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Corresponding author:
Christophe Dupichaud
christophe.dupichaud@univ-lyon1.fr

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Solutan echinoderms from the Lower Ordovician of the Montagne Noire (France): new data and palaeobiogeographic implications

Christophe Dupichaud[a], Bertrand Lefebvre[a] and Martina Nohejlová[b]

[a] Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France

[b] Czech Geological Survey, Klárov 3, Praha 1, 11821 Czech Republic

ABSTRACT

Solutans are relatively common members of echinoderm assemblages in the Saint-Chinian Formation (upper Tremadocian) of the Montagne Noire (France). The revision of all available material confirms that most specimens can be assigned to *Minervaecystis vidali*, which is here reconstructed for the first time. The occurrence of *Plasiacystis mobilis* is evidenced based on a single, well-preserved dististele. The interpretation of the small-sized individual as a putative dendrocystitid is rejected: it corresponds to a juvenile specimen of *M. vidali*. Early Ordovician solutans from the Montagne Noire partly fill the gap between Laurentian mid–late Cambrian syringocrinids and Avalonian-Gondwanan Early–Middle Ordovician taxa.

Introduction

In spite of some recent reports (e.g. Zhu et al. 2016), very few Furongian–Early Ordovician echinoderm faunas are known worldwide from this critical interval at the transition between the Cambrian explosion and the Great Ordovician Biodiversification Event (Smith 1988). Along with the Fillmore Formation in western Utah, USA (Sprinkle and Guensburg 1995), and the lower part of the Fezouata Formation in the Central Anti-Atlas, Morocco (Lefebvre et al. 2016), the Saint-Chinian Formation in the Montagne Noire, France, is one of the few lithostratigraphic units yielding abundant and diverse Tremadocian echinoderm remains (Thoral 1935; Vizcaïno and Lefebvre 1999; Vizcaïno et al. 2001). This situation probably results from their remarkable three-dimensional preservation in alumino-siliceous concretions and also from nearly 150 years of intensive, continuous sampling (Vizcaïno et al. 2001 and references therein). Echinoderm assemblages from the Saint-Chinian Formation comprise over 30 taxa belonging to eight classes. In terms of abundance and diversity, stylophorans (cornutes and mitrates) are the dominant group. The Saint-Chinian Formation also comprises some of the earliest representatives of the subphylum Asterozoa and of the class Crinoidea. This unit also yielded edrioasteroids, eocrinoids, rhombiferans and solutans (see Vizcaïno and Lefebvre 1999; Vizcaïno et al. 2001 and references therein).

Along with eocrinoids, glyptocystitid rhombiferans and stylophorans, solutans are typical members of the cosmopolitan, low-diversity, Furongian–Early Ordovician echinoderm assemblages (Sumrall et al. 1997; Lefebvre et al. 2013; Zhu et al. 2016). Late Cambrian and younger solutans were vagile members of benthos, generally interpreted as probable detritus-feeders, sweeping soft substrates with their unique feeding appendage (e.g. Kolata 1973; Noailles et al. 2014; Nohejlová and Lefebvre 2022). From Lower Ordovician sediments of the Montagne Noire, a single species of solutans has been described so far (*Minervaecystis vidali*) from the concretion-bearing shales of the Saint-Chinian Formation (Thoral 1935; Ubaghs 1970). Based on the examination of all available material (historical collections and additional specimens collected since Ubaghs' 1970 seminal description of *M. vidali*), the aims of this paper are (1) to revise the morphology and produce the first reconstruction of *Minervaecystis*; (2) to describe and document the first occurrence of *Plasiacystis mobilis* in the Lower Ordovician strata of southern France; and (3) to discuss the palaeobiogeographic affinities of the Montagne Noire solutans.

Materials and methods

The study material includes 42 solutan specimens collected from the Lower Ordovician of the Montagne Noire (southern France) and catalogued in the following public collections: Natural History Museum, London (BMNHUK: Miquel collection), Musée du Biterrois, Béziers (MBB: Griffe collection), Muséum National d'Histoire Naturelle, Paris (MNHN: Courtessole-Griffe collection), Lyon 1 University, Villeurbanne (UCBL.FSL: Lignières, Kundura, Villebrun, and Vizcaïno collections), and Montpellier University, Montpellier (UM: Azaïs, Roquefort, Thoral, and Villebrun collections). All specimens are from the Saint-Chinian Formation (late Tremadocian, *Euloma filacovi* Zone; see Vizcaïno and Álvaro 2003). In the Saint-Chinian area, this 500 m thick formation consists of relatively monotonous dark concretion-bearing siltstones with fine sandstone intercalations (Vizcaïno et al. 2001; Vizcaïno and Álvaro 2003). The Saint-Chinian Formation has yielded a particularly diverse fossiliferous assemblage typical of moderately deep, well-oxygenated shelf environments, below storm wave base, and comprising bivalves, brachiopods, cephalopods, conulariids, echinoderms, gastropods, graptolites, hyolithids, machaeridians, and trilobites (Thoral 1935; Vizcaïno et al. 2001).

All fossils are preserved three-dimensionally, as empty negative moulds, in alumino-siliceous concretions. So as to reveal their original aspect, solutans were cast with latex and coated with ammonium chloride (NH_4Cl) for drawing and photographic purposes. Observations and camera lucida drawings were made with a Zeiss SteREO Discovery.V8 binocular stereomicroscope, and photographs with a Canon 5DSR camera equipped with a MP-E 65 mm macro lens. Digital drawings were made with the help of the software Krita 5.0.2.

Results

The re-examination of Thoral's (1935) original type series and over 30 additional specimens (Fig. 1A–E) did not give any significant additional morphological information to the very detailed description of *Minervaecystis vidali* provided by Ubaghs (1970). However, this abundant material made it possible to elaborate on the first detailed, specimen-based reconstruction of this solutan (Fig. 2). Tentative reconstructions of *M. vidali* were already provided by Lefebvre et al. (2012, fig. 2.1) and Rozhnov (2022, fig. 4h), but they were simply combining two original camera lucida drawings figured in Ubaghs (1970, figs 39.1 and 41.1). Moreover, the observation of all available individuals of *M. vidali* indicates that, when preserved, their twisted dististele is not straight but consistently curved to the right (Fig. 1A, C). *Minervaecystis* shares with *Pahvanticystis* and *Plasiacystis* the possession of a non-apical, laterally inserted brachiole, a relatively large, inflated, ovoid theca, and a flattened, twisted dististele (Lefebvre and Lerosey-Aubril 2018). *Minervaecystis* differs from *Pahvanticystis* in the more posterior insertion of its brachiole, a proportionately longer proxistele (comprising over 20 tetramerous rings), and the morphology of its dististele (narrower, and with lateral comb-like spikes). *Minervaecystis* mostly differs from *Plasiacystis* in having a proxistele consisting of numerous, regularly arranged tetramerous rings (this region is composed of numerous, unorganized, imbricate, scale-like plates in *P. mobilis*), and an elongate, stem-like dististele, instead of a short, broad, paddle-like distal structure (Prokop and Petr 2003; Lefebvre et al. 2012).

Lefebvre and Lerosey-Aubril (2018) questioned the possibility that the smallest known individual assigned to *Minervaecystis* (UM.ACI.636) and figured by both Thoral

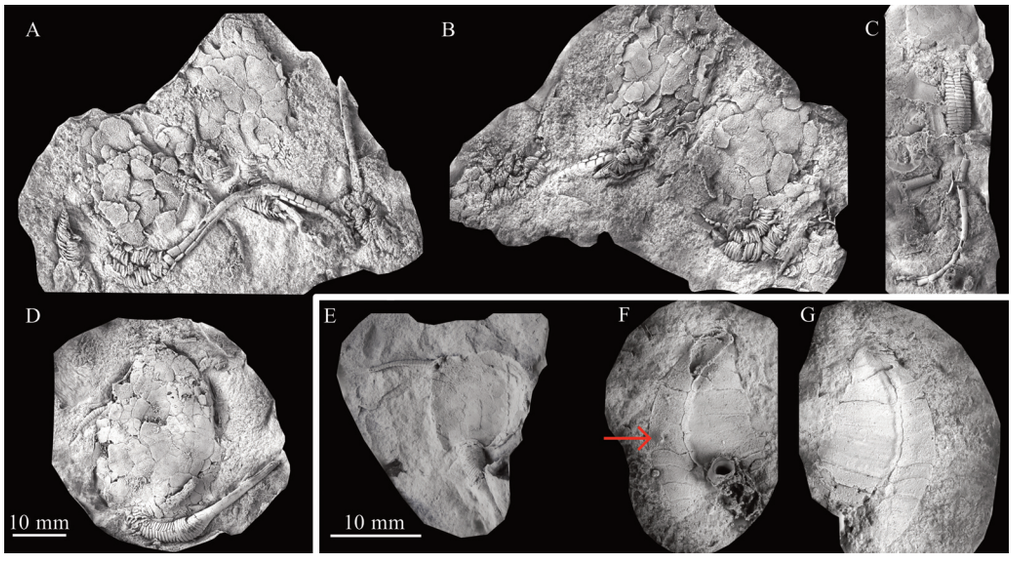

Fig. 1. Solutans from the Saint-Chinian Formation (upper Tremadocian), Montagne Noire (Hérault, France); latex casts of original specimens. **A**–**E** – *Minervaecystis vidali* (Thoral, 1935); **A**–**B** – cluster of four individuals (part and counterpart); BMNHUK.E.23695 (Miquel coll.), locality Cassagnoles; **A** – nearly complete individual (in lower aspect) in the centre of the cluster, with a fully articulated brachiole and a long, strongly curved, twisted dististele; **B** – same individuals (in upper aspect); **C** – well-preserved individual (in lower aspect) with a strongly curved, twisted dististele; UCBL.FSL.713595 (Kundura coll.), locality Prades-sur-Vernazobre; **D** – fully articulated theca (in upper aspect) with a brachiole and a well-preserved anal pyramid, to the right of homoiostele insertion; lectotype, UM.ACI.634 (Villebrun coll.), locality Saint-Chinian; **E** – juvenile individual; UM.ACI.636 (Thoral coll.), locality Prades-sur-Vernazobre; **F**–**G** – *Plasiacystis mobilis* Prokop and Petr, 2003; latex casts of the dististele (part and counterpart) of the single known specimen (MBB.GG.6, Griffe coll.), locality Saint-Chinian; note the presence of a well-defined spike-shaped tubercle on one of the two sides (**F**, red arrow).

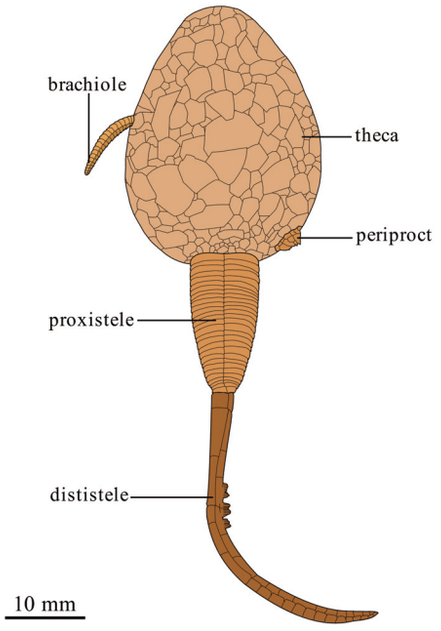

Fig. 2. Reconstruction of *Minervaecystis vidali* (Thoral, 1935), Saint-Chinian Formation (upper Tremadocian), Montagne Noire (France).

(1935, pl. 11, fig. 2) and Ubaghs (1970, pl. 16, fig. 5) could represent one of the oldest known dendrocystitid solutans. Their suggestion relied on the quadrangular aspect of the theca and, mostly, on the location and morphology of the periproct (relatively large, rounded, low structure formed of several elongate tapered plates forming a well-defined anal rosette). However, the re-examination of the original specimen (Fig. 1E) does not support this interpretation but confirms its identification as a juvenile individual of *M. vidali* (Thoral, 1935; Ubaghs 1970). Its unusual aspect results from the combination of a theca preserved as a hollow internal mould, with two appendages (brachiole and homoiostele) occurring as three-dimensional external moulds. Consequently, contrary to most other specimens of *Minervaecystis*, the periproct of UM.ACI.636 is visible in internal view. Its regular arrangement into a well-defined, closed rosette suggests that the prominent, cone-shaped (external) morphology of the periproct observed in most individuals is possibly preservational and/or results from its ability to open outwards (valvular structure). As in all other specimens of *Minervaecystis*, the brachiole of UM.ACI.636 is inserted laterally, away from the apex and on the antanal side of the theca (i.e. opposite the periproct).

Although the occurrence of *Plasiacystis mobilis* in the Lower Ordovician of the Montagne Noire was regularly mentioned (e.g. Lefebvre et al. 2012, 2016), no remains of this solutan have been formally described or illustrated from this region so far. The detailed re-examination of the historical collections made it possible to confirm the presence of *P. mobilis*, based on a single, well-preserved, isolated dististele (MBB.GG.6, part and counterpart) collected from the Saint-Chinian Formation. Its short and broad, bean-shaped, flattened morphology (Fig. 1F–G) is typical of *Plasiacystis* and identical to the dististele in Czech specimens of *P. mobilis* (see Prokop and Petr 2003; Lefebvre et al. 2012). The distally incomplete paddle-like appendage of MBB.GG.6 consists of two unequal series of wide, flattened plates, with those forming the concave lateral edge about twice as long as those on the opposite, convex margin. The dististele slightly increases in thickness along the longitudinal suture running along the opposite sets of plates, left and right. In MBB.GG.6, a well-defined tubercle (spike) occurs on one side of the dististele. It cannot be formally excluded that some poorly preserved solutan thecae traditionally assigned to *Minervaecystis* may indeed belong to *Plasiacystis*.

Discussion

Their abundant and almost continuous fossil record from the lower Drumian to the upper Floian of (modern) North America (Alabama, Nevada and Utah) suggests that solutans very likely originated in Laurentia (Zamora et al. 2013a; Lefebvre and Lerosey-Aubril 2018), possibly from a gogiid-like ancestor (Parsley 1997). The yet undescribed solutans from the Sandu Formation (Jiangshanian) of South China represent the earliest known occurrence of this clade outside Laurentia (Zamora et al. 2013b; Zhu et al. 2016). In this context, the late Tremadocian solutans from the Montagne Noire correspond, along with coeval occurrences from the Central Anti-Atlas (Morocco), to the earliest known record of this class in high-latitude Gondwanan regions (Lefebvre et al. 2013, 2016). The two taxa occurring in the Lower Ordovician of southern France (*Minervaecystis* and *Plasiacystis*) are closely related to Cambrian syringocrinids from Laurentia (*Castericystis*, and mostly *Pahvanticystis*; see Lefebvre and Lerosey-Aubril 2018). Although *Minervaecystis vidali* is so far considered endemic to the Montagne Noire, very similar isolated homoiosteles sp. from the Whipple Cave Formation (upper Furongian) of Nevada (Ubaghs 1963; Sumrall et al. 1997) have been tentatively assigned to this genus (*Minervaecystis*? sp.), and the yet undescribed remains of minervaecystids are also known from the Wah Wah Formation (late Floian) of Utah (Sprinkle and Guensburg 1993). In sharp contrast to the Montagne Noire, where it is extremely rare, *Plasiacystis mobilis* is particularly abundant and widespread in the Lower Ordovician of Morocco, with occurrences ranging from the late Tremadocian to the late Floian (Lefebvre et al. 2016; Saleh et al. 2022; Dupichaud and Lefebvre 2022). The latter solutan has a remarkably long temporal range, as it is also present in the Darriwilian of Shropshire, UK (Hope Shale; Lefebvre et al. 2012), and of the Prague Basin, Czech Republic (Šarka Formation; Prokop and Petr 2003; Lefebvre et al. 2012).

Conclusions

Solutans were relatively common members of late Tremadocian benthic communities in the southern Montagne Noire (France). The revision of all available specimens from the Saint-Chinian Formation made it possible to confirm the occurrence of two distinct taxa: (1) the most abundant one, *Minervaecystis vidali*, is here reconstructed for the first time, with new information on the morphology of its periproct;

(2) *Plasiacystis mobilis*, which is particularly rare in the Lower Ordovician of the Montagne Noire, is described and figured for the first time; and (3) the occurrence of putative dendrocystitids is not confirmed. The Montagne Noire solutan assemblage documents a key evolutionary transition, with a mixture of plesiomorphic morphologies inherited from the worldwide expansion of syringocrinids outside Laurentia in the late Cambrian (*Minervaecystis*), and the onset of new, highly derived morphotypes in Avalonia and Gondwana (*Plasiacystis*) in the Early and Middle Ordovician. During the Darriwilian, the persistence and diversification of solutans in the latter two geographic areas fuelled their expansion to Baltica and Laurentia (where they had disappeared at the end of the Floian) in the Late Ordovician.

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