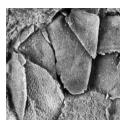


Morphological variability within the mitrate *Mitrocystella incipiens* (Echinodermata, Stylophora) from the Darriwilian (Middle Ordovician) of high-latitude peri-Gondwanan regions

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The mitrate *Mitrocystella incipiens* (Barrande, 1887) is a locally abundant stylophoran echinoderm, with a short stratigraphic range but a wide palaeobiogeographic distribution in the high-latitude peri-Gondwanan regions of the Mediterranean Province: Czech Republic (Prague Basin, Bohemia), France (Armorican Massif, Brittany), northern Portugal and Spain (Iberian Massif). Two regional subspecies were previously identified based on the morphology of their thecal outlines: *M. incipiens incipiens* (Barrande, 1887) (Prague Basin), and *M. incipiens miloni* Chauvel, 1937 (Armorican Massif and Iberian Peninsula). A sample of 40 complete and well-preserved individuals from the Armorican Massif, the Iberian Peninsula, and the Prague Basin was selected to assess whether these morphotypes could be distinguished through quantitative analysis. Geometric morphometric analysis of their theca confirmed the existence of morphological differences between the Armorican and Czech populations, but also identified that the Iberian specimens are morphologically intermediate between those from the Armorican Massif and Prague Basin. Furthermore, the antero-lateral margins of the Iberian specimens present a delicate pustulose ornamentation, while the lower thecal surface of the Armorican and Czech individuals is completely smooth. The Iberian specimens are thus assigned to a new subspecies: *M. incipiens pustulosa* ssp. nov. These results support the idea that all populations of *Mitrocystella* belong to the same species, *M. incipiens*, which is characterized by a broad phenotypic variation. Together with geographic isolation, subtle environmental differences between the three regions (e.g. depth) may have contributed to shape these ecophenotypes. Finally, the first example of abnormal thecal plating in *Mitrocystella incipiens* is described in a specimen from Spain and its possible phylogenetic implications are discussed. • Key words: *Mitrocystella incipiens*, Echinodermata, Stylophora, Bohemia, Armorican Massif, Iberia.

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Stylophorans are an extinct class of vagile and epibenthic echinoderms (Miaolingian–Bashkirian) characterized by the possession of a single ambulacral structure (aulacophore) inserted into a flattened and asymmetric theca (Ubaghs 1968, Chauvel 1981, Parsley 1994, David *et al.* 2000, Lefebvre *et al.* 2019, Boisset *et al.* 2024, Rahman & Zamora 2024). During the late Cambrian (Furongian) and earliest Ordovician (Tremadocian), stylophorans were one of the main components of the low-diversity,

cosmopolitan echinoderm communities thriving on soft substrates (Sumrall *et al.* 1997, Ubaghs 1998, Zamora *et al.* 2013). In low latitude regions, stylophorans subsequently disappeared or played a minor role in echinoderm faunas dominated by new groups rapidly diversifying on soft substrates (e.g. crinoids, paracrinoids, pleurocystitids) (Lefebvre & Fatka 2003, Sprinkle & Guensburg 2004, Lefebvre *et al.* 2013). In contrast, in high-latitude peri-Gondwanan regions of the Mediterranean Province (e.g.

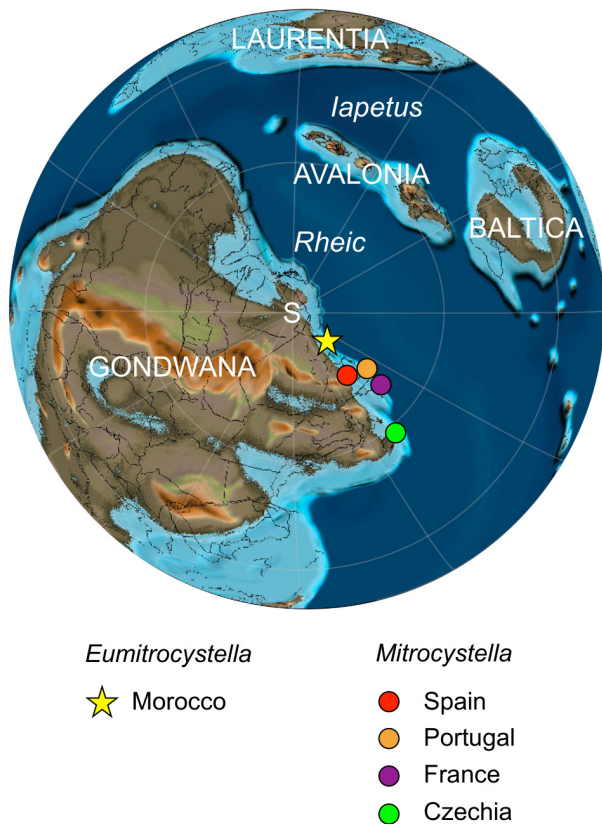


Figure 1. Late Middle Ordovician palaeogeography (460 Ma; south polar view) based on Scotese's (2001) paleomap project, with plotted occurrences of the two closely related mitrate genera *Eumitrocystella* and *Mitrocystella*.

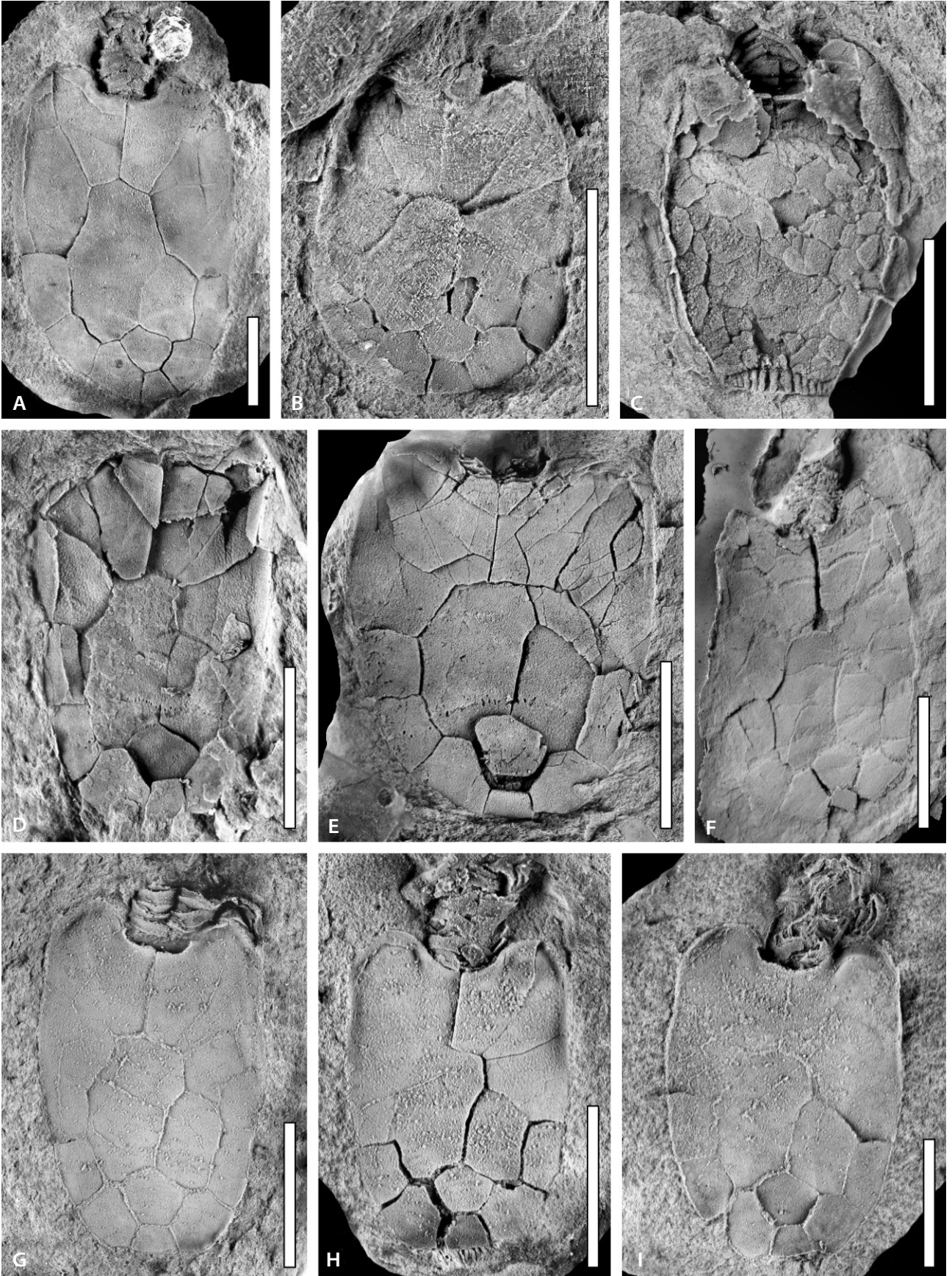
Czech Republic, France, Morocco, Portugal, Spain) (Fig. 1), stylophorans remained, along with aristocystitid diploporites and ophiuroids, a key member of echinoderm communities throughout most of the Ordovician, (Lefebvre & Fatka 2003; Lefebvre 2007; Lefebvre *et al.* 2013, 2016, 2022).

Mitrocystella incipiens (Barrande, 1887) (Fig. 2) probably represents one of the most emblematic and most studied stylophorans from the Middle Ordovician of the Mediterranean Province (see *e.g.* Barrande 1887; Chauvel 1937, 1941, 1981; Jefferies 1968, 1986; Gutiér-

rez-Marco & Meléndez 1987; Hunter *et al.* 2007; Lefebvre & Régnault 2009; Renaud *et al.* 2023). This mitrate was palaeobiogeographically widespread with occurrences reported from the Prague Basin, Bohemia, Czech Republic (*e.g.* Barrande 1887, Prokop & Petr 1999); the Armorican Massif, Brittany, France (Chauvel 1937, 1941, 1981; Jefferies 1968; Lefebvre 2000; Hunter *et al.* 2007; Lefebvre & Régnault 2009; Renaud *et al.* 2023), and the Iberian Massif, including Portugal and Spain (Chauvel & Meléndez 1978, Gutiérrez-Marco *et al.* 1984a, Gutiérrez-Marco & Meléndez 1987, Couto & Gutiérrez-Marco 2000, Jacinto *et al.* 2015) (Fig. 1). Almost all known occurrences of *M. incipiens* are restricted to a very short stratigraphic interval in the late Darriwilian (early Dobrotivian), corresponding to the *Hustedograptus teretiusculus* graptolite Zone and the top of the *Placoparia tournemini* trilobite Zone (Gutiérrez-Marco & Meléndez 1987, Renaud *et al.* 2023). The only exception was a single occurrence at the base of both biozones in the locality of Alía (province of Cáceres: locality PSV-IV in Rábano 1990). However, possible earlier occurrences of the species (middle Darriwilian, early Oretanian) comprise specimens from the Crozon Peninsula (Armorican Massif, Brittany, France) (Renaud *et al.* 2023) and Almuradiel (Ciudad Real, Spain) (see below).

Although dozens of specimens of this mitrate stylophoran were collected from concretions of the Traveusot Formation (late Darriwilian) near Guichen (Armorican Massif, Brittany, France) in the early 1850s by Marie Rouault, this material remained unexplored for more than 80 years (see Chauvel 1941, Lefebvre 2000b, Lefebvre & Régnault 2009). This taxon was originally described as *Anomalocystites incipiens* by Barrande (1887), based on several specimens from the Prague Basin (Bohemia, Czech Republic) preserved in black shales of the Dobrotivá Formation (late Darriwilian) (Fig. 2A, B). The genus *Mitrocystella* was later created by Jaekel (1901), with *M. incipiens* (Barrande, 1887) designated as the type species. Jaekel (1901) also correctly pointed out that some of the specimens originally described as *Mitrocystites mitra* by Barrande (1887) were distinct from it and

Figure 2. *Mitrocystella incipiens* (Barrande, 1887), late Darriwilian (*H. teretiusculus* Zone). • A, B – *Mitrocystella incipiens incipiens* (Barrande, 1887), Dobrotivá Formation, Prague Basin, Czech Republic. A – NMP L 67019: smooth lower thecal surface and proximal aulacophore of a very large individual; Malé Přílepy. B – NMP L 9295: smooth lower thecal surface of a small individual originally figured by Barrande (1887, pl. 5, Fig. 1.13–14); Svatá Dobrotivá. • C–E – *Mitrocystella incipiens pustulosa* ssp. nov., Guindo Shale, Calzada de Calatrava (Ciudad Real), Central Iberian Zone, Spain. C – MGM-85970: upper thecal surface, with periproct, and proximal rings of the aulacophore. D – MGM-85930 (holotype): lower thecal surface, with delicate spiny ornamentation on antero-lateral marginals (M'_2 , M'_3 , M_2 , and M_c). E – MGM-85940: lower thecal surface, with slightly displaced posterior infracentral element (I'_3) and delicate spinose ornamentation on antero-lateral marginals. • F – *Mitrocystella incipiens pustulosa?* ssp. nov., Valongo Formation, San Pedro de Cova (Douro Litoral), Central Iberian Zone, northern Portugal; UCBL-FSL 718480: lower thecal surface. • G–I – *Mitrocystella incipiens miloni* Chauvel, 1937, Traveusot Formation, Traveusot en Guichen, Ille-et-Vilaine, Armorican Massif, France. G – IGR 15337: proximal rings of the aulacophore and smooth lower thecal surface. H – IGR 15430: stylocone, proximal aulacophore, and smooth lower thecal surface. I – IGR 15498: smooth lower thecal surface and disarticulated remains of the aulacophore. All scale bars = 1 cm.



morphologically closer to *Mitrocystella incipiens*. He therefore placed them in a new taxon: “*Mitrocystella barrandei*”, before Lefebvre (2000a) placed them in a new genus as *Promitrocystites barrandei* (see below).

Several hundred specimens of *Mitrocystella* from the Traveusot Formation were thoroughly studied by Chauvel (1937, 1941, 1981), who identified morphological differences with the material from the Prague Basin. Chauvel (1937, 1941) pointed out that the theca of Armorican specimens is characterized by a deep anterior cavity for the aulacophore insertion (Fig. 3D), and a straight posterior margin, while the aulacophore insertion is shallower, and the posterior thecal margin rounded in Czech specimens (see also Gutiérrez-Marco & Meléndez 1987). Therefore, Chauvel (1937, 1941) suggested assigning all Armorican specimens to a new subspecies, *M. incipiens miloni* (Fig. 2G–I), distinct from the Bohemian one, *M. incipiens incipiens* (see e.g. Chauvel 1981; Jefferies 1968, 1975, 1981, 1984, 1986; Ubaghs 1968; Jefferies & Lewis 1978, Parsley 1994). Long suspected in the Middle Ordovician of the Iberian Peninsula (Chauvel & Meléndez 1978, Gutiérrez-Marco *et al.* 1984b), the presence of *M. incipiens* in the late Darriwilian of both Ciudad Real, Spain (Guindo Shales; Fig. 2C–F) and northern Portugal (Valongo Formation) was clearly established by Gutiérrez-Marco & Meléndez (1987). All Iberian specimens were assigned to *M. incipiens miloni* (see also Couto & Gutiérrez-Marco 2000, Jacinto *et al.* 2015).

The detailed morphology and anatomy of mitrocystitid mitrates from the Middle Ordovician of the Prague Basin were analysed by Parsley (1994), based on the examination of over 500 specimens three-dimensionally preserved in silico-aluminous concretions of the Šárka Formation (Oretanian, middle Darriwilian) and assigned to *Mitrocystites mitra* (Fig. 3A) and *Mitrocystella incipiens incipiens*. This study not only extended the stratigraphic range of *M. incipiens*, but also identified additional morphological differences between its two subspecies. In 2024, re-examination by two of the co-authors (MN and BL) of the original material studied by Parsley (1994) did not confirm his taxonomic identifications: all specimens from the Šárka Formation assigned to *Mitrocystella incipiens incipiens* by Parsley (1994) actually correspond to “*Mitrocystella barrandei*” (Fig. 3B). Consequently, Parsley’s (1994) study of Czech mitrocystitids contributed to making their systematics and stratigraphic range more confusing. Moreover, it also questioned the validity of the two subspecies of *M. incipiens* identified by Chauvel (1937, 1941), because the morphological features considered as typical of *M. incipiens incipiens* (shallow anterior cavity for the aulacophore insertion and rounded posterior thecal margin) are also found in “*Mitrocystella barrandei*” (see Lefebvre 2000a, b; Hunter *et al.* 2007;

Lefebvre & Régnault 2009; Renaud *et al.* 2023). Accordingly, Lefebvre (2000a) assigned “*Mitrocystella barrandei*” to a new genus, *Promitrocystites*, morphologically intermediate (with 13 marginals and a single infracentral area; Fig. 3B) between *Mitrocystites* (with 13 marginals and two infracentral areas; Fig. 3A) and *Mitrocystella* (with 12 marginals and one infracentral area; Fig. 3C).

Despite the record of an abundant, often well-preserved material, the existence of two morphologically distinct regional subspecies of *Mitrocystella incipiens* has not been quantitatively assessed so far. Therefore, the main objective of this study is to produce the first morphometric analysis of the outlines and plate pattern of the lower thecal surface of a sample of 40 specimens of *Mitrocystella incipiens* from different regions, in order to test the validity of the existence of two morphologically distinct subspecies *M. incipiens incipiens* and *M. incipiens miloni*.

Material and methods

Material

Armorican Massif (Brittany, France). – All available material of *Mitrocystella incipiens miloni* from its type locality (Traveusot en Guichen, Ille-et-Vilaine, France; upper part of the Traveusot Formation, late Darriwilian) is deposited in the public collections of the University of Rennes (IGR), France (over 800 specimens, including Chauvel’s original material) and the palaeontological collections of the Université Claude Bernard Lyon 1 (UCBL-FSL), Villeurbanne, France (35 specimens) was examined. As pointed out by Chauvel (1941, 1981), most specimens of *Mitrocystella* from Traveusot are more or less strongly disarticulated, with the supracentrals sometimes collapsed, but generally absent, thus exposing the internal aspect of the lower thecal surface. Except for its taphonomically more resistant proximal elements (tetramerous rings and stylocone), the aulacophore is rarely preserved (Figs 2G–I, 3D) (see Chauvel 1941, 1981; Lefebvre *et al.* 2022). Despite the very large quantity of specimens available, only 24 of them possessed a sufficiently well-preserved lower thecal surface (with all skeletal elements present and in anatomical connection) and were therefore selected for morphometric analysis (see supplementary data).

All studied specimens from the Traveusot Formation are preserved as three-dimensional imprints in silico-aluminous and terrigenous concretions (Fig. 2G–I). They are associated with a particularly abundant and diverse marine fauna composed of bivalves, brachiopods, cephalopods, gastropods, graptolites, hyoliths, ostracods,

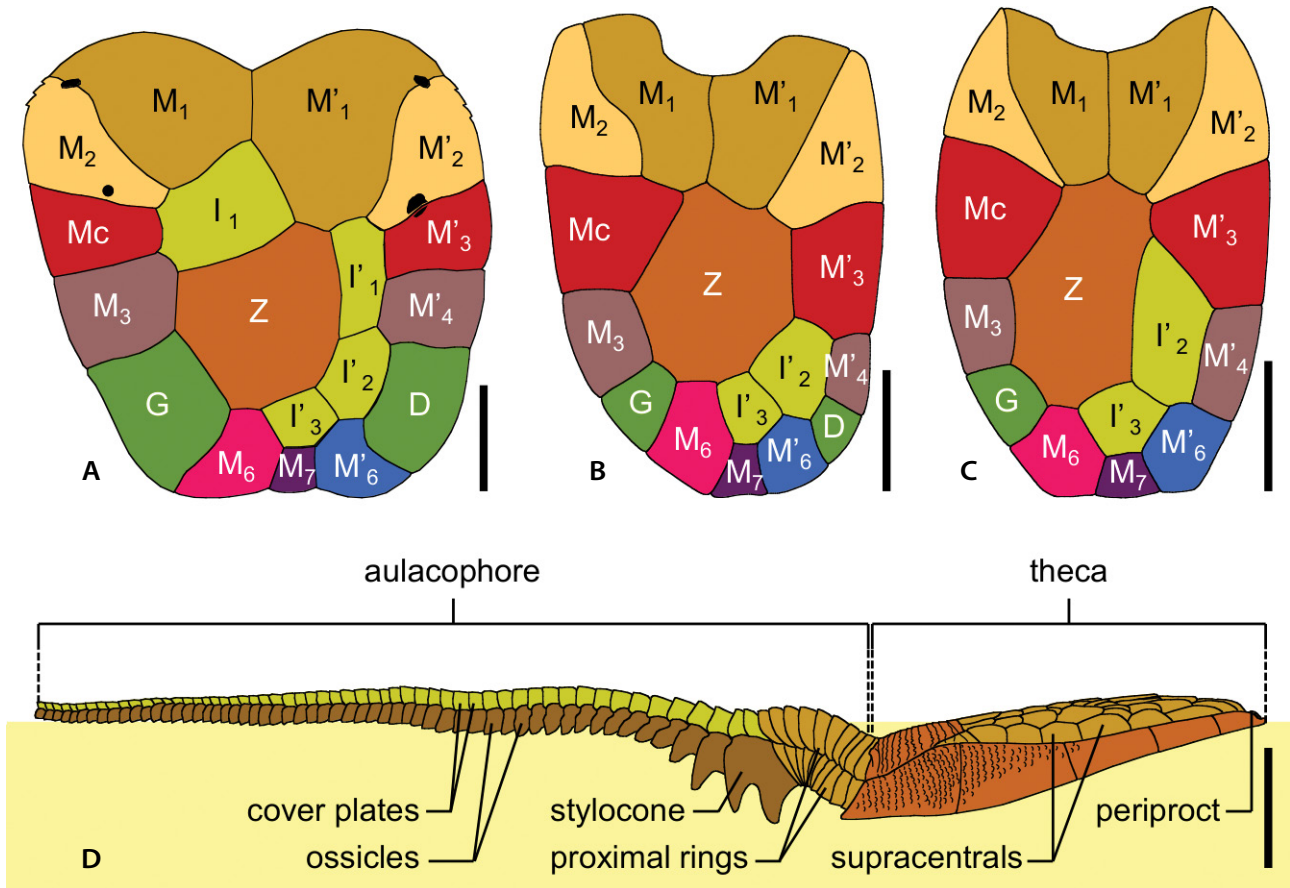


Figure 3. Thecal plate homologies and morphology of selected mitrocystitidan mitrates belonging to the paranacystid stem-lineage. A–C – plate homologies on the lower thecal surface of selected mitrocystitidans (aulacophore not represented). • A – *Mitrocystites mitra* Barrande, 1887, Šárka Formation (middle Darriwilian), Prague Basin (Czech Republic); redrawn and modified after Ubaghs (1968). • B – *Promitrocystites barrandei* Jaekel, 1901, Šárka Formation (middle Darriwilian), Prague Basin (Czech Republic); redrawn and modified after Ubaghs (1968). • C – *Mitrocystella incipiens miloni* Chauvel, 1937, Traveusot Formation (late Darriwilian), Armorican Massif (France); redrawn and modified after Jefferies (1968). • D – morphology and presumed life position of *Mitrocystella incipiens* (Barrande, 1887) (late Darriwilian), in left lateral view; redrawn and modified after Lefebvre & Régnault (2009). All scale bars = 5 mm.

trilobites, as well as numerous other echinoderms (crinoids, diploporites, stenuroids, and other stylophorans) (see e.g. Chauvel 1941; Babin 1966; Mélou 1973, 1975; Henry 1980, 1989; Gendry et al. 2013; Lefebvre et al. 2022). The composition of this diverse benthic fauna and its taphonomic features (e.g. preservation of delicate trilobite exuviae and many decayed and collapsed echinoderm skeletons) suggest relatively distal, well-oxygenated and quiet environmental conditions (below storm wave base) (Henry 1980, 1989; Lefebvre et al. 2022).

In the Armorican Massif, additional material of *Mitrocystella* is also known from the same stratigraphic interval (*H. teretiusculus* Zone) in several other localities (e.g. Bain-de-Bretagne, Gourin, Guignen, La Croixille, Langon), as well as possibly from slightly older deposits in the Crozon Peninsula (lower part of the Postolonnet Formation; *Didymograptus artus* Zone) (Chauvel 1941, 1981; Lefebvre 2000b; Hunter et al. 2007; Renaud et al. 2023). However, most of these specimens are found

in shales (e.g. Crozon Peninsula, Gourin), and were too poorly preserved to be included in the analysis.

Iberian Massif (Portugal and Spain). – All known specimens of *Mitrocystella* from the Middle Ordovician of the Iberian Peninsula deposited in public collections were examined. This material includes the isolated adoral (IGR 15624) originally figured by Chauvel & Meléndez (1978); the two Spanish specimens described by Gutiérrez-Marco & Meléndez (1987) and deposited in the collections of the Área de Paleontología of the Complutense University of Madrid, Spain (MT); the specimen from Portugal mentioned by Gutiérrez-Marco & Meléndez (1987), now deposited in the palaeontological collections of the Université Claude Bernard Lyon (UCBL-FSL); and finally, 14 new specimens from Spain, deposited in the collections of the Museo Geominero, Madrid, Spain (MGM). Most Spanish specimens are preserved as three-dimensional imprints in relatively dark siltstones

(Fig. 2C–E), while the material from the Valongo Formation (Portugal) occurs in black shales and is more strongly flattened (Fig. 2F). With the exception of one specimen (MGM-8605O), which was collected in early Oretanian (middle Darriwilian) dark micaceous siltstones near Almuradiel (Ciudad Real, Spain), all specimens of Iberian *Mitrocystella* were sampled in early Dobrotivian (late Darriwilian, *H. teretiusculus* Zone) deposits. The Oretanian specimen from Almuradiel was too incomplete (anterior part of the theca not preserved) to be selected for morphometric analysis. Only five specimens, all from the late Darriwilian, were sufficiently well preserved and were included in the analysis: five are from the Guindo Shale, Spain (Fig. 2C–E), and one from the Valongo Formation, Portugal (Fig. 2F) (see supplementary data).

Examined specimens of late Darriwilian *Mitrocystella* from Spain were collected in the lower part of the Guindo Shales, at three distinct localities, all situated within the Central Iberian Zone (Iberian Massif): Almodóvar del Campo, Calzada de Calatrava, and Fontanosas (Ciudad Real, Spain); a single specimen is from a fourth locality in the lower part of the upper Navatrasiera (= Navalaceite) Shales at Alía (Cáceres, Spain). In these levels, mitrates are associated with a particularly abundant and diverse fauna, including bivalves, brachiopods, cephalopods, gastropods, graptolites, trilobites, and many other echinoderms (e.g. diploporites, ophiuroids) (see e.g. Gutiérrez-Marco *et al.* 1984a, 1984b; Hammann & Schmincke 1986; Gutiérrez-Marco & Meléndez 1987; Rábano 1990; Babin & Gutiérrez-Marco 1991, 1992; Reyes-Abril *et al.* 2011; Paul & Gutiérrez-Marco 2022). Associated palaeoenvironmental conditions were interpreted as relatively distal, well-oxygenated, and quiet, with episodic, storm-generated obrution deposits (e.g. Hammann & Schmincke 1986). This interpretation agrees well with the preservation of fully articulated ophiuroids (*Taeniaster ibericus*) and nearly complete specimens of *Mitrocystella* with their distal aulacophore preserved (Figs 2F, 3D), suggesting the burial of living (or freshly killed) organisms.

The unique specimen of *Mitrocystella* from northern Portugal was sampled near San Pedro de Cova (Douro Litoral) in the upper half of the Valongo Formation (Gutiérrez-Marco & Meléndez 1987, Couto & Gutiérrez-Marco 2000, Jacinto *et al.* 2015). It is associated with a diverse fauna including brachiopods, conulariids, crinoids, diploporites, graptolites, hyoliths, molluscs, machaeridians, and mostly, trilobites (Romano 1976, 1991; Tauber *et al.* 1997; Sá & Gutiérrez-Marco 2006; Sá *et al.* 2007). Compared to specimens collected elsewhere in the Czech Republic, France and Spain, the Portuguese material of *Mitrocystella* stands out for its particularly large size. The same phenomenon, also observed in trilobites and most other associated invertebrates, was

first interpreted as possible evidence of polar gigantism (see e.g. Gutiérrez-Marco *et al.* 2009). However, it more likely results from a tectonic homothetic expansion (Sá *et al.* 2021). The shales of the Valongo Formation were deposited in relatively quiet, distal settings, with highly fluctuating oxygenation levels (Gutiérrez-Marco *et al.* 2009, Sá *et al.* 2021).

In any case, the records of *Mitrocystella* from the late Darriwilian of Spain and Portugal correspond to somewhat shallower environments than those of the Traveusot Formation and the Prague Basin, where *Mitrocystella* co-occurs with *Lagynocystis pyramidalis* – a widespread mitrate unknown from the Central Iberian Zone, but reported from deeper-water settings in the Ossa-Morena Zone of SW Spain (Lefebvre & Gutiérrez-Marco 2007). A study of the sandy tempestites from the late Darriwilian of the Central Iberian Zone reveals the existence of a broad, shallow marine platform with a slight north- to northeastward dip (gradient < 1°), such that the greatest relative depths were reached in the Valongo and Mounts of Toledo areas, which lay below storm wave base (Brenchley *et al.* 1986).

Prague Basin (Bohemia, Czech Republic). – Reexamination of all specimens assigned to *Mitrocystella* in Czech public collections has shown that most of them come from the Šárka Formation and belong to *Promitrocystites barrandei* (see above). Only 23 specimens of *Mitrocystella incipiens incipiens* could be identified in the collections of the Dr. Bohuslav Horák Museum, Rokycany (BHMR), the Czech Geological Survey, Prague (CGS), and the Národní Muzeum, Prague (NMP). This material includes all specimens from Svatá Dobrotivá (Sancta Benigna) originally described by Barrande (1887), and thus, specimen NMP L 9292 (Barrande 1887, pl. 5, I.3–4) designated as the lectotype of *M. incipiens* by Chauvel (1941, p. 174). The observed material of *Mitrocystella* deposited in Czech public collections was collected from dark shales of the Dobrotivá Formation (*H. teretiusculus* Zone; Fig. 2A, B). Most specimens are strongly flattened and poorly preserved, so that only ten were selected for morphometric analysis (see supplementary data). Rare additional material of Czech *Mitrocystella* is also present in private collections, and includes specimens preserved in both shales and silico-aluminous concretions from the Dobrotivá Formation (O. Zicha, pers. comm., April 2022). This material was not included in the study.

In the Prague Basin, the black shales of the Dobrotivá Formation have yielded a relatively diverse echinoderm fauna comprising crinoids, diploporites, ophiuroids, rhombiferans, and stylophorans (see e.g. Barrande 1887, Prokop & Petr 1999, Lefebvre *et al.* 2022). Although *Mitrocystella* is a rare member of the echinoderm assemblage, the presence of abundant remains of the mitrate

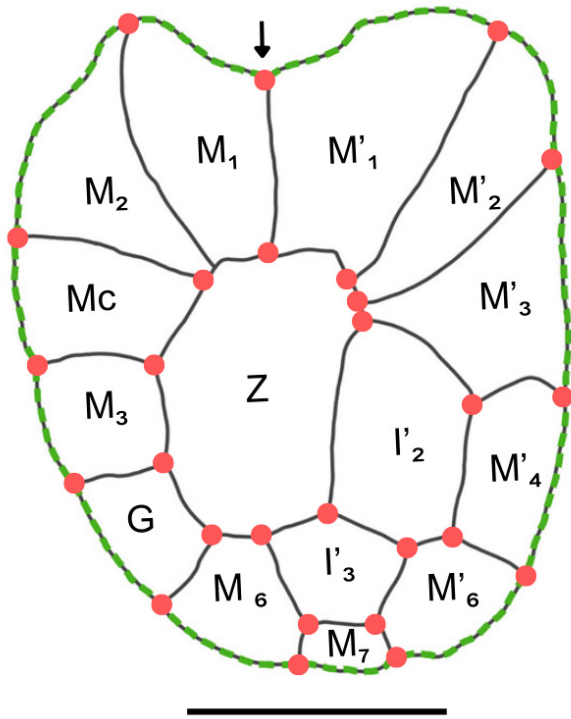


Figure 4. Placement of 28 landmarks (red dots) identifying plate boundaries and 200 semi-landmarks (green dots) outlining a continuous curve along the thecal margin of *Mitrocystella*. The black arrow marks the starting point for semi-landmark placement. *Mitrocystella incipiens pustulosa* ssp. nov., MGM-85940. Scale bar = 1 cm.

Lagynocystis pyramidalis suggests the existence of deep and dysoxic environmental conditions on the seafloor (Henry *et al.* 1997, Lefebvre 2007, Lefebvre *et al.* 2010). This interpretation is supported by the coexistence of an atheloptic trilobite assemblage (*i.e.* composed of small-eyed and blind benthic taxa) with cyclopygids (large-eyed, nektonic trilobites), which is generally considered typical of deep offshore environments, well below the photic zone (Fortey & Owens 1987, Henry *et al.* 1997, Kraft *et al.* 2023). Other faunal elements include bivalves, brachiopods, cephalopods, chelicerates, conulariids, gastropods, graptolites, hyoliths, machaeridians, ostracods, palaeoscolecid, phyllocarids, and sponges (see *e.g.* Havlíček & Vaněk 1966, 1990; Havlíček 1982; Kraft *et al.* 2023). In the Early and Middle Ordovician, the Prague Basin was an actively subsiding and rifting area, with relatively intense volcanic activity in its western part (Kraft *et al.* 2023).

Palaeoenvironmental synthesis. – In the Armorican Massif (Brittany, France), *Mitrocystella incipiens miloni* from the Traveusot Formation occurs in silico-aluminous concretions associated with a diverse benthic fauna, indicating quiet, distal, well-oxygenated settings below storm wave base. In the Iberian Massif (Spain and Por-

tugal), late Darriwilian specimens from the Guindo and Valongo formations are found in siltstones and shales with abundant, well-preserved benthic assemblages, reflecting relatively distal but shallower, well-oxygenated conditions, episodically affected by storm-induced deposits. Portuguese material from the Valongo Formation also records fluctuating oxygen levels. In the Prague Basin (Bohemia, Czech Republic), *M. incipiens incipiens* occurs in the black shales of the Dobrotivá Formation, associated with deep-water, dysoxic faunas including *Lagynocystis pyramidalis*, atheloptic trilobites, and cyclopygids, consistent with deposition in offshore environments below the photic zone.

Methods

Casts and drawings. – As all specimens are preserved as imprints in the rock, latex casts were made to reveal their original, three-dimensional morphology. For drawing and photographic purposes, the latex peels were coated with ammonium chloride (NH₄Cl) to enhance morphological details (see Parsley *et al.* 2018). Drawings were made using a camera lucida apparatus mounted on a Zeiss SteREO Discovery V8 binocular stereomicroscope. Photographs of the specimens were taken using a Canon EOS 5Ds R camera equipped with a 100mm macro lens and then edited with Krita 5.2.9 software.

Geometric morphometrics. – Geometric morphometric analysis focused on the lower thecal surface, consisting of a fixed number of large thecal plates (12 marginals, one zygal, and two left infracentrals in *Mitrocystella incipiens*) with a well-defined and regular pattern (Figs 3C, 4). The plate pattern on the opposite (upper) thecal side is more irregular, with two large anterior skeletal elements (left and right adorals), and a broad supracentral area consisting of numerous unorganized platelets, and bearing the transversely elongated, posterior anal opening (Fig. 2C).

The 40 selected specimens were assigned to a regional group, based on their geographic origin: France (24 specimens), Czech Republic (10 specimens), and Iberia consisting of both Portugal (1 specimen) and Spain (5 specimens).

A landmark-based geometric morphometric analysis was performed to assess morphological variation among specimens. This approach captures shape differences using anatomical points (“landmarks”) and semi-landmarks along curves, describing the morphology of each fossil (Fig. 4) and comparable among specimens. Landmarks and semi-landmarks were collected on the drawings of the specimens using the TPSdig2 software (Rohlf 2010). Twenty-eight fixed points (landmarks) marking plate

boundaries in a consistent sequence across all specimens were defined. The description of the geometry was completed by a series of 200 semi-landmarks, describing the external outline of the theca, the curve starting at the upper junction between plates M_1 and M'_1 (Fig. 4).

A Generalized Procrustes Analysis (GPA) was applied to the (x, y) coordinates of the landmarks and semi-landmarks to normalize variation in size, position, and orientation between individuals (Rohlf & Slice 1990). During the superimposition, semi-landmarks were allowed sliding along their tangent vectors until their positions minimized the shape difference between specimens, the criterion being bending energy (Bookstein 1997).

The GPA resulted in aligned (x, y) coordinates (a.k.a. Procrustes coordinates) of the landmarks and semi-landmarks. A Principal Component Analysis (PCA) was performed on the aligned coordinates to visualise the pattern of shape variation. Shape differences between groups were tested on the full set of aligned coordinates using permutation-based Procrustes ANOVA with 9999 permutations and associated pairwise tests.

All analyses were conducted in R (R Core Team 2018). The GPA, permutation-based Procrustes ANOVA, and the PCAs were performed using the R package geomorph (Adams & Otárola-Castillo 2013).

Results

Geometric morphometric analysis

A PCA on the aligned coordinates was performed to analyze shape and allowed to visualize the pattern of shape variation without *a priori* geographic presupposition (Fig. 5A). French and Czech specimens occupy different ranges on this morphospace, with French ones having globally negative scores along PC1, while Czech specimens tend to display positive scores. A unique Czech specimen plots within the negative PC1 range. This position may be related to the morphology of its M'_3 plate, which is larger and more elongated than in other Czech specimens, and resembles the M'_3 morphology observed in Armorican material.

Iberian specimens are scattered over the entire morphospace and overlap both the Armorican and Czech groups. The Czech group is characterized by a regularly convex posterior thecal margin, a shallow anterior cavity for the aulacophore insertion, and more asymmetrical thecal outlines, with a short, straight left side, and a longer, slightly curved right side (Fig. 5B). The French group has more quadrangular and symmetrical thecal outlines, with a straight posterior margin, subequal and nearly parallel lateral sides, and a deeper anterior cavity for the insertion of the aulacophore (Fig. 5B).

This visual impression is confirmed by pairwise tests of shape differences between geographic groups. Armorican and Czech groups appeared to be significantly different in shape (Procrustes ANOVA: $p = 0.0004$). In contrast, the Iberian group was not different from either the Armorican group (Procrustes ANOVA: $p = 0.2830$) nor from the Czech group (Procrustes ANOVA: $p = 0.4162$).

New observations on thecal morphology

Abnormal plating – Among more than 800 examined specimens of *Mitrocystella incipiens*, only one individual from Spain (MGM-85950) shows an abnormal plate pattern, with 11 marginals instead of the usual 12 due to the absence of M_7 (Fig. 6). This results in a shorter, concave posterior margin and an enlarged M_6 plate (see Discussion). Because of its atypical plating, this specimen was not incorporated in the morphometric analysis.

Pustulose ornamentation – All examined Iberian individuals share a distinctive feature consisting of a delicate pustulose ornamentation on the lower thecal surface, restricted to the antero-lateral marginals ($M'_2 - M'_3$ and $M_2 - M_6$) (Fig. 2D–F). This ornamentation is absent in Armorican and Czech material, which consistently show a smooth lower thecal surface (Fig. 2A, B, G–I). The consistent presence of pustules in all Spanish specimens supports their assignment to a distinct subspecies, *M. incipiens pustulosa* ssp. nov. (see Discussion).

Discussion

The geometric morphometric analysis validated the significant difference between French and Czech regional groups based on their thecal shape. In contrast, the thecal shape of Iberian specimens showed no significant geometrical difference from the French or Czech groups, due to substantial within-group variation overlapping both.

Identification of two subspecies: *M. incipiens incipiens* and *M. incipiens miloni*

The statistically significant shape difference between the French and Czech specimens confirms Chauvel's (1937) interpretation of these two populations being distinct subspecies: *Mitrocystella incipiens miloni* (Armorican Massif, Brittany, France) and *M. incipiens incipiens* (Prague Basin, Bohemia, Czech Republic).

Two main non-mutually exclusive hypotheses can be considered to explain the divergence between these two subspecies. The first one would correspond to a vicariant

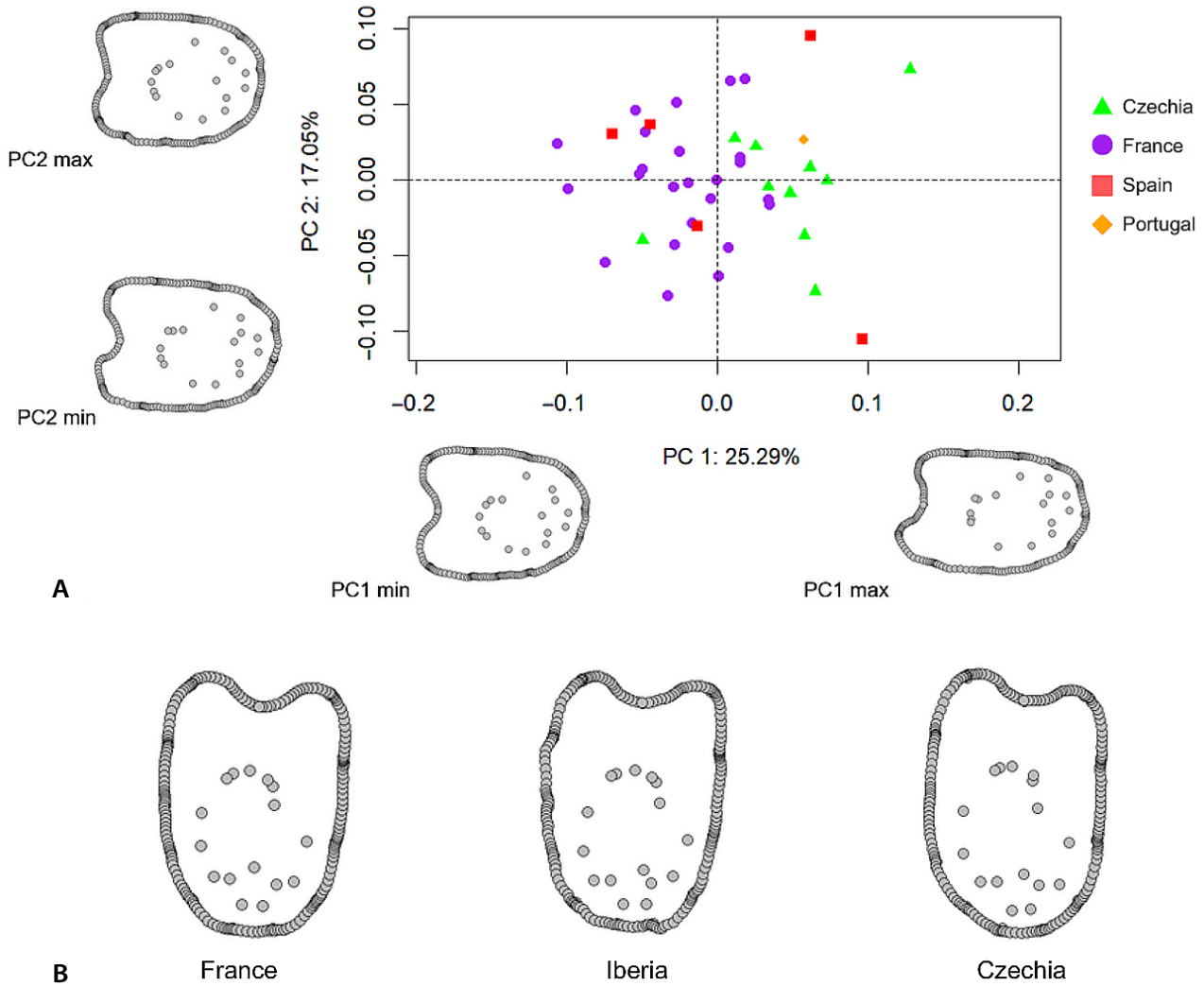


Figure 5. A – morphospace describing the variation in thecal shape, defined by the first two axes of a Principal Component Analysis (PCA) on the aligned coordinates of the landmarks and semi-landmarks. The different geographic groups are represented with different symbols. • B – mean shapes of *Mitrocystella* populations from France, Iberia (Spain and Portugal), and Czech Republic. Shapes are represented by landmark and semi-landmarks configurations.

event: the morphological differences would result from evolutionary divergence due to a prolonged breakdown of gene flow due to geographic isolation, while the two incipient subspecies would continue to share similar ecological preferences.

Alternatively, morphological variation may be partly shaped by local ecological conditions rather than by vicariance alone. In this scenario, morphological differences would be adaptive responses to environmental differences. Cases of phenotypic variation influenced by environmental conditions (*e.g.* depth, oxygenation, pH, predation pressure, temperature) have been documented in many extant echinoderms (see *e.g.* Rogacheva *et al.* 2013). As both the Armorican Massif and the Prague Basin were located at relatively similar high palaeolatitudes in the Middle Ordovician (Fig. 1), it

seems unlikely that seawater temperature was significantly different in these two regions. In contrast, depth was strongly different, with populations of *M. incipiens incipiens* inhabiting deeper, less oxygenated, and more restricted environments. Another obvious difference concerns the presence of widespread tholeiitic and alkaline volcanism in the Prague Basin (Kraft *et al.* 2023), while the populations of *M. incipiens miloni* were living on a passive shelf, without volcanic activity (Lefebvre *et al.* 2023). Volcanic processes can alter marine geochemistry, including localized acidification due to elevated dissolved gas concentrations (*e.g.* H₂S, CH₄, CO, CO₂). Such environmental stressors have been shown induce morphological changes in modern echinoderms under decreasing pH conditions (Bednařek *et al.* 2021). Furthermore, echinoderm morphology can be

influenced by a complex interplay of factors. Apart from bathymetric differentiation, oxygenation and pH, other variables may have contributed to subspecies divergence, including nutrient availability, hydrodynamic energy, subtle variations in predator abundance, and differences in salinity.

Specimens occur in substrates of varying consistency but are preserved in calm, shallow to moderately shallow environments dominated by fine-grained sediments (shales and black shales). Such conditions likely limited mechanical abrasion, suggesting that the overall thecal outline remained largely unaffected by taphonomic processes. While substrate characteristics do not appear to strongly shape the overall thecal architecture of the living animal, they may influence certain functional traits, particularly those related to locomotion, stabilization, and interaction with the sediment, which are mainly guaranteed by the length and robustness of the aulacophore (Lefebvre 2007). Such factors could influence the width and orientation of the aulacophore, which does not seem to vary significantly between the specimens studied. Moreover, previous studies indicate that stylophoran morphology is primarily structured by palaeobiogeographic and bathymetric factors, with substrate effects playing a more localized, functionally relevant role (Lefebvre 2007). On the other hand, especially in the Portuguese material, advanced fossil-diagenetic deformation mainly affected specimen size rather than overall thecal shape, suggesting that size variation is largely taphonomic and not indicative of biological differentiation between populations. Finally, the two mechanisms mentioned above (vicariance and environmentally-driven variation) are not mutually exclusive and may have acted in concert. Moreover, the Iberian specimens, exhibiting intermediate morphology, do not provide unequivocal support for either hypothesis. This population inhabited the shallowest environment among the three localities and is geographically located to the south of both the Prague Basin and Armorican Massif. This pattern suggests that neither vicariance nor the environmental factors previously discussed alone can account for the observed intermediate morphology, and that one or both processes, potentially act in conjunction with additional unknown environmental variables.

Iberian specimens as a new subspecies: *M. incipiens pustulosa* ssp. nov.

The overall morphology of the Iberian *Mitrocystella* is very variable and overlaps the French and Czech morphotypes. The Iberian dataset includes only six specimens, compared to 24 for the Armorican Massif and ten for the Prague Basin. This limited sample size might

not adequately reflect the morphological variance present within the Iberian population. Alternatively, the Iberian specimens could represent a morphological intermediate between the other two subspecies and anyway illustrating complex intraspecific variation.

However, detailed observation of the lower thecal surface of Spanish specimens shows the presence of a delicate pustulose ornamentation on their antero-lateral marginals: M'_2 and M'_3 (on the left), and M_2 and M_c (on the right) (Fig. 2D–F). In contrast, the lower thecal surface of Armorican and Czech specimens is always completely smooth (Fig. 2A–B, G–I) (see e.g. Barrande 1887; Chauvel 1941, 1981; Jefferies 1968). This ornamentation, clearly visible in all examined specimens of *Mitrocystella incipiens* from the Central Iberian Zone suggests that Spanish specimens should be placed in a third, distinct subspecies: *Mitrocystella incipiens pustulosa* ssp. nov. (see systematic section, below).

It should be noted, however, that the broad morphological variance of the Iberian specimens – particularly the Spanish ones – does not itself constitute a diagnostic feature. Their morphological variation prevents reliable identification based solely on general shape.

A teratologic case and its possible phylogenetic implications

Stylophorans are characterized by highly stable plate patterns on their lower thecal surface (Lefebvre 2001, Lefebvre *et al.* 2022). This feature allows the identification of class-wide plate homologies, and is a keystone of their systematics. Rare cases of abnormal thecal platings (*i.e.* an unusual number of plates, resulting from the addition or the loss of one skeletal element) have been documented in stylophorans (see e.g. Chauvel 1941, Ubaghs 1970, Ruta 1998, Lefebvre 2003, Ware & Lefebvre 2007). Such teratological cases are particularly important to better understand the underlying mechanisms of ontogenetic development leading to the acquisition of standardized and “normal” plate patterns (Lefebvre 2003, Ware & Lefebvre 2007). For example, the description of a teratological specimen of *Mitrocystites mitra* from the Šarká Formation demonstrated that the increasing number of marginals in basal mitrocystitids results from repeated insertions of left infracentral elements between the posterior marginals (Lefebvre 2003).

The thecal morphology of *M. incipiens incipiens* shares several plesiomorphic features with *Promitrocystites barrandei* (rounded posterior margin, asymmetric outlines with the left side shorter than the right), which are lost in *M. incipiens miloni* and more derived taxa of the paranacystid clade (e.g. *Eumitrocystella savilli*; see Lefebvre *et al.* 2025). In some respects, the morphology

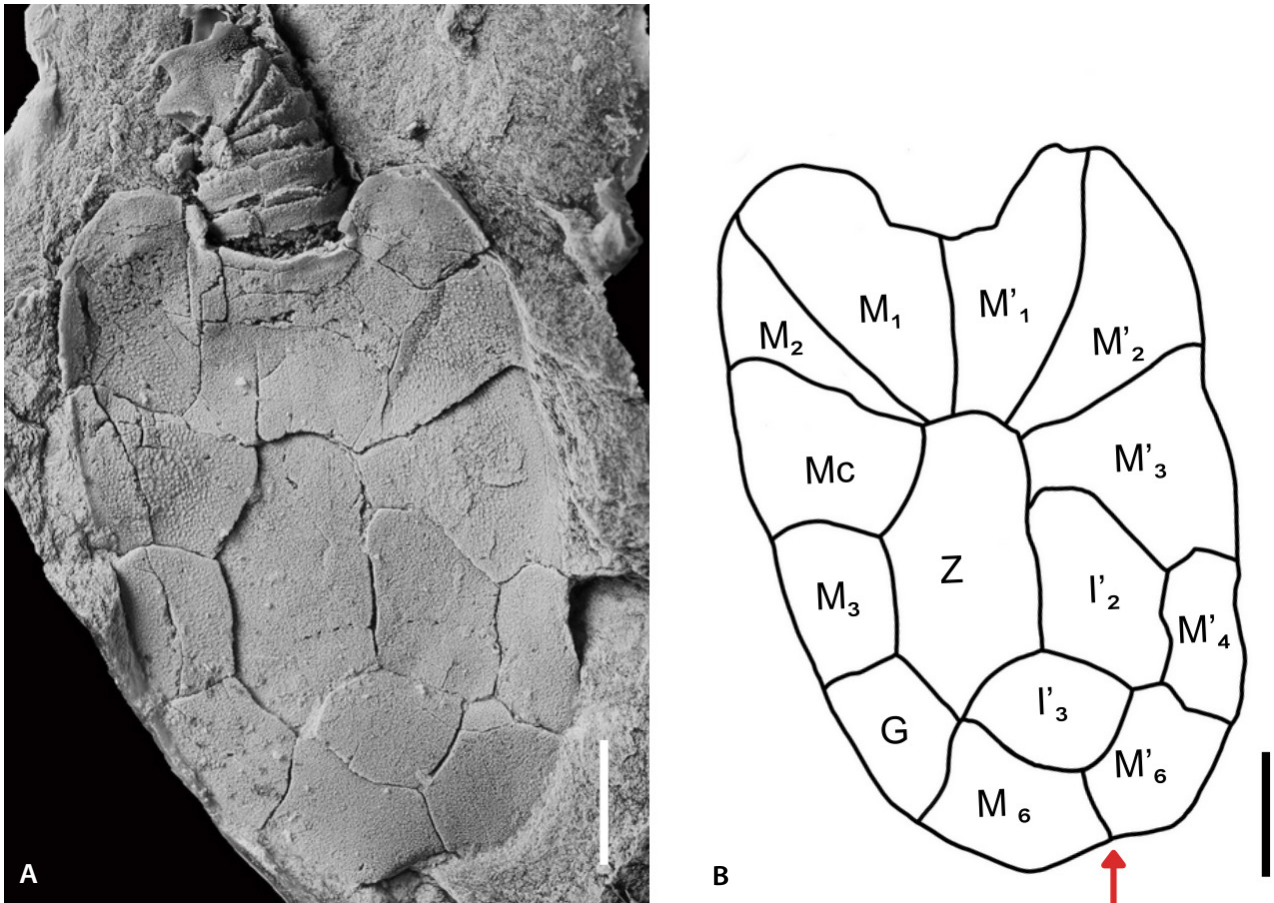


Figure 6. *Mitrocystella incipiens pustulosa* ssp. nov.: abnormal (teratological) plating of the lower thecal surface (M_7 missing); MGM-85950, Guindo Shale, late Darriwilian (early Dobrotivian), Middle Ordovician; Calzada de Calatrava, Ciudad Real, Spain. A – photograph of the latex cast. B – interpretative, camera-lucida drawing of the plate pattern. Arrow indicates expected position of missing M_7 plate. Scale bars = 0.5 cm.

of the Czech population of *Mitrocystella* thus appears more primitive than that of Armorican specimens. This morphological framework provides useful context for interpreting rare deviations from the standard plating pattern observed within the species.

More than 800 specimens of *Mitrocystella incipiens* were examined for the present study, and only one case of abnormal plating was observed in a specimen from Spain (Fig. 6). The lower thecal surface of MGM-85950 has 11 marginals, instead of 12 in all other specimens. Detailed examination of its plate pattern indicates that this unusual number of marginals results from the loss of M_7 , at the posterior end of the theca. As a consequence, the posterior margin is shorter, unusually concave, and slightly shifted to the left. The morphology of the other thecal plates remains almost unchanged, except for M_6 , which is significantly larger. Whereas M_6 forms the right posterior corner of the theca in “normal” specimens of *M. incipiens pustulosa*, it constitutes a slightly prominent median posterior expansion in the abnormal individual (Fig. 6).

The abnormal plating of MGM-85950 (Fig. 7B) is remarkably intermediate between that of regular individuals of *Mitrocystella incipiens* (Fig. 7A) and that of the closely related taxon *Eumitrocystella savilli* (Fig. 7C) from the Ouine-Inirne and Izegguirène formations (late Darriwilian–early Sandbian) of the Anti-Atlas, Morocco (Beisswenger 1994, Lefebvre 2000a, Lefebvre et al. 2025). *Eumitrocystella* is consistently considered to have evolved from a *Mitrocystella*-like ancestor (see e.g. Beisswenger 1994; Parsley 1997; Ruta & Jell 1999; Lefebvre 2000a, 2005; Ruta 2003; Lefebvre et al. 2025). *Eumitrocystella* differs from *Mitrocystella* mainly by the loss of two posterior skeletal elements: M_7 and the left infracentral plate I'_3 (Beisswenger 1994, Ruta & Jell 1999, Lefebvre et al. 2025). The morphology of the abnormally plated specimen MGM-85950 therefore suggests that this transition may have occurred in two steps, with the loss of M_7 preceding that of I'_3 . This only known teratological case in *Mitrocystella* is documented in the Iberian population, which also presents the greatest morphological variation.

Systematic palaeontology

Phylum Echinodermata Klein, 1778
 Subphylum Blastozoa Sprinkle, 1973
 Class Stylophora Gill & Caster, 1960
 Order Mitrata Jaekel, 1918
 Suborder Mitrocystitida Caster, 1952

Remarks. – The suborder Mitrocystitida comprises two well-defined clades (the families Anomalocystitidae and Paranacystidae), both deriving from a paraphyletic assemblage of more basal taxa (family Mitrocystitidae) (Lefebvre & Ausich 2021). New fossil evidence from the Lower Ordovician Fezouata Shale of Morocco suggests that anomalocystitids originate from an *Aspidocarpus*-like mitrocystitid, while *Eumitrocystella* has recently been reinterpreted as the earliest and basal-most paranacystid (Lefebvre & Ausich 2021, Lefebvre *et al.* 2025). This implies that *Mitrocystites*, *Promitrocystites*, and *Mitrocystella* belong to the paranacystid stem-lineage.

Family Mitrocystitidae Ubaghs, 1968

Genus *Mitrocystella* Jaekel, 1901

Type species. – *Anomalocystites incipiens* Barrande, 1887.

Mitrocystella incipiens (Barrande, 1887)

Mitrocystella incipiens pustulosa ssp. nov.
 Figures 2C–F, 6A–B, 7B

- ? 1978 *Mitrocystella* cf. *incipiens miloni*. – Chauvel & Meléndez, p. 83, pl. 2, fig. 70.
- ? 1984b *Mitrocystella incipiens miloni*. – Gutiérrez-Marco *et al.*, p. 426, tab. 1.
- v1987 *Mitrocystella incipiens miloni*. – Gutiérrez-Marco & Meléndez, p. 43, figs 1–6.
- v2000 *Mitrocystella incipiens miloni*. – Couto & Gutiérrez-Marco, p. 191.
- v2015 “*Mitrocystella*” *incipiens miloni*. – Jacinto *et al.*, p. 164, tab. 1.

LSID. – Zoobank.org:act:A4E3B533-D382-4A84-89BF-462E2C4603A1

Holotype. – MGM-85930 (Fig. 2D), fully articulated lower thecal surface; aulacophore and opposite (upper) side not preserved.

Type horizon and locality. – Guindo Shale (20 m above its base). *Hustedograptus teretiusculus* Biozone, upper lower Dobrotivian, upper Darriwilian (Middle Ordovician). The type locality lies at the base of the Fresneda reservoir dam, 12 km SE from Calzada de Calatrava, Ciudad Real, Spain (Latitude 38° 37' 02" N, Longitude 3° 40' 52" W).

Other material. – Specimens MGM-85940 (Fig. 2E), MGM-85950 (Figs 6A, B; 7B), and MGM-85970 (Fig. 2C), all from the same locality and horizon as the holotype. Please note that the lower thecal surface of MGM-85950 is abnormally plated (teratological case; see above).

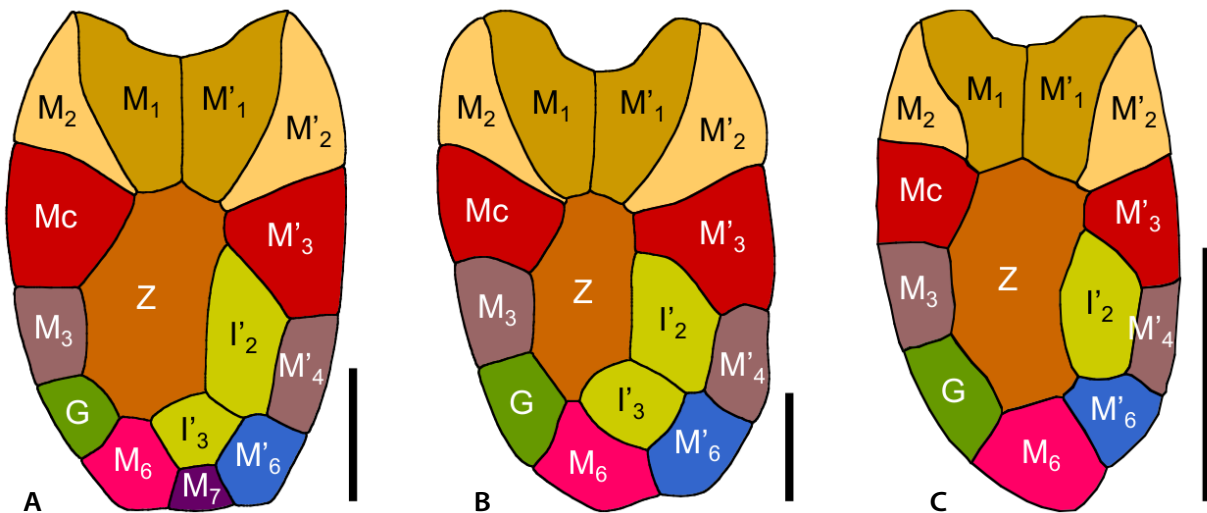


Figure 7. Plate homologies on the lower thecal surface of selected mitrocystitidans, based on Lefebvre & Ausich (2021) and Lefebvre *et al.* (2025). • A – *Mitrocystella incipiens miloni* Chauvel, 1937, Traveusot Formation (late Darriwilian), Armorican Massif (France); redrawn and modified after Jefferies (1968). • B – MGM-85950: teratological specimen of *Mitrocystella incipiens pustulosa* ssp. nov.; Guindo Shale (late Darriwilian), Iberian Massif (Spain). • C – *Eumitrocystella savilli* Beisswenger, 1994, Ouine-Inirne and Izeguirène formations (late Darriwilian–early Sandbian), Anti-Atlas (Morocco); redrawn and modified after Beisswenger (1994). All scale bars = 5 mm.

Etymology. – From the Latin *pustulosa*, meaning “covered with pustules”, referring to the presence of small, rounded calcareous protrusions – pustules – on the lower thecal surface.

Diagnosis. – A subspecies of *Mitrocystella* with a delicate pustulose ornamentation extending on the lower surface of antero-lateral marginals.

Remarks. – Three distinct regional subspecies can be identified in the late Darriwilian mitrocystitid *Mitrocystella incipiens* (see above). The Spanish morphotype, *M. incipiens pustulosa*, is characterised by the presence of a pustulose ornamentation on its lower thecal surface. The two other subspecies differ from *M. incipiens pustulosa* by their completely smooth lower thecal surface. The Czech subspecies *M. incipiens incipiens* is characterised by a shallow anterior cavity for the aulacophore insertion, a rounded posterior margin, and asymmetrical thecal outlines. In the Armorican morphotype *M. incipiens miloni*, the aulacophore insertion is deeper, the posterior margin is almost straight, and thecal outlines are more symmetrical and quadrangular.

The unique Portuguese specimen cannot be assigned to *M. incipiens pustulosa*, as no pustulose ornamentation is visible on the lower thecal surface. However, the absence of ornamentation may reflect taphonomic bias since the upper half of Valongo Formation is affected by tectonic homothetic expansion that likely obliterated fine surface structures. In the absence of additional material, the taxonomic position of the Portuguese specimen remains uncertain.

Conclusion

Geometric morphometric analysis of 40 specimens of *Mitrocystella incipiens* from the Armorican Massif, the Iberian Peninsula and the Prague Basin demonstrates the existence of significant differences between the thecal morphologies of Armorican and Czech specimens, thus supporting their assignment to two distinct subspecies, *M. incipiens miloni* and *M. incipiens incipiens*, respectively, as originally suggested by Chauvel (1937, 1941, 1981).

Relatively minor regional morphological variation in these populations indicates expected ecophenotypic variation, resultant from variable palaeoenvironmental conditions. Pinpointing the exact causes are unknown, but wide distribution alone suggests adaptability among mitrate taxa to a range of palaeoenvironmental conditions. The thecal morphology of Iberian specimens of *Mitrocystella* does not differ significantly from that of the other two subspecies, suggesting that Iberian populations may be morphologically intermediate between *M. incipiens*

and *M. incipiens miloni*, illustrating a case of intraspecific variation. However, the presence of a distinctive pustulose ornamentation on the lower thecal of Spanish specimens supports their assignment to a new subspecies, *M. incipiens pustulosa*.

Finally, the first reported case of abnormal plating in *Mitrocystella incipiens* is described in a Spanish specimen. This provides unexpected insights into the evolutionary transition between *Mitrocystella* and *Eumitrocystella*. It also highlights the possible palaeobiogeographic significance of Iberian faunas, morphologically intermediate between Armorican and Czech populations, but also suggesting strong faunal links with those from the Moroccan Anti-Atlas.

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References

- ADAMS, C.D. & OTAROLA-CASTILLO, E. 2013. Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* 4, 393–399. DOI 10.1111/2041-210X.12035
- BABIN, C. 1966. *Mollusques bivalves et céphalopodes du Paléozoïque armoricain. Etude systématique. Essai sur la phylogénie des Bivalves. Esquisse paléoécologique*, 470 pp. Imprimerie commerciale et administrative, Brest.
- BABIN, C. & GUTIÉRREZ-MARCO, J.C. 1991. Middle Ordovician bivalves from Spain and their phyletic and palaeogeographic significance. *Palaeontology* 34, 109–147.

- BABIN, C. & GUTIÉRREZ-MARCO, J.C. 1992. Intérêt paléobiogéographique de la présence du genre *Trocholites* (Cephalopoda, Nautiloidea) dans le Dobrotivá (Llandeilo) inférieur d'Espagne. *Neues Jahrbuch für Geologie und Paläontologie Monashefte* 1992, 519–541.
DOI 10.1127/njgpm/1992/1992/519
- BARRANDE, J. 1887. *Système Silurien du centre de la Bohême. 1^{ère} Partie. Recherches Paléontologiques. Volume 7. Classe des Echinodermes. Ordre des Cystidées*, 233 pp. Gerhard, Leipzig & Řivnáč, Prague.
- BEDNARŠEK, N., CALOSI, P., FEELY, R.A., AMBROSE, R., BYRNE, M., CHAN, K.Y.K., DUPONT, S., PADILLA GAMIÑO, J.L., SPICER, J.I., KESSOURI, F., ROETHLER, M., SUTULA, M. & WEISBERG, S.B. 2021. Synthesis of thresholds of ocean acidification impacts on echinoderms. *Frontiers in Marine Science* 8, 602601.
DOI 10.3389/fmars.2021.602601
- BEISSWENGER, M. 1994. A calcichordate interpretation of the new mitrate *Eumitrocystella savilli* from the Ordovician of Morocco. *Paläontologische Zeitschrift* 68, 443–462.
DOI 10.1007/BF02991355
- BOISSET, T., LEFEBVRE, B., MOOI, R., KROH, A., WINKLER, V., ADRIEN, J. & MARTIN, M.J. 2024. Insights into stylophoran anatomy and taphonomy based on an exceptionally preserved mitrate from the Lorraine Group (Upper Ordovician) of New York, USA. *Cahiers de Biologie Marine* 65, 511–516.
DOI 10.21411/CBM.A.33CFD1AB
- BOOKSTEIN, F.L. 1997. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. *Medical Image Analysis* 1, 225–243.
DOI 10.1016/S1361-8415(97)85012-8
- BRENCHLEY, P.J., ROMANO, M. & GUTIÉRREZ-MARCO, J.C. 1986. Proximal and distal Hummocky cross-stratified facies on a wide Ordovician Shelf in Iberia, 241–255. In KNIGHT, R.J. & MCLEAN, J.R. (eds) *Shelf Sands and Sandstones. Canadian Society of Petroleum Geologists, Calgary, Memoir II*.
- CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoïd Echinodermata. *Bulletins of American Paleontology* 34, 1–47.
- CHAUVEL, J. 1937. Les hétérostélées armoricaines. *Compte-Rendu Sommaire des Séances de la Société Géologique et Minéralogique de Bretagne* 3(2), 1–3.
- CHAUVEL, J. 1941. Recherches sur les cystoïdes et les carpoïdes armoricains. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 5, 1–286.
- CHAUVEL, J. 1981. Étude critique de quelques échinodermes stylophores du Massif armoricain. *Bulletin de la Société Géologique et Minéralogique de Bretagne* 13, 67–101.
- CHAUVEL, J. & MELÉNDEZ, B. 1978. Les échinodermes (cystoïdes, astérozoaires, homalozoaires) de l'Ordovicien moyen des Monts de Tolède (Espagne). *Estudios Geológicos* 34, 75–87.
- COUTO, H. & GUTIÉRREZ-MARCO, J.C. 2000. Alguns fósseis raros ou pouco conhecidos da Formação de Valongo (Ordovício Médio, Norte de Portugal), 191–192. In DIEZ, J.B. & BALBINO, A.C. (eds) *I Congresso Ibérico de Paleontología. XVI Jornadas de la Sociedad Española de Paleontología*. Universidade de Évora, Évora.
- DAVID, B., LEFEBVRE, B., MOOI, R. & PARSLEY, R.L. 2000. Are homalozoans echinoderms? An answer from the extraxial-axial theory. *Paleobiology* 26, 529–555.
DOI 10.1666/0094-8373(2000)026<0529:AHEAAF>2.0.CO;2
- FORTEY, R.A. & OWENS, R.M. 1987. The Arenig Series in South Wales. *Bulletin of the British Museum (Natural History), Geology* 41, 69–307.
- GENDRY, D., COURVILLE, P., SAUCÈDE, T., LAFFONT, R. & PARIS, F. 2013. Contribution of morphometrics to the systematics of the Ordovician genus *Neseuretus* (Calymenidae, Trilobita) from the Armorican Massif, France. *Journal of Paleontology* 87, 456–471. DOI 10.1666/12-046.1
- GILL, E.D. & CASTER, K.E. 1960. Carpoïd echinoderms from the Silurian and Devonian of Australia. *Bulletins of American Paleontology* 41, 5–71.
- GUTIÉRREZ-MARCO, J.C. & MELÉNDEZ, B. 1987. Nuevos hallazgos de Estilóforos (Homalozoos) en los materiales ordovícicos de la zona Centroibérica. *Coloquios de Paleontología* 41, 41–50.
- GUTIÉRREZ-MARCO, J.C., RÁBANO, I., PRIETO, M. & MARTÍN, J. 1984a. Estudio bioestratigráfico del Llanvirn y Llandeilo (Dobrotiviense) en la parte meridional de la zona Centroibérica (España). *Cuadernos de Geología Ibérica* 9, 287–319.
- GUTIÉRREZ-MARCO, J.C., CHAUVEL, J., MELÉNDEZ, B. & SMITH, A.B. 1984b. Los equinodermos (Cystoidea, Homalozoa, Stellerioidea, Crinoidea) del Paleozoico inferior de los Montes de Toledo y Sierra Morena (España). *Estudios Geológicos* 40, 421–453. DOI 10.3989/geol.84405-6680
- GUTIÉRREZ-MARCO, J.C., SÁ, A.A., GARCÍA-BELLIDO, D.C., RÁBANO, I. & VALÉRIO, M. 2009. Giant trilobites and trilobite clusters from the Ordovician of Portugal. *Geology* 37(5), 443–446. DOI 10.1130/G25513A.1
- HAMMANN, W. & SCHMINCKE, S. 1986. Depositional environment and systematics of a new ophiuroid, *Taeniaster ibericus* n. sp. from the Middle Ordovician of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 173(1), 47–74. DOI 10.1127/njgpa/173/1986/47
- HAVLÍČEK, V. 1982. Ordovician of Bohemia: development of the Prague Basin and its benthic communities. *Sborník geologických věd, Geologie* 37, 103–136.
- HAVLÍČEK, V. & VANĚK, J. 1966. The biostratigraphy of the Ordovician of Bohemia. *Sborník geologických věd, Paleontologie* 8, 7–69.
- HAVLÍČEK, V. & VANĚK, J. 1990. Ordovician invertebrate communities in black shale lithofacies (Prague Basin, Czechoslovakia). *Věstník Ústředního ústavu geologického* 65, 223–236.
- HENRY, J.-L. 1980. Trilobites ordoviciens du Massif armoricain. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 22, 1–250.
- HENRY, J.-L. 1989. Paléoenvironnements et dynamique de faunes de trilobites dans l'Ordovicien (Llanvirn supérieur – Caradoc basal) du Massif armoricain (France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 73, 139–153.
DOI 10.1016/0031-0182(89)90049-7
- HENRY, J.-L., LEFEBVRE, B. & CHAUVIN, D. 1997. Stratification thermique probable des eaux marines sur la marge gondwanienne (Massif Armoricain) pendant l'Ordovicien

- (Llanvirn): implications paléogéographiques. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 205, 373–392. DOI 10.1127/njgpa/205/1997/373
- HUNTER, A.W., LEFEBVRE, B., RÉGNAULT, S., ROUSSEL, P. & CLAVERIE, R. 2007. A mixed ophiuroid-stylophoran assemblage (Echinodermata) from the Middle Ordovician (Llandeilian) of western Brittany, France, 71–86. In ÁLVARO, J.J., ARETZ, M., BOULVAIN, F., MUNNECKE, A., VACHARD, D. & VENNIN, E. (eds) *Palaeozoic Reefs and Bioaccumulations: Climatic and Evolutionary Controls*. Geological Society London, Special Publication 275. DOI 10.1144/GSL.SP.2007.275.01.05
- JAEKEL, O. 1901. Ueber Carpoideen, eine neue Klasse von Pelmatozoen. *Zeitschrift der Deutschen geologischen Gesellschaft* 52, 661–677. DOI /10.1127/zdgg/52/1900/661
- JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. *Paläontologische Zeitschrift* 3, 1–124. DOI 10.1007/BF03190413
- JACINTO, A.F.M., GUTIÉRREZ-MARCO, J.C. & ZAMORA, S. 2015. Situación actual de las investigaciones sobre equinodermos del Ordovícico portugués, 163–167. In DOMINGO, L., DOMINGO, S., FESHARAKI, O., GARCÍA YELO, B., GÓMEZ CANO, A.R., HERNÁNDEZ-BALLARIN, V., HONTECILLAS, D., CANTALAPIEDRA, J.L., LÓPEZ GUERRERO, P., OLIVER, A., PELEGRÍN, J., PÉREZ DE LOS RÍOS, M., RÍOS, M., SANISIDRO, O. & VALENCIANO, A. (eds) *Current Trends in Paleontology and Evolution. XIII EJIP. Conference Proceedings*. Universidad Complutense de Madrid, Madrid.
- JEFFERIES, R.P.S. 1968. The subphylum Calcichordata (Jefferies 1967) primitive fossil chordates with echinoderm affinities. *Bulletin of the British Museum (Natural History) (Geology)* 16, 243–339. DOI 10.5962/p.313838
- JEFFERIES, R.P.S. 1975. Fossil evidence concerning the origin of the chordates. *Symposia of the Zoological Society of London* 36, 253–318.
- JEFFERIES, R.P.S. 1981. In defence of the calcichordates. *Zoological Journal of the Linnean Society* 73, 351–396. DOI 10.1111/j.1096-3642.1981.tb01601.x
- JEFFERIES, R.P.S. 1984. Locomotion, shape, ornament, and external ontogeny in some mitrate calcichordates. *Journal of Vertebrate Paleontology* 4, 292–319. DOI 10.1080/02724634.1984.10012011
- JEFFERIES, R.P.S. 1986. *The Ancestry of the Vertebrates*. 376 pp. British Museum (Natural History), London.
- JEFFERIES, R.P.S. & LEWIS, D.N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. *Philosophical Transactions of the Royal Society, B* 282, 205–323. DOI 10.1098/rstb.1978.0013
- KLEIN, J.T. 1778. *Naturalis Dispositio Echinodermatum. Accesserunt Lucubratiuncula de Aculeis Echinorum Marinarum et Specilegium de Belemnitis. Edita et Descriptionibus Novisque Inventis et Synonymis Auctorum Auca a Nathanaele Godofredo Leske*. 278 pp. Officina Gleditschiana, Lipsiae (Leipzig).
- KRAFT, P., LINNEMANN, U., MERGL, M., BRUTHANSOVÁ, J., LAIBL, L. & GEYER, G. 2023. Ordovician of the Bohemian Massif, 433–464. In HARPER, D.A.T., LEFEBVRE, B., PERCIVAL, I.G. & SERVAIS, T. (eds) *A Global Synthesis of the Ordovician System Part 1*. Geological Society London, Special Publication 532. DOI 10.1144/SP532-2022-191
- LEFEBVRE, B. 2000a. A new mitrate (Echinodermata, Stylophora) from the Tremadoc of Shropshire (England) and the origin of the Mitrocystitida. *Journal of Paleontology* 74, 890–906. DOI 10.1666/0022-3360(2000)074<0890:ANMESF>2.0.CO;2
- LEFEBVRE, B. 2000b. Les échinodermes stylophores du Massif armoricain. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France* 22, 101–122.
- LEFEBVRE, B. 2001. A critical comment on ‘ankyroids’ (Echinodermata, Stylophora). *Geobios* 34, 597–627. DOI 10.1016/S0016-6995(01)80024-3
- LEFEBVRE, B. 2003. Stephen J. Gould, les mitrates et les monstres. *Comptes Rendus Palevol* 2, 509–522. DOI 10.1016/j.crpv.2003.09.011
- LEFEBVRE, B. 2005. Stylophoran supertrees revisited. *Acta Palaeontologica Polonica* 50, 477–486.
- LEFEBVRE, B. 2007. Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran echinoderms. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245, 156–199. DOI 10.1016/j.palaeo.2006.02.021
- LEFEBVRE, B. & AUSICH, W.I. 2021. New Siluro-Devonian anomalocystitids (Echinodermata, Stylophora) from Bolivia and Canada, and a reevaluation of skeletal homologies in mitrates. *Paleontological Journal* 55, 932–965. DOI 10.1134/S0031030121090070
- LEFEBVRE, B. & FATKA, O. 2003. Palaeogeographical and palaeoecological aspects of the Cambro-Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 73–97. DOI 10.1016/S0031-0182(03)00303-1
- LEFEBVRE, B. & GUTIÉRREZ-MARCO, J.C. 2007. Echinoderms from the Middle Ordovician of Ossa Morena (SW Iberian Peninsula): Palaeobiogeographic and palaeoenvironmental implications, 15. In ÁLVARO, J.J. & VILLAS, E. (eds) *IGCP Project 503. Regional Meeting and Field-trip Zaragoza 2007*. Publicaciones Universidad de Zaragoza.
- LEFEBVRE, B. & RÉGNAULT, S. 2009. Les stylophores, fossiles énigmatiques du Paléozoïque: échinodermes, crustacés ou vertébrés? *Penn ar Bed* 207, 35–41.
- LEFEBVRE, B., RÉGNAULT, S., LARDEUX, H., KUNDURA, J.P. & ROUSSEL, P. 2010. New Ordovician mitrates (Echinodermata, Stylophora) from the Ancenis Basin (South Armorican Domain, France): palaeogeographic and palaeoenvironmental implications, 37–44. In HARRIS, L.G., BÖTTGER, S.A., WALKER, C.W. & LESSER, M.P. (eds) *Echinoderms: Durham*. Balkema, Rotterdam. DOI 10.1201/9780203869543-c6
- LEFEBVRE, B., SUMRALL, C.D., SHROAT-LEWIS, REICH, M., WEBSTER, G.D., HUNTER, A.W., NARDIN, E., ROZHNOV, S.V., GUENSBURG, T.E., TOUZEAU, A., NOAILLES, F. & SPRINKLE, J. 2013. Palaeobiogeography of Ordovician echinoderms, 173–198. In HARPER, D.A.T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society London, Memoir 38. DOI 10.1144/M38.14
- LEFEBVRE, B., ALLAIRE, N., GUENSBURG, T.E., HUNTER, A.W., KOURAÏSS, K., MARTIN, E.L.O., NARDIN, E., NOAILLES, F.,

- PITTET, B., SUMRALL, C.D. & ZAMORA, S. 2016. Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460, 97–121. DOI 10.1016/j.palaeo.2016.02.039
- LEFEBVRE, B., GUENSBURG, T.E., MARTIN, E.L.O., MOOI, R., NARDIN, E., NOHEJLOVÁ, M., SALEH, F., KOURAÏSS, K., EL HARIRI, K. & DAVID, B. 2019. Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes. *Geobios* 52, 27–36. DOI 10.1016/j.geobios.2018.11.001
- LEFEBVRE, B., NOHEJLOVÁ, M., MARTIN, E.L.O., KAŠIČKA, L., ZICHA, O. & GUTIÉRREZ-MARCO, J.C. 2022. New Middle and Late Ordovician cornute stylophorans (Echinodermata) from Morocco and other peri-Gondwanan areas, 345–522. In HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco*. The Geological Society London, Special Publication 485. DOI 10.1144/SP485-2021-99
- LEFEBVRE, B., ÁLVARO, J.J., CASAS, J.M., GHENNE, J.-F., HERBOSCH, A., LOI, A., MONCERET, E., VERNIERS, J., VIDAL, M., VIZCAÍNO, D. & SERVAIS, T. 2023. The Ordovician of France and neighbouring areas of Belgium and Germany, 375–408. In HARPER, D.A.T., LEFEBVRE, B., PERCIVAL, I.G. & SERVAIS, T. (eds) *A Global Synthesis of the Ordovician System Part 1*. Geological Society London, Special Publication 532. DOI 10.1144/SP532-2022-268
- LEFEBVRE, B., NOIRIT, F., DE OLIVEIRA SANTOS, V. & NOHEJLOVÁ, M. 2025. Mitrates paranacystidés (Echinodermata, Stylophora) dans le Dévonien moyen de la rade de Brest (Finistère): affinités et implications paléobiogéographiques. *Bulletin de la Société Géologique et Minéralogique de Bretagne Série D* 23, 19–34.
- MÉLOU, M. 1973. Le genre *Aegiromena* (brachiopode – Strophomenida) dans l'Ordovicien du Massif armoricain (France). *Annales de la Société Géologique du Nord* 93, 253–264. DOI 10.3406/asn.1973.1751
- MÉLOU, M. 1975. Le genre *Heterorthina* (Brachiopoda, Orthida) dans la Formation des Schistes de Postolonnec (Ordovicien), Finistère, France. *Geobios* 8, 191–208. DOI 10.1016/S0016-6995(75)80038-6
- PARSLEY, R.L. 1994. Mitrocystitid functional morphology, evolution and their relationships with other primitive echinoderm classes, 167–172. In DAVID, B., GUILLE, A., FÉRAL, J.-P. & ROUX, M. (eds) *Echinoderms Through Time*. Balkema, Rotterdam. DOI 10.1201/9781003077831-29
- PARSLEY, R.L. 1997. The echinoderm classes Stylophora and Homoiostelea: non Calcichordata, 225–248. In WATERS, J.A. & MAPLES, C.G. (eds) *Geobiology of Echinoderms*. Paleontological Society Papers 3. DOI 10.1017/S1089332600000279
- PARSLEY, R.L., LAWSON, M.H. & POJETA, J. JR. 2018. A practical and historical perspective on the how and why of whitening fossil specimens and casts as a precursor to their photography. *Fossil Imprint* 74(3–4), 237–244. DOI 10.2478/if-2018-0016
- PAUL, C.R.C. & GUTIÉRREZ-MARCO, J.C. 2022. Pentaradiate diploporites (Echinodermata) from the Spanish Middle Ordovician and their taxonomic significance. *Spanish Journal of Palaeontology* 37(2), 153–176. DOI 10.7203/sjp.25498
- PROKOP, R.J. & PETR, V. 1999. Echinoderms in the Bohemian Ordovician. *Journal of the Czech Geological Society* 44, 63–68.
- R CORE TEAM. 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- RÁBANO, I. 1990. Trilobites del Ordovícico Medio del sector meridional de la zona Centroibérica española. *Publicaciones Especiales del Boletín Geológico y Minero* 1990, 1–233.
- RAHMAN, I.A. & ZAMORA, S. 2024. Origin and early evolution of echinoderms. *Annual Review of Earth and Planetary Sciences* 52, 295–320. DOI 10.1146/annurev-earth-031621-113343
- RENAUD, M., LEFEBVRE, B., BAILLIOT, D., BAILLIOT, M.-N., COAT, S., GAUDU, C. & VIDAL, M. 2023. First report of the mitrate *Mitrocystella* (Echinodermata, Stylophora) in the Middle Ordovician of the Crozon Peninsula, Brittany (France). *Estonian Journal of Earth Sciences* 72(1), 86–89. DOI 10.3176/earth.2023.57
- REYES-ABRIL, J., GUTIÉRREZ-MARCO, J.C. & VILLAS, E. 2011. Biostratigraphy of the Middle Ordovician brachiopods from Central Spain. *Cuadernos del Museo Geominero* 14, 463–472.
- ROGACHEVA, V., MIRONOV, A.N., MININ, K. & GEBRUK, A.V. 2013. Morphological evidence of depth-related speciation in deep-sea Arctic echinoderms. *Invertebrate Zoology* 10(1), 143–166. DOI 10.15298/invertzool.10.1.07
- ROHLF, F.J. 2010. *TPSdig2, Digitize Landmarks and Outlines*. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.
- ROHLF, F.J. & SLICE, D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39, 40–59. DOI 10.2307/2992207
- ROMANO, M. 1976. The trilobite genus *Placoparia* from the Ordovician of Valongo area, north Portugal. *Geological Magazine* 113, 11–28.
- ROMANO, M. 1991. Trilobites from the Ordovician of Portugal. *Palaeontology* 34, 329–355. DOI 10.1017/S0016756800042977
- RUTA, M. 1998. An abnormal specimen of the Silurian anomalcystitid mitrate *Placocystites forbesianus*. *Palaeontology* 41(1), 173–182.
- RUTA, M. 2003. A species-level supertree for stylophoran echinoderms. *Acta Palaeontologica Polonica* 48, 559–568.
- RUTA, M. & JELL, P.A. 1999. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Formation and Lochkovian Humevale Formation of central Victoria. *Memoirs of the Queensland Museum* 43, 377–398.
- SÁ, A.A. & GUTIÉRREZ-MARCO, J.C. 2006. *Trilobites gigantes das ardósias de Canelas (Arouca)*. 207 pp. Ardosias Valério & Figueiredo, Madrid.
- SÁ, A.A., GUTIÉRREZ-MARCO, J.C., RÁBANO, I. & VALÉRIO, M. 2007. Palaeontology and Stratigraphy of the Ordovician in the Arouca Region (Central Portugal). *Acta Paleontologica Sinica* 46(Suppl.), 434–439.

- SÁ, A.A., PEREIRA, S., RÁBANO, I. & GUTIÉRREZ-MARCO, J.C. 2021. Giant trilobites and other Middle Ordovician invertebrate fossils from the Arouca UNESCO Global Geopark, Portugal. *Geoconservation Research* 4(1), 121–130. DOI 10.30486/gcr.2021.1913689.1057
- SCOTSE, C.R. 2001. *Computer Animations on CD-ROM, PALEOMAP Project*. Arlington, Texas.
- SPRINKLE, J. 1973. *Morphology and Evolution of Blastozoan Echinoderms*. 283 pp. Museum of Comparative Zoology Harvard University, Cambridge (Massachusetts). DOI 10.5962/bhl.title.66379
- SPRINKLE, J. & GUENSBURG, T.E. 2004. Crinozoan, blastozoan, echinozoan, asterozoan, and homalozoan echinoderms, 266–280. In WEBBY, B.D., PARIS, F., DROSER, M.L. & PERCIVAL, I.G. (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press, New York. DOI 10.7312/webb12678-027
- SUMRALL, C.D., SPRINKLE, J. & GUENSBURG, T.E. 1997. Systematics and paleoecology of Late Cambrian echinoderms from the western United States. *Journal of Paleontology* 71, 1091–1109. DOI 10.1017/S0022336000036052
- TAUBER, E.H., ROMANO, M. & REIS, J.M. 1997. The trilobite *Actinopeltis (Valongia) wattisoni* Curtis, 1961 from the Valongo Formation (Ordovician) of North Portugal. *Comunicações de Instituto Geológico e Mineiro* 83, 3–16.
- UBAGHS, G. 1968. Stylophora, S495–S565. In MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology, Echinodermata 1(2)*. Geological Society of America, Lawrence & University of Kansas Press, Boulder.
- UBAGHS, G. 1970. *Les échinodermes « carpoïdes » de l'Ordovicien inférieur de la Montagne Noire (France)*. 110 pp. Éditions du CNRS, Cahiers de Paléontologie, Paris.
- UBAGHS, G. 1998. Echinodermes nouveaux du Cambrien supérieur de la Montagne Noire (France méridionale). *Geobios* 31, 809–829. DOI 10.1016/S0016-6995(98)80111-3
- WARE, D. & LEFEBVRE, B. 2007. Abnormalities in the Lower Ordovician cornute *Phyllocystis* Thoral (Echinodermata: Stylophora) of Montagne Noire (southern France): implications for plate homology and phylogeny. *Journal of Paleontology* 81, 779–787. DOI 10.1666/pleo0022-3360(2007)081[0779:AITLOC]2.0.CO;2
- ZAMORA, S., ZHU, X.J. & LEFEBVRE, B. 2013. A new Furongian (Cambrian) Echinoderm-Lagerstätte from the Sandu Formation (South China). *Cahiers de Biologie Marine* 54, 565–569.

Supplementary data

List of selected specimens for morphometric analysis.

Mitrocystella incipiens incipiens (Prague Basin, Czech Republic): NMP L 9294, NMP L 9295, NMP L 9301, NMP L 67013, NMP L 67014, NMP L 67015, NMP L 67016, NMP L 67017, NMP L 67018.

Mitrocystella incipiens miloni (Armorican Massif, France): IGR 15014, IGR 15239, IGR 15253, IGR 15269, IGR 15273, IGR 15352, IGR 15411, IGR 15413, IGR 15420, IGR 15430, IGR 15498, IGR 15498, IGR 15593, IGR 15645, IGR 15651, IGR 15658, IGR 15688, IGR 15797, IGR 15814, IGR 15885, IGR 15900, IGR 15911, IGR 15919, IGR 15923, IGR 15999.

Mitrocystella incipiens pustulosa (Spain): MGM-8592O, MGM-8593O, MGM-8594O, MGM-8595O, MGM-8601O.

Mitrocystella incipiens pustulosa? (Portugal): UCBL-FSL 718 480 (= plaster cast MT-230 in Gutiérrez-Marco & Meléndez 1987).