast with the ‘Hercynian’ (hercynotypic) or ‘Bohemian’ facies that chiefly includes pelagic faunas reflecting offshore palaeoenvironments with calm water and predominantly argillaceous and calcareous sedimentation (Jansen, 2016).

Our knowledge of echinoderms from the rhenotypic facies of southern Belgium is restricted essentially to the crinoids that can be abundant as columnals or stem fragments in some levels of the thick, essentially siliciclastic Lochkovian (~ Gedinnian), Pragian (~ Siegenian), and Emsian successions (e.g. Leriche, 1912; Asselberghs, 1930, 1946; Maillieux, 1931, 1933, 1938,

1940, 1941). Nevertheless, they remain inadequately known notably due to the rarity of well-preserved specimens (Figs 7, 8A–C). Indeed, calyxes are particularly scarce as reflected by the few discoveries reported in the literature (Schmidt in Maillieux, 1936; Maillieux, 1938 [note that *Platycrinus lommanus* Maillieux, 1938 (Fig. 8C) could be late Emsian or early Eifelian in age]; Ubahgs, 1945a, 1945b, 1947; Closset, 1970). It is obvious that the taxonomic revision of the Early

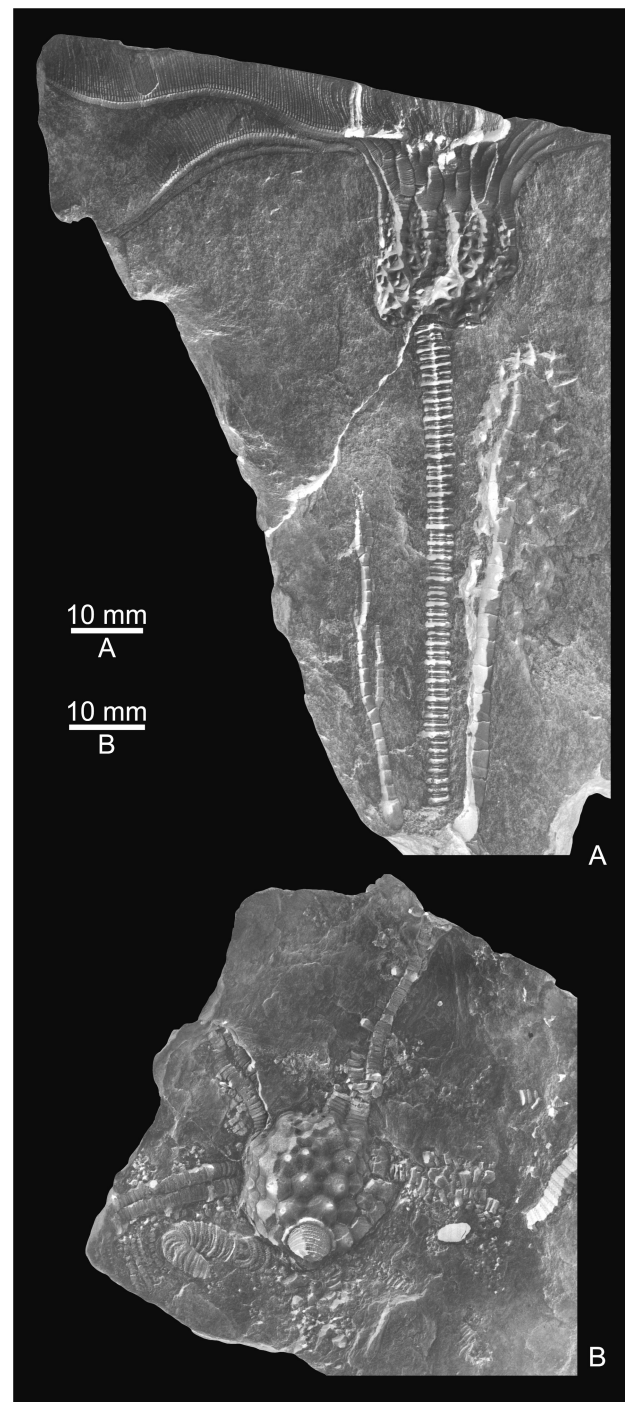


Figure 7. Crinoids from the Lower Devonian of Belgium; both are negatives of pictures of the external moulds that were coated with ammonium chloride sublimate. See Denayer & Mottequin (2024) for the lithostratigraphic units. **A.** *Diamenocrinus stellatus* Jaekel, 1895 (fide Schmidt in Maillieux, 1936), RBINS a1057 (= specimen D₁ in Ubahgs, 1947); Martelange (Fauvillers 7a), Longlier Formation, Pragian. **B.** *Ctenocrinus pyramidalis* Ubahgs, 1945a, RBINS a7679 (holotype); south of Petigny, Hierges Formation, upper Emsian.

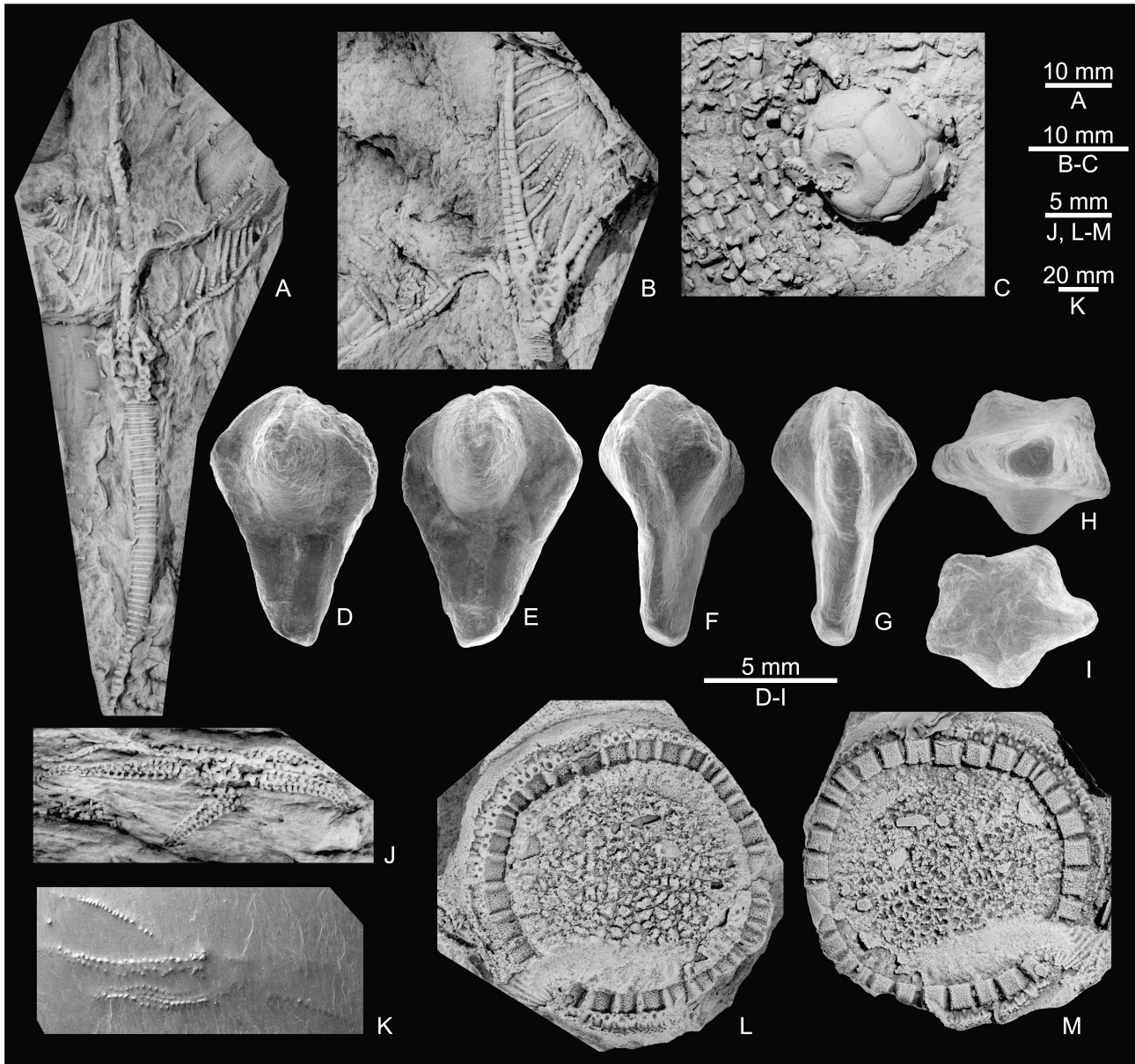


Figure 8. Crinoids (A–C), blastoid (D–I), ophiuroids (J–K), and cyclocystoid (L–M) from the Lower Devonian of Belgium (except otherwise stated). See Denayer & Mottequin (2024) for the lithostratigraphic units. All specimens are coated with ammonium chloride sublimate (except otherwise stated). **A.** *Ctenocrinus aculeatus* Ubaghs, 1945a, RBINS a7674 (holotype), artificial cast; railway trench between Grupont and Mirwart, Ruisseau de la Forge Formation (Pèrnelle Member), upper Pragian. **B.** *Ctenocrinus arduennensis* Closset, 1970, RBINS a172 (holotype), artificial cast; railway trench between Grupont and Mirwart, Ruisseau de la Forge Formation (Pèrnelle Member), upper Pragian. **C.** *Platycrinus lommanus* Maillieux, 1938, RBINS (holotype), artificial cast; Rochefort 31(2), Moulin de la Foulerie Formation (Eau Noire Member), upper Emsian or lower Eifelian (see fig. 2 in Denayer et al., 2024). **D–I.** *Pentremitidea fraiponti* ('Fraipont, 1884'), PA.ULg.20250109-1 (holotype by monotypy), calyx in lateral (D–G), aboral (H) and oral (I) views (SEM); Champlon-Famenne, Moulin de la Foulerie Formation (Saint-Joseph Member or Eau Noire Member), upper Emsian or lower Eifelian (see fig. 2 in Denayer et al., 2024). **J.** *Bohemura constellata* (Thorent, 1839), RBINS a7666, artificial cast; Brûly-de-Pesche, Mondrepuis Formation, Lochkovian. **K.** Unidentified pyritised ophiuroid, RBINS a14162; Linglé slate underground quarry (Mortehan), La Roche Formation, Pragian. **L–M.** *Sievertsia concava* Smith & Paul, 1982, RBINS a9588 (holotype), external mould and artificial cast; Rochefort, 8649, Hierges Formation, upper Emsian.

Devonian crinoids from Belgium is needed to better assess their diversity and their close relationships with those from the contemporaneous successions of the nearby Rhenish Massif. This is notably the case for those from the Longlier Formation (Pragian), which were identified by Schmidt (in Maillieux, 1936) (Fig. 7A), who noted strong similarities with the German species, but they mostly remain undescribed. Pyritised crinoids are also known from the Herbeumont slate underground quarries west of Warmifontaine (RBINS collections). Apart from crinoids, reports of other echinoderms are scarce in the literature. A single blastoid (*Pentremitidea*) occurrence is

known from the upper Emsian–lower Eifelian Moulin de la Foulerie Formation of the southern margin of the Dinant Synclinorium (Fraipont, 1884; Etheridge & Carpenter, 1886) (Fig. 8D–I). Asterozoans (asteroids and ophiuroids) can be counted on the fingers of the two hands (Leriche, 1912; Asselberghs, 1930; Ubaghs, 1942, 1943) (Fig. 8J–K). To this point, as is the case for the aforementioned pyritised crinoids, large asteroids are known from the Linglé slate underground quarry (Fig. 1) at Mortehan (RBINS collections) (Fig. 8K). A single specimen (holotype) of the cyclocystoid *Sievertsia concava* Smith & Paul, 1982 (Fig. 8L–M), first reported by

Maillicux (1926) and illustrated by Sieverts-Doreck (1951), is known from the upper Emsian Hierges Formation. Consequently, the first reports of *Dehmicystis?* sp. and a peltocystidan mitrate in the Belgian Lower Devonian deserved to be thoroughly documented.

The identification of the representatives of the two echinoderm classes *Soluta* (*Dehmicystis?* sp.) and *Stylophora* (peltocystidan indet.) significantly increases the taxonomic diversity of invertebrate marine assemblages from the Martelange Member (La Roche Formation), which was up to now considered as yielding poorly diverse invertebrate fossils (e.g. Asselberghs, 1946). The two echinoderms identified in Warmifontaine suggest strong affinities with slightly younger taxa from the Hunsrück Slate of Germany (early Emsian): *Dehmicystis globulus* and *Mitrocystites? styloideus*. Faunal affinities between these two regions, palaeogeographically close to each other in the Early Devonian, are not surprising and were already suggested (see references in Mottequin & Jansen, 2025). However, as far as solutans and stylophorans are concerned, palaeobiogeographic implications remain limited, because of the scarcity of other occurrences worldwide. Similarities with Devonian taxa from Germany may also simply reflect the existence of relatively similar environmental and/or taphonomic conditions, associated with relatively deep settings.

Acknowledgements

This paper is part of the project B2/202/P1/VERTIGO of the Belgian Science Policy Office (Belspo). We thank Herman Borré for authorising the collection of samples on his property, Guy Conard the neighbour of the quarry who provided assistance, our numerous colleagues for taking part in the field work, Laetitita Despontin (RBINS) for the SEM photographic work, and Thierry Hubin (RBINS) for photographing the echinoderm, mollusc and trilobite specimens from Warmifontaine and Bertrix. We are grateful to Manuela Aiglstorfer, David Kuhlmann and Kai Nungesser (Naturhistorisches Museum Mainz), who warmly welcomed us in the collections in their care and provided us with photographs of specimens. We thank A. Folie (RBINS), J. Lalanne (RBINS) and V. Fischer (ULiège) for access to the collections under their care. We thank SOLEIL synchrotron for provision of beamtime (proposal 20220721). Object Research Systems (ORS; Montreal, Canada, <https://www.theobjects.com/dragonfly/index.html>) and GOM (<https://www.gom.com/>) are thanked for allowing the use of their Dragonfly ORS (Version 4.1.0.647 for Windows) and GOM Inspect softwares. We are grateful to M. Reich (Germany) and an anonymous reviewer for their comments and suggestions.

Author contribution

All the authors contributed to the writing of the paper, but BL is responsible for the systematic description and interpretation.

Data availability

All studied specimens are housed in an official repository ensuring their long-term safekeeping and availability to other researchers for future studies.

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