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Corresponding author:
Bertrand Lefebvre
bertrand.lefebvre@univ-lyon1.fr

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First report of the mitrate *Mitrocystella* (Echinodermata, Stylophora) in the Middle Ordovician of the Crozon Peninsula, Brittany (France)

Maxime Renaud[a], Bertrand Lefebvre[a], Denis Bailliot[b], Marie-Noëlle Bailliot[b], Sophie Coat[c], Christian Gaudu†[d] and Muriel Vidal[e]

[a] Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France
[b] 84 Avenue du Maréchal Leclerc, F-29610 Plouigneau, France
[c] Réserve naturelle régionale des sites d'intérêt géologique de la presqu'île de Crozon – Communauté de communes presqu'île de Crozon - Aulne maritime, F-29160 Crozon, France
[d] 21, Poul Ranet, F-22970 Ploumagoar, France
[e] Laboratoire Géo-Océan, UMR 6538, UBO, Ifremer, CNRS, IUEM, F-29280 Plouzané, France

ABSTRACT

The mid-Ordovician mitrocystitid mitrate *Mitrocystella incipiens* was one of the most widespread stylophorans in the high latitude Mediterranean Province, with occurrences in the Armorican Massif (France), the Iberian Peninsula (Portugal and Spain) and the Prague Basin (Czech Republic), all restricted so far to the late Darriwilian (*Hustedograptus teretiusculus* Zone). The description of this taxon in the Corréjou Member (Postolonnec Formation) of the Crozon Peninsula (western Brittany, France) not only extends its spatial distribution within the Armorican Massif, but also its stratigraphic range into the mid-Darriwilian (*Didymograptus artus* Zone). The remarkable preservation of the new material and associated sedimentological evidence both suggest rapid burial by storm deposits.

Introduction

Stylophorans (cornutes, mitrates) are a clade of extinct, vagile echinoderms, which initially diversified on soft substrates during the Miaolingian (Zamora et al. 2013). In the Furongian–Floian interval, they were, along with eocrinoids and glyptocystitid rhombiferans, one of the dominant members of the low-diversity echinoderm faunas occurring worldwide before the major diversification of crinoids on hard substrates (Lefebvre and Fatka 2003). After this late Cambrian–Early Ordovician peak in both diversity and palaeobiogeographic distribution, stylophorans remained minor elements of benthic communities until their last appearance in the fossil record, in the Pennsylvanian of Oklahoma (Kolata et al. 1991). During the Darriwilian, the Armorican Massif (western France; Fig. 1) represents, along with the Prague Basin (Czech Republic), one of the two major diversity hotspots for stylophorans (Lefebvre and Fatka 2003; Lefebvre et al. 2022). This situation possibly results from the combination of originally favourable environmental conditions (widespread siliciclastic soft substrates) and over 150 years of regional sampling and scientific descriptions. Specimen labels in the collections of Rennes University indicate that in April 1850 several individuals of the mitrate *Mitrocystella incipiens* were collected at Guichen (Ille-et-Vilaine; Fig. 1.1) by Marie Rouault in concretions of the Traveusot Formation (Darriwilian). Although possible occurrences of *Anatifopsis* sp. were mentioned by Tromelin and Lebesconte (1876) and Kerforne (1901) in regional faunal lists of Ordovician taxa, the first descriptions of Darriwilian stylophorans from the Armorican Massif were made by Chauvel (1937, 1941).

In the last decades, ten stylophoran taxa were described in the Middle Ordovician of six distinct areas of the Armorican Massif (see Lefebvre 2000; Lefebvre et al. 2022

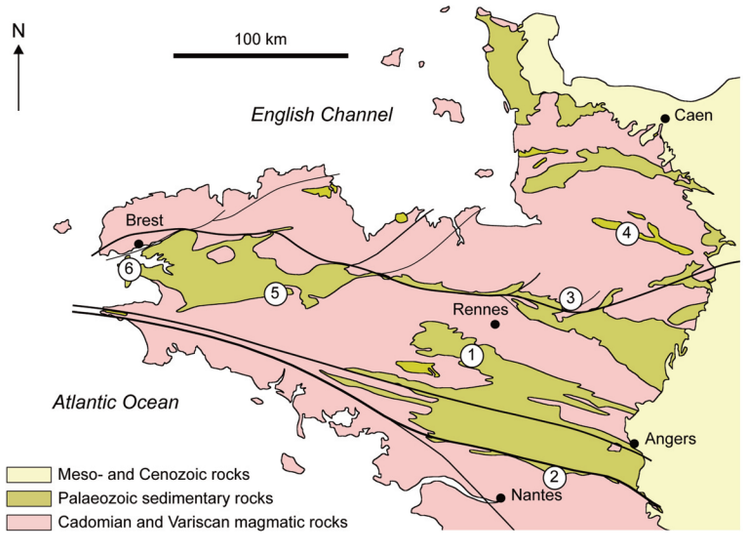

Fig. 1. Simplified geological map of the Armorican Massif (western France) showing the six main areas yielding Darriwilian stylophorans: 1 – Martigné-Ferchaud Syncline (Traveusot Formation); 2 – Ancenis Syncline (Pierre Meslière Formation); 3 – Menez-Belair Syncline (Andouillé Formation); 4 – Mortain-Domfront Syncline (Le Pissot Formation); 5 – eastern part of the Châteaulin Basin (Postolonnec Formation); 6 – Crozon Peninsula (Postolonnec Formation).

and references therein). In the Martigné-Ferchaud Syncline (Fig. 1.1), fine siltstones of the lower part of the Traveusot Formation (*Didymograptus artus* Zone) provided rare specimens of poorly preserved cornutes (*Domfrontia*? sp.) and mitrocystitid mitrates (*Aspidocarpus* sp.). In the same area, silico-aluminous concretions and shales of the upper part of the Traveusot Formation (*Hustedograptus teretiusculus* Zone) yielded the most diverse stylophoran assemblage of the Armorican Massif. This assemblage is dominated by extremely abundant remains of *M. incipiens*, associated with relatively common kirkocystid mitrates (*Anatifopsis minuta* and *Balanocystites primus*), and rare representatives of anomalocystitids (*Diamphidiocystis regnaulti*), cornutes (*Domfrontia pissotensis*, *Milonicystis kerfornei* and *Thoralicarpus guilloui*), and lagynocystids (*Lagynocystis pyramidalis*). In the Ancenis Syncline (Fig. 1.2), the concretions of the Pierre Meslière Formation (*D. artus–Didymograptus murchisoni* zones) yielded rare individuals of the two mitrates *Lagynocystis pyramidalis* and *Mitrocystites mitra*. In the Menez-Belair Syncline (Fig. 1.3), several specimens of *M. incipiens* were found at La Croixille, in upper Darriwilian shales (*H. teretiusculus* Zone) of the Andouillé Formation. In the Mortain-Domfront Syncline (Fig. 1.4), abundant remains of the cornute *Domfrontia pissotensis* were described in the fine siltstones of the Le Pissot Formation (*H. teretiusculus* Zone). In the eastern part of the Châteaulin Syncline (Fig. 1.5), a single echinoderm-rich bed in shales of the upper part of the Postolonnec Formation (*H. teretiusculus* Zone) provided several flattened specimens of the mitrates *M. incipiens* and *D. regnaulti*. Finally, in the Crozon Peninsula (Fig. 1.6), the same levels yielded three specimens of *Aspidocarpus* sp.

The aims of this paper are to report the first occurrence of the mitrate *Mitrocystella* in the Crozon Peninsula and to discuss its preservation and palaeobiogeographic implications.

Materials and methods

In March 2021, several mitrate-like pyritized fossils were identified in the lowermost part of the Corréjou Member of the Postolonnec Formation (*D. artus* Zone, mid Darriwilian; Dabard et al. 2015) exposed on the Notinau beach in Camaret (Crozon Peninsula, Finistère; Fig. 1.6), on the territory of the regional natural reserve of Crozon Peninsula (for a detailed description of local stratigraphy and palaeontology, please see e.g. Henry 1980; Guillocheau 1983; Loi and Dabard 2002; Dabard et al. 2007, 2015; Vidal et al. 2011). Once all official authorizations were obtained, a large rock sample containing the two side-by-side, best preserved specimens (Fig. 2A) was extracted from the cliff and registered in the palaeontological collections of the University of Western Brittany in Brest. Two thin sections (also registered at the Brest University) were made perpendicular to the bedding plane (Fig. 2B), so as to describe the associated lithology. As the two mitrates are preserved as 'negative' empty moulds in the rock, they were cast with latex to better visualize their original 'positive' morphology. The two individuals were drawn with a camera lucida apparatus mounted on a Zeiss SteREO Discovery.V8 stereomicroscope binocular. Photographs were taken with a Canon 5DSR camera equipped with a MP-E 65 mm macro lens.

Results and discussion

Although they are strongly flattened, the two individuals can be unambiguously identified as stylophorans, based on the presence of two distinct parts: a relatively massive, polyplated theca and, articulated to it, a single feeding appendage (aulacophore) comprising a wide proximal region made of several telescopic rings, and a narrower distal part (Fig. 2A). Moreover, the preservation of their aulacophore in a recurved position indicates that these two stylophorans correspond to mitrates (cornutes were unable to flex their distal appendage; Lefebvre 2003). The absence of posterior spines (digital and/or glossal), along with the main features of their plate pattern on the two contrasted thecal sides, makes it possible to unambiguously assign these two mitrates to the mitrocystitid *M. incipiens* (see, e.g., Hunter et al. 2007 for similarly preserved specimens of *M. incipiens* in the shales of the same formation, in the eastern part of Châteaulin Basin; Fig. 1.5).

The material collected in Camaret (Notinau beach; Fig. 1.6) at the base of the Corréjou Member thus represents the stratigraphically earliest occurrence of *M. incipiens* in the

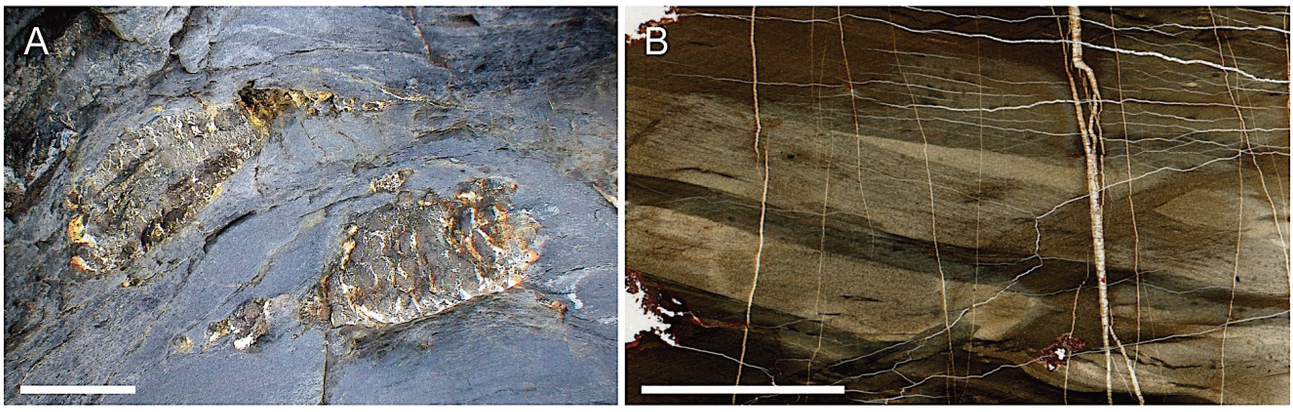

Fig. 2. **A** – two original individuals of *Mitrocystella incipiens* in the lower (left specimen) and upper aspect (right specimen), LPB 10711, Corréjou Member, Postolonnec Formation (*Didymograptus artus* Zone, middle Darriwilian), Notinau beach (Camaret, Finistère); **B** – thin section (BR3184/Notinau1) cut perpendicular to the mitrate-bearing rock sample, with two distinct beds of very fine siltstones (distal tempestites) embedded within thinly laminated mudstones (background sedimentation). All scale bars: 10 mm.

Armorican Massif (*D. artus* Zone, middle Darriwilian). In all other localities (Martigné-Ferchaud and Menez-Belair synclines, eastern part of the Chateaulin Basin; Fig. 1.1,3,5), it was always found within the same, younger stratigraphic interval (*H. teretiusculus* Zone, upper Darriwilian). However, the palaeobiogeographic distribution of *M. incipiens* is not restricted to the Armorican Massif. During the Middle Ordovician, this mitrate was widely distributed in several other regions of the high-latitude Mediterranean Province. It was originally described in the Prague Basin, where it is relatively common in silico-aluminous concretions of the Dobrotivá Formation (*H. teretiusculus* Zone) (Barrande 1887; Chauvel 1941; Prokop and Petr 1999). Rare specimens of *M. incipiens* were also reported in the lower Guindo Shales (*H. teretiusculus* Zone) in the Hesperian Massif, Spain (Chauvel and Meléndez 1978; Gutiérrez-Marco and Meléndez 1987), and in the Valongo Formation (*H. teretiusculus* Zone) in northern Portugal (Gutiérrez-Marco and Meléndez 1987; Couto and Gutiérrez-Marco 2000). Finally, a single specimen of mitrocystitid from the Pontyfenni Formation (Dapingien) of Wales was tentatively described as *Mitrocystella*? sp. by Jefferies (1987). However, its incomplete preservation (posterior half of the theca is missing) precludes any firm taxonomic assignment. Consequently, this overview of all known occurrences of *M. incipiens* indicates that the specimens from the lowermost levels of the Corréjou Member in Camaret represent the earliest known record of this taxon. Everywhere else, its stratigraphic distribution is restricted to the late Darriwilian.

Thin sections (Fig. 2B) exhibit thinly laminated sediment, with mudstones interbedded with two distinct beds, each with a sharp base and consisting of siltstones to very fine sandstones with low-angle to planar, wavy laminations. These observations suggest the occurrence of two distinct 'event beds' (very fine sandstones), probably corresponding to relatively distal storm deposits, interbedded with thinly laminated mudstones suggesting relatively quiet environmental shelf conditions (background sedimentation). This interpretation is in good accordance with previous field observations and detailed sedimentological analyses of the lower part of the Postolonnec Formation (base of the Corréjou Member) in Crozon Peninsula, all of which indicate environmental conditions corresponding to a storm-influenced shelf (Guillocheau 1983; Loi and Dabard 2002; Dabard et al. 2007, 2015).

Similarly to the situation regarding extant echinoderms (Brett et al. 1997), it is very likely that the stylophoran multiplated endoskeleton disarticulated rapidly (i.e. within a few weeks) after the death of the organism (Lefebvre 2007). Consequently, the preservation of intact, fully articulated mitrates in Camaret (Fig. 2A) implies that they were buried either alive or shortly after death. This interpretation is further supported by the preservation of their aulacophores in a flexed position, which is generally interpreted as either a distressed posture and/or resulting from the post-mortem, ligament-induced contraction of the appendage (Lefebvre 2003). When they are preserved in life position, mitrates have their feeding appendage held almost straight over the sea floor (Parsley and Gutiérrez-Marco 2005; Lefebvre and Ausich 2021). Moreover, the opposite, upside-down orientations of the two side-by-side individuals (one is in the upper aspect and the other one in the lower aspect) clearly demonstrate that they are not preserved in life position. These taphonomic observations are in good accordance with sedimentological data (see above), suggesting storm-influenced environmental conditions. Consequently, the remarkable preservation of the two specimens of *M. incipiens* from Camaret probably results from their rapid burial, soon after death, by storm deposits.

Conclusions

The description of the mitrate *Mitrocystella incipiens* in the lower part of the Postolonnec Formation (Corréjou Member) in the Crozon Peninsula not only increases its distribution across the Armorican Massif, but it also represents the earliest known record of this taxon in the whole Mediterranean Province. Both the taphonomic characteristics of the specimens and the associated sedimentological structures suggest that the Notinau mitrates were very likely buried soon after death by storm deposits.

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