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A mixed ophiuroid–stylophoran assemblage (Echinodermata) from the Middle Ordovician (Llandeilian) of western Brittany, France

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Abstract: In the abandoned slate quarry of Guernanic, Gourin (Morbihan, France), a single horizon (Upper Member of the Schistes de Postolonnec Formation) has yielded an exquisitely preserved Llandeilian (Middle Ordovician) echinoderm assemblage composed of the ophiuroid *Taeniaster armoricanus* sp. nov. and the mitrate *Mitrocystella incipiens*. These two groups of echinoderms represent the first fossils formally described from the Middle Ordovician of the Gourin area. The brittlestar *T. armoricanus* sp. nov. is the third and oldest ophiuroid reported so far in the Palaeozoic of the Armorican Massif. The mitrate *Mitrocystella* is also described for the first time from western Brittany. Taphonomic features of this ophiuroid–stylophoran aggregation suggest that it probably corresponds to the rapid burial of a life assemblage in an otherwise quiet and moderately deep setting (shelf) below, but close to, storm wave base. This echinoderm association represents the oldest evidence for a gregarious mode of life for ophiuroids, as well as the oldest indisputable example of a mixed ophiuroid–stylophoran meadow.

Large concentrations of non-colonial organisms such as, for example, ophiuroids and crinoids are good sources of taphonomic, palaeoecological and taxonomic information (see Donovan 1991). Observations of modern communities from submersibles demonstrate that such accumulations could reach a great extent, not only in tropical waters but also on shallow temperate shelves, abyssal plains and even around the fringes of Antarctica (Aronson & Blake 1997; Juterzenka & Soltwedel 2004). Understanding such assemblages allows us to reconstruct ancient palaeo-communities and isolate the factors that control biofacies and taphofacies (Hunter & Donovan 2005). Recent work on modern environments has allowed us to understand mass accumulations and their relevance to fossil bioaccumulations as far back as the Palaeozoic (e.g. Brett *et al.* 1997).

In modern seas, ophiuroid meadows probably represent one of the most significant and widely distributed examples of such accumulations of echinoderms (Aronson & Blake 1997). They correspond to extensive, dense populations (several tens to several hundreds of individuals per m²)

of infaunal or epibenthic ophiuroids forming an actual living ‘carpet’ in or on the sea floor (Fujita & Ohta 1989, 1990; Aronson & Blake 1997). For example, the sea floor off the northern coast of Japan is nearly totally blanketed by dense beds of the modern ophiuroid *Ophiura sarsii*, between depths of 200 and 600 m (Fujita & Ohta 1990). Such assemblages are usually monospecific or largely dominated by a single species (Brun 1969; Fujita & Ohta 1990; Hily 1991). They are also typically characterized by a rare and poorly diversified associated fauna (Fujita & Ohta 1989, 1990; Ball *et al.* 1995). Several examples of comparable dense beds of ophiuroids have been also documented in the fossil record (Fujita 1992; Aronson & Blake 1997). The oldest indisputable occurrences of such ophiuroid meadows were reported from the Zahofany and Bohdalec formations (Caradoc, Upper Ordovician) of Bohemia (Petr 1989; Mikuláš *et al.* 1995). In the Middle Ordovician of Spain (Montes de Toledo), Hammann & Schmincke (1986) also reported the occurrence of several specimens of the ophiuroid

Taeniaster ibericus in a single horizon. However, this aggregation more probably results from the fortuitous local accumulation of several individuals transported by currents over a short distance, rather than an actual dense assemblage (Hammann & Schmincke 1986).

In this paper, we report on the discovery of an autochthonous assemblage consisting of a dozen, well-preserved, articulated individuals of the ophiuroid *Taeniaster* in the Upper Middle Ordovician (Llandeilian) of Gourin, Brittany (western France). This assemblage thus represents the oldest indisputable evidence of a gregarious mode of life for ophiuroids.

Interestingly, in the Middle Ordovician of Gourin, abundant remains of the mitrate stylophoran *Mitrocystella* were also sampled in the same horizon as well as specimens of ophiuroids. Stylophorans are an extinct class of free-living echinoderms (Middle Cambrian–Upper Carboniferous), characterized by a flattened theca and the possession of a single feeding arm (aulacophore: Ubaghs 1968; Chauvel 1981; Parsley 1988; Lefebvre 2003a). Their mode of life is supposed to be comparable to that of ophiuroids (Lefebvre 2003a, 2006). The occurrence of a dozen, fully articulated, autochthonous individuals of the mitrate *Mitrocystella* in a single horizon is indicative of a gregarious mode of life for these echinoderms. This interpretation is in good accordance with several previous records suggesting a gregarious mode of life for stylophorans: such stylophoran-dominated meadows are documented from the Middle Cambrian (Ubaghs & Robison 1988) to at least the Devonian (Ruta & Bartels 1998). However, the co-occurrence of abundant ophiuroids and mitrates in the same horizon in the Middle Ordovician of Gourin is an extremely significant observation from a palaeoecological point of view. Several examples of such mixed ophiuroid-stylophoran meadows have been reported in younger deposits of the Upper Ordovician (e.g. Lefebvre 2006) to Lower Devonian (e.g. Caster 1954). Consequently, this paper reports on the oldest definitive example of a mixed ophiuroid–stylophoran assemblage documented so far, and it demonstrates that the co-occurrence of these two echinoderm groups is a not uncommon occurrence in the fossil record. This study incorporates data from recent research on brittlestar preservation, palaeoecology and observations of modern communities from submersibles, along with numerous recent works on the probable palaeoecology of stylophorans (see Lefebvre 2003a) to track the early evolution of such bioaccumulations.

Finally, this paper describes the oldest remains of ophiuroids reported so far in the Armorican Massif and the third species of this Class ever described in the Palaeozoic of this region. The two previously described brittlestars are both early Devonian in age, and have been reported from Daoulas, Finistère (*Protaster daoulasensis*: Davy 1886), and from Saulges, Mayenne (*Ophiurina armoricana*: Morzadec & Ubaghs 1969). The comparable Middle Ordovician successions and faunas observed in Spain, Portugal and the Armorican Massif are considered by most authors as evidence for a direct geographic continuity between these three regions (e.g. Paris & Robardet 1977; Romano & Henry 1982; Young 1990; Gutiérrez-Marco *et al.* 1999). Consequently, the rarity of ophiuroids in the Middle Ordovician of Brittany is intriguing, as at least three different forms have been reported in coeval levels from elsewhere (Llandeilian) in Spain (Chauvel & Meléndez 1978; Gutiérrez-Marco *et al.* 1984; Hammann & Schmincke 1986). This paper also presents the first report of the mitrate *Mitrocystella* in the Chateaulin Basin (western Brittany). In the Armorican Massif, this stylophoran was previously only documented from several localities in eastern Brittany (e.g. Guichen), where most specimens were collected in siliceous concretions of the Traveusot Formation (Llandeilian: Chauvel 1941, 1981; Lefebvre 2000a). In eastern Brittany, this type of fossil occurrence severely limits palaeoecological interpretations (especially as far as a putative gregarious mode of life is concerned). Apart from the Armorican Massif, the mitrate *Mitrocystella* was also reported from the Middle Ordovician (Llandeilian) of Bohemia (Barrande 1887; Jefferies 1967, 1984; Parsley 1994), Spain and Portugal (Gutiérrez-Marco & Meléndez 1987; Couto & Gutiérrez-Marco 2000).

Repositories

The material referred to in this paper is deposited in the following public institutions: MHNN (Muséum d'Histoire naturelle de Nantes, France) and NMP (Narodni Muzeum Prague, Czech Republic).

Geological setting and associated fauna

Both the ophiuroids (consisting entirely of the genus *Taeniaster*) and the mitrate stylophoran (*Mitrocystella*) were sampled from a single unit within the Upper Member of the Schistes de Postolonnec Formation (Llandeilian) in the abandoned slate quarry of Guernanic, near Gourin, Morbihan (grid ref. (GR) 157210688),

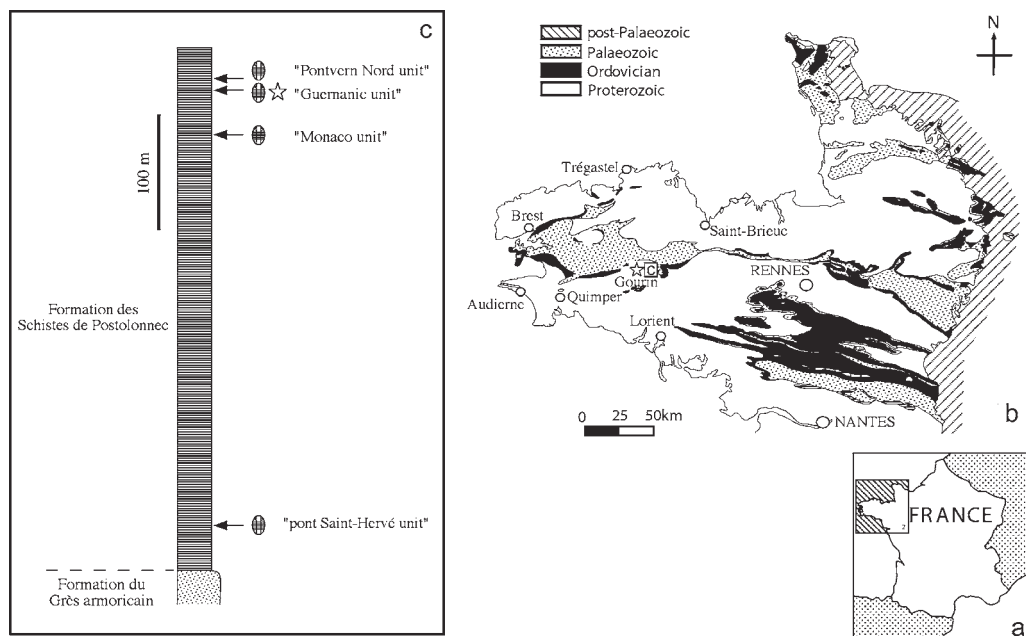


Fig 1. (a) Location of the Armorican Massif. (b) Geological map of the Armorican Massif focusing on the areas of Ordovician outcrop. (c) Synthetic stratigraphic column of Middle Ordovician sections in Gourin area, showing identified fossiliferous horizons (star signifies the echinoderm bed).

in the central 'synclinerium' system of Brittany (western France). The occurrence of Middle Ordovician fossils in the Gourin area was first documented by Tromelin & Lebesconte (1876), who mentioned the presence of bivalves (*Redonia deshayesiana*, *R. duvaliana*) and trilobites (*Calymene aragoi*, *C. salteri*, *C. tristani*, *Dalmanites macrophthalma*, *Illaeus beaumonti*, *I. giganteus*) in the 'schiste ardoisier'. Later on, Barrois (1884, 1885) reported a comparable, although more diverse, fossil assemblage in the 'schistes ardoisiers d'Angers' (Middle Ordovician) of Roch-Arvrán (north of Gourin), including bivalves (*Redonia deshayesiana*, *R. duvaliana*), brachiopods (*Orthis berthoisii*), graptolites and trilobites (*Calymene aragoi*, *C. tristani*, *Dalmanites macrophthalma*, *Illaeus giganteus*). The presence of Middle Ordovician echinoderm remains in the area of Gourin was quoted by Chauvel (1941, p. 65), who mentioned the probable occurrence of diploporite cystoids (*Aristocystites* cf. *bohemicus*). However, contrary to the situation in other regions of the Armorican Massif (e.g. Crozon peninsula, synclinals south of Rennes), where Middle Ordovician successions and faunas have been intensively studied (e.g. Kerforne 1901; Chauvel 1941, 1980, 1981; Babin 1966; Henry 1980, 1989; Henry *et al.* 1993), those

occurring in the Gourin area remained very poorly investigated (Pruvost & Le Maître 1949; Le Gall *et al.* 1992). Consequently, this study represents the first systematic description of Middle Ordovician fossils collected in the eastern part of the Chateaulin Basin.

In the Gourin area, the Schistes de Postolonnec Formation (Aberiddian–Llandeilian) corresponds to a thick succession (at least 450 m thick) of shales and slates lying conformably above the sandstones of the Grès Armoricain Formation (Arenig). The uncertain presence of the Middle Member of the Schistes de Postolonnec Formation (Grès de Kerarvail) has not yet been definitively established in the Gourin area (Le Gall *et al.* 1992). In more western outcrops (Crozon peninsula), the Kerarvail Member corresponds to a relatively thick sandstone intercalation (up to 30 m thick) between the shales of the Lower Member (Aberiddian) and those of the Upper Member (Llandeilian) of the Schistes de Postolonnec Formation (see Barrois 1889; Kerforne 1901; Babin *et al.* 1976; Henry 1989). In spite of a difficult geological context (numerous faults, absence of continuous sections), intensive field studies lead since the mid 1990s by two of the authors (P. Roussel and R. Clavierie) has made it possible to recognize at

least four distinct fossiliferous intervals (typically 10–50 cm thick) within the Schistes de Postolonnec Formation (Fig. 1). These four intervals are characterized by their different faunal content and can be correlated between outcrops. They are designated here, from bottom to top, as the ‘Pont Saint-Hervé’, ‘Monaco’, ‘Guernanic’ and ‘Pontvern Nord’ units. Fossils collected in these four intervals of the Schistes de Postolonnec Formation are flattened and some of them are preserved in pyrite.

The Pont Saint-Hervé unit occurs about 40 m above the contact between the Grès Armoricaïn and Schistes de Postolonnec formations. It has yielded a rich Aberdeiddian assemblage, with abundant remains of cystoid echinoderms (*Calix*), graptolites and trilobites (e.g. *Neseuretus*, *Plaesiacomia*). The second fossiliferous interval (Monaco) is located about 350 m above the pont Saint-Hervé unit, and it corresponds to a Llandeilian assemblage, dominated by trilobites (e.g. *Placoparia*, *Prionocheilus*). The third fossiliferous unit (Guernanic) occurs about 40 m above the Monaco unit. It is characterized by the presence of numerous micas (absent in the underlying Monaco unit). The Guernanic unit has yielded a rich and diverse fossil assemblage, dominated by articulated trilobites (e.g. *Salterocoryphe*, illaenid indet., *Zeliskella*), associated with echinoderms (e.g. crinoids, diploporite cystoids, mitrate stylophorans), brachiopods, bivalve and cephalopod molluscs. The presence of tarphicerid cephalopods is indicative of a possible late Llandeilian age. In one locality (abandoned slate quarry of Guernanic), a well-defined echinoderm-rich horizon occurring within this fossiliferous interval has yielded a dozen specimens of ophiuroids (*Taeniaster*) associated with a comparable proportion of mitrate stylophorans (*Mitrocystella*). It is this assemblage that will be described herein. It is apparent that this echinoderm horizon contains very little associated fauna. Finally, the fourth fossiliferous unit (Pontvern Nord) is located about 10 m above the Guernanic unit. It consists in a well-defined, mica-rich interval. The Pontvern Nord unit has yielded a late Llandeilian assemblage dominated by bivalves and trilobites (e.g. *Phacopidina micheli*).

The composition of the four fossiliferous assemblages recognized so far in the Middle Ordovician of Gourin shows clear affinities with coeval faunas reported from elsewhere in Brittany (e.g. western part of the Chateaulin Basin, synclinals south of Rennes: Chauvel 1941, 1980, 1981; Henry 1980, 1989) but also in Portugal and Spain (see Chauvel & Meléndez 1978; Henry

1980; Gutiérrez-Marco *et al.* 1984; Gutiérrez-Marco & Meléndez 1987). However, in the absence of a complete survey of the Gourin fauna (and especially of the trilobites), it is beyond the scope of this paper to elaborate further on its biostratigraphic and/or palaeobiogeographic significance.

Taphonomy

Both ophiuroids and stylophorans are regarded universally as having echinoderm skeletons (e.g. Jefferies 1967; Ubaghs 1968; Chauvel 1981). In the taphonomic classification proposed by Brett *et al.* (1997), these two groups can be classified as ‘type 1 echinoderms’ in that they possess a skeleton composed of loosely articulated plates, and require exceptional preservation to prevent fragmentation. In spite of comparable taphonomic attributes, brittlestars are much better understood owing to being present in modern environments and will thus be discussed first. However, the preservation and palaeoecology of stylophorans have been compared with those of ophiuroids (Lefebvre 2006). The fossil record of ophiuroids is considered so patchy that their former diversity is often misunderstood. This is primarily owing to their calcareous endoskeleton being composed of ossicles, which completely disarticulate and disassociate in a very short period after death. Such ossicles have long been thought to be unclassifiable (see Mortensen 1938). However, subsequent studies using fragmentary remains have tried to readdress this balance in the Mesozoic (see Jagt 1999, 2000; Hunter 2004). As yet only Hotchkiss *et al.* (1999) have applied this treatment to Palaeozoic echinoderms. This study looks at the exceptional instances when ophiuroids are preserved in obrution deposits. Owing to the apparent similarities between extant and fossil ophiuroids it would be expected that the history of preservation would be well understood, especially in such obrutions. However, this is not the case, although Schäfer (1972) noted that the arms of extant ophiuroids begin to disintegrate within 15 h of death and noted that catastrophic burial would be reasonable for articulated brittlestar assemblages, such as those that are observed in the Lower Jurassic in Dorset, UK. More rigorous studies were not conducted until recently by Kerr & Twitchett (2004). It is this study that is critical to understanding the Middle Ordovician assemblage from Gourin. Using experiments analogous to those carried out by Briggs & Kear (1994), specimens of the extant ophiuroid *Ophiura texturata* were decayed for 14 days at temperatures ranging from 15 to 25 °C, with

frequent tumbling of specimens to represent the turbidity of the environment. These experiments produced several stages of decay that could be quantified ranging from fully articulated carcasses to complete disarticulation. The ophiuroids in the present study could be classified in two of the decay stages identified in Kerr & Twitchett's (2004) study. Some specimens (including the paratype) could be classified as stage 1 (i.e. loss of ventral plates, oral shields, tooth papillae and jaws, and full articulation of the arms) (Figs 2a, d & 3a, MHNN.P.025955 and MHNN.P.025956), while most of them (including the holotype) would belong to stage 2 (i.e. arms begin to break off at/near the disk, and at least one arm remains attached) (see Figs 2b, c & 3c, MHNN.P.025954b and MHNN.P.025954a). However, interpretation of stage 2 preservation is difficult, as ophiuroids can sometimes autotomize their arms under environmental stress, so that forms lacking arms could have been buried before decay or shed arms during the catastrophic burial event itself. Kerr & Twitchett (2004) observed this type of preservation in brittlestars of the British Lower Jurassic and considered that burial occurred around the time of death, which implies the existence of a single community. However, such an observation could be a result of collector bias (see Hunter & Donovan 2005). In this study we have to assume an error caused by dealing with more distant Palaeozoic forms where the Recent brittlestar morphology is not strictly analogous with those in the Lower Palaeozoic.

The most fossiliferous starfish bed known in the Lower Palaeozoic is the Lady Burn starfish beds of Girvan, Scotland, UK. This assemblage is so diverse that in the most recent survey of Palaeozoic asterozoans (Shackleton 2003) approximately 60% of the taxonomic data came from this locality. The Lady Burn starfish beds have lenticular thinning from 15 to 1 cm within 1.5 m. This occurrence was interpreted by Goldring & Stephenson (1972) as resulting from the rapid entombment by storm deposits of a living, shallow-water assemblage, with limited transport and redeposition in a region where the fossilization potential is much higher than the environment of origin. However, more recent analyses based on the regional geological context, the composition of the faunal associations, as well as available sedimentological and taphonomic features of the Lady Burn starfish beds, all suggest that these assemblages more probably correspond to the rapid downslope transportation (by turbiditic currents), accumulation and burial of shallower, but relatively deep (i.e. outer shelf), living assemblages (e.g. Ingham 1978; Harper 1982, 2001; Daley 1992). In the

Ordovician, the geological context of Gourin (i.e. continental shelf, with relatively shallow deposits, at or below storm wave base) was clearly distinct from that documented in Girvan (i.e. outer edge of the Laurentian plate continental shelf). Moreover, contrary to the situation in the Lady Burn starfish beds, the Guernanic unit does not contain any evidence of lenticular thinning or several episodes of transport. Instead the whole horizon (including the echinoderm level) seems to be laterally continuous suggesting that the fauna was preserved *in situ*. Consequently, it is proposed here that the Guernanic fauna must have been entombed by a rapid influx of sediment as seen in ophiuroids from the Lower Lias of SW England (Kerr & Twitchett 2004). It is most probable that the ophiuroid-stylophoran association represented the termination of a period of echinoderm colonization extinguished by sediment influx (as possibly suggested by the local abundance of floated micas). This would best explain the odd faunal content of the isolated echinoderm level atypical of the sampled horizon, primarily composed of trilobites, associated with rare brachiopods and molluscs (see Table 1). This trilobite-dominated assemblage would be more akin to the assemblages of the Middle Ordovician of Spain, where *T. ibericus* occurs at the base of a channel (5 × 2 cm). These channels are considered to be traps for the ophiuroids caught in the channel and covered quickly by channel fill (Hammann & Schmincke 1986). Although there is an absence of such channels in Guernanic, there are considerable similarities both in the monogeneric nature of the assemblage and the sedimentology.

In Guernanic, the stylophorans are well preserved, and occur in 'clusters' on the rock surface (see Fig. 3b). Like the ophiuroids, stylophorans can also occur in deep low-energy distal shelf or slope environments (Lefebvre 2006). In most Gourin specimens, the preservation of the whole theca is likely to be the result of a quick burial to prevent disarticulation seen in type 1 skeletons. It is also likely that the plates of the theca are preserved in the same manner as regular echinoid tests (see Aslin 1968), where the theca is quickly filled with sediment through the openings in the cavity, thus preventing crushing of the theca. Another indicator of swift preservation is the absence in several specimens of the typical post-mortem kinking of their appendage (e.g. MHNN.P.025958 and MHNN.P.025960, see Fig. 3b). In mitrates, such a flexed position of the aulacophore is generally interpreted as a distressed posture and/or as resulting from the post-mortem contraction of this structure (Dehm 1932; Jefferies 1984; Parsley 1988; Ruta & Bartels

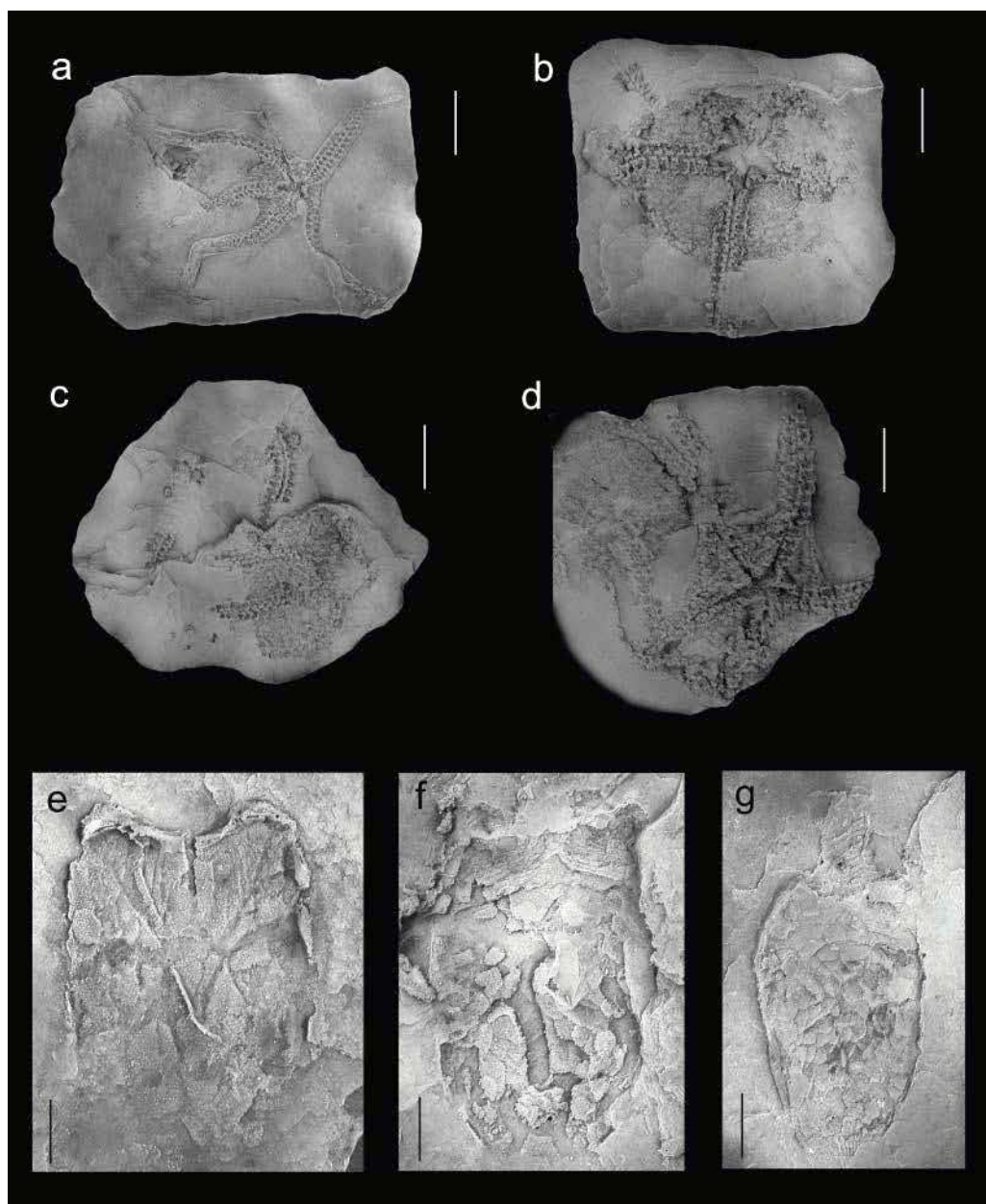


Fig. 2. (a)–(d) Morphology of the ophiuroid *Taeniaster armoricanus* and (e)–(g) of the mitrate stylophoran *Mitrocystella incipiens*, Upper Member, Postolonnec Formation (Llandeilian), Guernanic quarry, Gourin (Morbihan), Brittany, France. (a) MHNN.P.025955. (b) MHNN.P.025954b. (c) MHNN.P.025954a. (d) MHNN.P.025956. (e) MHNN.P.025957, partly disarticulated lower thecal surface (upper aspect) showing the zygial crest. (f) MHNN.P.025961, articulated lower thecal surface (upper aspect), with adorals and some supracentrals. (g) MHNN.P.025960, articulated upper thecal surface, with adorals, supracentrals, and aulacophore (in extended position). Scale bar represents 1 cm.

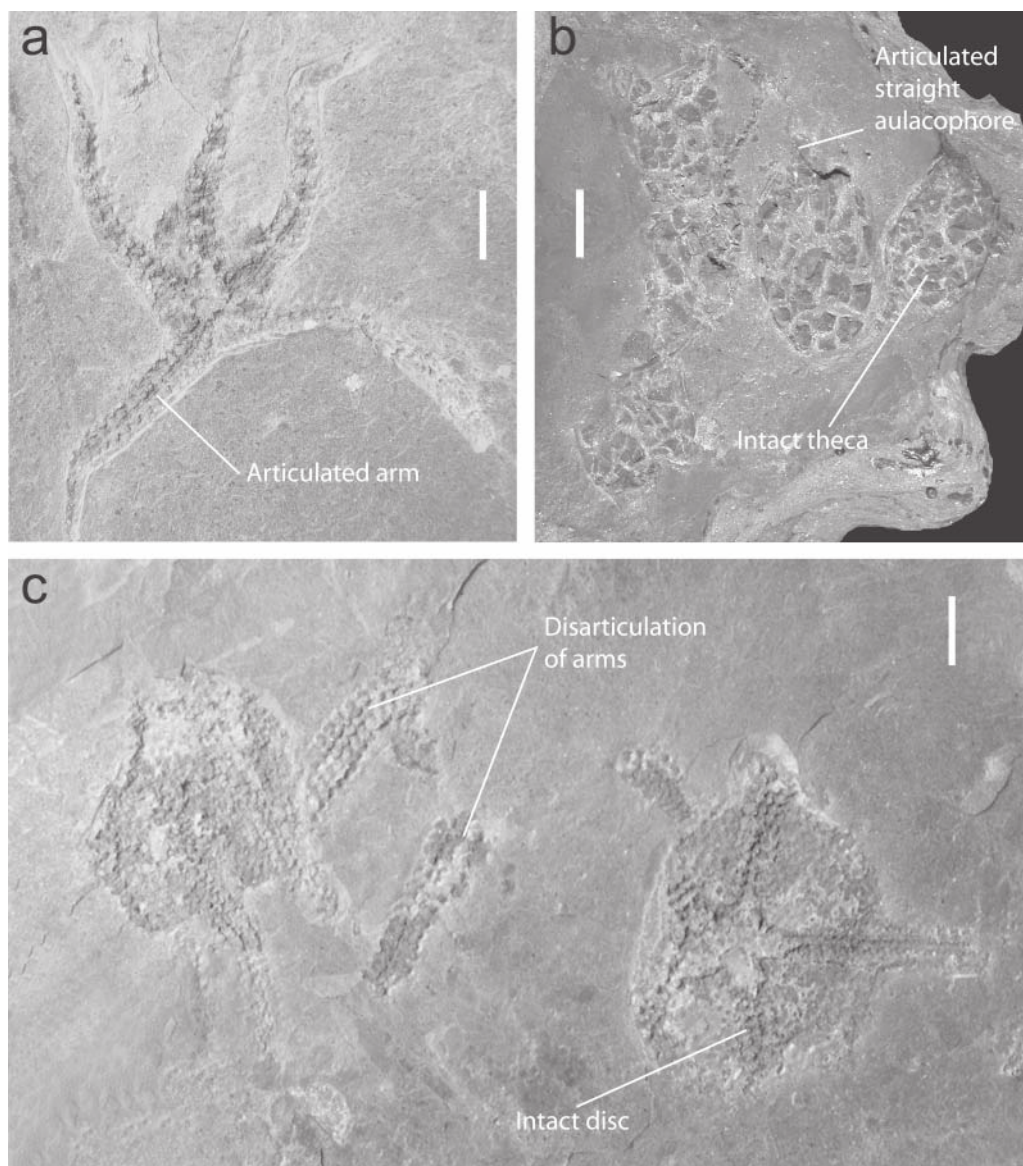


Fig. 3. (a) & (c) Taphonomy of the ophiuroid *Taeniaster armoricanus* and (b) of the mitrate stylophoran *Mitrocystella incipiens*, Upper Member, Postolonnec Formation (Llandeilian), Guernanic quarry, Gourin (Morbihan), Brittany, France. (a) MHNN.P.025955, articulated specimen. (c) MHNN.P.025955a-b, semi-articulated specimens. (c) MHNN.P.025958, cluster of articulated specimens. Scale bar represents 1 cm.

1998; Lefebvre 2003a). Consequently, the preservation of several specimens showing both their arm in the extended position and their cover plates ajar strongly suggests that these individuals were probably buried alive.

In Gourin, the presence of some slightly disarticulated specimens of *Mitrocystella* (e.g.

MHNN.P.025957, see Fig. 3b) suggests that all mitrates were not alive when buried. However, the low degree of disarticulation of the Gourin *Mitrocystella*, combined with the absence of epibionts on their thecal plates, are both indicative of a short time of exposure on the sea floor. This preservation is clearly different from that

Table 1. Faunal list of macrofossils found in Guernanic quarry, Gourin (Morbihan, France), in the Guernanic unit, Upper Member of the Schistes de Postolonnec Formation (Llandeilian), with an indication of their abundance (C, common; R, rare)

Brachiopods		Trilobites
lingulids indet. (R)		<i>Colpocoryphe</i> (C)
<i>Aegiromena</i> (R)		<i>Coplapararia</i> (R)
<i>Eorhipidomella</i> (Crozonorthis)?(R)		<i>Iliaenid</i> indet (C)
articulate forms indet. (R)		<i>Isabelinia</i> (C)
		<i>Neseuretus</i> (C)
Echinoderms		<i>Nobiliasaphus</i> (C)
<i>Calix</i> (C)		<i>Panderia</i> (C)
crinoids (C)		<i>Parabarrandia</i> (R)
<i>Diamphidiocystis</i> (R)		<i>Phacopidina</i> (R)
<i>Mitrocystella</i> (C)		<i>Prionocheilus</i> (R)
<i>Taeniaster</i> (C)		<i>Salterocoryphe</i> (C)
		<i>Selenopeltis</i> (R)
Molluscs		<i>Zeliszella</i> (R)
<i>Trocholites</i> (R)		
nautiloids indet. (R)		Other fossils
<i>Glyptarca</i> (R)		conulariids (R)
<i>Praemucula</i> (R)		hyolithids (R)
<i>Redonia</i> (R)		
bivalves indet. (R)		
<i>Ribeiria</i> (R)		

observed in specimens of *Mitrocystella* from the Dobrotiva Formation (Llandeilian) of Bohemia. Although they are usually exquisitely preserved, and not much disarticulated, Bohemian mitrates are frequently relatively intensively bioeroded (e.g. numerous *Arachnostega*-like tubes on both the internal and external side of their lower thecal surface: see Bruthansová & Kraft 2003; Lefebvre 2006). These taphonomic features suggest that carcasses of Bohemian *Mitrocystella* were exposed for a long time on the seafloor, in quiet palaeoenvironmental conditions. Consequently, contrary to the situation in Gourin, the Bohemian assemblage clearly represents a taphocoenosis (accumulation of dead organisms).

To sum up, several lines of evidence suggest instantaneous preservation of the Gourin echinoderm specimens (fully articulated, with even the most fragile portions still intact) and are suggestive of rapid burial in an otherwise low-energy environment. With such quick preservation, it seems extremely likely that both ophiuroids and stylophorans occurred together in the same environment.

Autecology of ophiuroids and stylophorans

The above taphonomic section has established that fully articulated specimens of *Taeniaster* and *Mitrocystella* from Gourin are very probably

preserved in life position and correspond to an *in situ* assemblage, suddenly and deeply buried by obrution deposits, in a moderately deep-shelf environment, below, but close to, storm wave base. In Palaeozoic sediments, the frequent simultaneous occurrences of abundant stylophorans and ophiuroids in the same layers could indicate that these two groups of echinoderms shared comparable palaeoecology or functional morphology, or at least inhabited the same habitat. Mixed assemblages of ophiuroids and stylophorans are relatively common in the late Ordovician–early Devonian time interval. Notable examples that will be discussed here are the Izegguirene Formation of Anti-Atlas, Morocco (early Caradoc: Lefebvre 2006), the South Threave Formation of Girvan, Scotland, UK (Ashgill: Spencer 1950; Donovan *et al.* 1996; Jefferies & Daley 1996), the Ponta Grossa Formation of Parana, Brazil (Emsian: Caster 1954) and the Hunsrück Slate, Bundenbach, Germany (Emsian: Dehm 1932; Ruta & Bartels 1998; Glass 2005). Such an association is not entirely unexpected, as both stylophorans and ophiuroids were small, flattened, free-living, unattached, gregarious, epibenthic or infaunal echinoderms, which were using their flexible arms for feeding and anchoring to the substrate for limited mobility (Lefebvre 2006).

Comprising approximately 1800 species in 250 genera, ophiuroids are the largest group of

extant echinoderms and today range across all modern environments from the Arctic regions to the Equator (Simms *et al.* 1993). In terms of ecology, modern ophiuroids can be epifaunal suspension feeders or infaunal detritus feeders. However, the morphology of even the modern fauna is not mutually exclusive to one feeding habit, although many interpretations have been proved to be ambiguous. For instance, Spencer (1951) suggested that aboral paxillae in Palaeozoic asteroids could indicate an infaunal behaviour. However, in modern brittlestars, such a character occurs in both epifaunal and infaunal forms (Gale 1987). Although it is possible that Palaeozoic ophiuroids were probably low-level suspension feeders, with some of them adapted to occasional scavengers (see Petr 1989), they however lacked the mobility of the arms seen in more recent forms, so that a more advanced filter-feeding habit may have not been possible (Shackleton 2005).

With many anatomical characters common to both ophiuroids and stylophorans (Nichols 1972; Lefebvre 2006), it is probable that comparable feeding techniques were used in these two groups of echinoderms. Thus, observations of modern ophiuroid meadows can probably help to understand not only the palaeoecology of fossil brittlestars, but also that of stylophorans.

Indisputable ophiuroid remains have not been documented before the Lower Ordovician (Tremadocian: Thorall 1935; Spencer 1950, 1951; Fell 1963), and a possible gregarious or social mode of life for this echinoderm group (so typical of their modern relatives) was not evident before the Late Ordovician (Caradoc: Petr 1989; Fujita 1992; Mikuláš *et al.* 1995). The oldest dense assemblages of ophiuroids known so far have been documented in the Caradoc of Morocco and Bohemia (Petr 1989; Lefebvre 2006). On the other hand, stylophorans have been described as far back as the Middle Cambrian, and a gregarious mode of life seems to be the rule for most of them (Ubaghs 1968; Ubaghs & Robison 1988).

The distribution of modern dense beds of epibenthic ophiuroids is relatively substrate-independent, but strongly controlled by depth (and water temperature). Extensive, dense populations of modern epibenthic ophiuroids are nearly exclusively restricted to the bathyal zone (depths of between 200 and 3000 m: Blaber *et al.* 1987; Fujita & Ohta 1989; Fujita 1992; Gage & Brey 1994). In shallower environments, very rare, small, patchy aggregations of epibenthic ophiuroids have been documented in the infralittoral zone (depths of between 10 and 50 m), as for example on the SW coast of England (Warner

1971; Broom 1975), or in a salt lake of the Bahamas (Aronson & Harms 1995; Aronson & Blake 1997).

As argued above, ophiuroids can occur in dense aggregations (also known as 'brittlestar beds'), in which representatives of other echinoderm groups (e.g. echinoids, asteroids) are frequently present (Hunter 2004), whilst members of other major groups of marine invertebrates (e.g. crustaceans, molluscs, sea anemones, sponges) are generally rare and poorly diversified (Fujita & Ohta 1989). A gregarious mode of life, with very high densities of individuals and low-diversity-associated faunas are features, which are not only observed in modern and fossil ophiuroid assemblages (see Petr 1989; Mikuláš *et al.* 1995) but seem to be a conservative characteristics of most echinoderm dense populations as far back as the early Palaeozoic (Lefebvre 2006). Such a gregarious mode of life can be highly advantageous not only for reproductive success (Lawrence 1987; Emson 1998), but also for a greater efficiency of filter feeding: in large aggregations of modern ophiuroids the presence of numerous arms facing the current locally slows down the current flow, and thus increases the deposition of food particles into the feeding structures (Warner 1971; Fujita 1992). A gregarious mode of life may also provide a better resistance against both high current flows (Warner 1971; Broom 1975) and predation ('principle of strength in numbers': Warner 1971; Fujita & Ohta 1989; Fujita 1992; Aronson & Blake 1997).

Several studies based on modern and fossil ophiuroids have indicated that the presence and spatial extension of brittlestar beds were both strongly inversely correlated with the abundance of putative predators (e.g. sea-stars, teleost fishes: Aronson 1992; Fujita 1992; Aronson & Blake 1997). More generally, the distribution of dense populations of both fossil and modern sessile, suspension-feeding, epibenthic echinoderms (e.g. crinoids, ophiuroids) appears to be strongly influenced by the intensity of predation pressure (Bottjer & Jablonski 1988; Fujita 1992; Aronson & Blake 1997; Meyer 1997). This important interpretation suggests that, in the Palaeozoic, dense assemblages of stylophorans and/or other free-living epibenthic suspension-feeding echinoderms (e.g. cinctans, ophiuroids, solutes) were probably also restricted to palaeo-environments where predators were rare and even absent (Lefebvre 2006). However, observation of modern and fossil brittlestar beds indicate that in such echinoderm meadows not only predators are rare, but the whole associated fauna is also scarce and poorly diversified. Consequently, the comparison with modern

brittlestar beds demonstrates that the low diversity observed in most dense assemblages of ophiuroids and stylophorans (e.g. in the Middle Ordovician of Gourin or Traveusot, or in the Upper Ordovician of Bohemia: see Petr 1989; Mikulas *et al.* 1995) probably does not result from a preservational bias, but corresponds to a general feature of most gregarious echinoderm faunas (Lefebvre 2006).

Echinoderm meadows represent major bioaccumulations and are in urgent need of further consideration. Such bioaccumulations are not only important in tropical waters, but in modern Arctic waters as well. This study shows that such gregarious occurrences of echinoderms are not uncommon in the fossil record.

Conclusions

- In the Llandeilian Guernanic unit (Upper Member of the Schistes de Postolonnec Formation) of Gourin (Brittany), sedimentological, taphonomic (e.g. bivalves preserved with their valves in connection) and palaeontological evidence (e.g. composition of trilobite assemblages) all suggest that deposition was at or below storm wave base.
- In Gourin, the fossils are largely complete and some of them in life position (e.g. mitrates with extended aulacophore), suggesting rapid sedimentation.
- An application of experimental taphonomy on ophiuroids has allowed the greater understanding of the origin of bioaccumulations and whether they are allochthonous (e.g. Girvan) or autochthonous (e.g. Gourin). Thus, establishing that the ophiuroids like the mitrates were preserved quickly after death
- Large echinoderm bioaccumulations are recorded early in the fossil record and could have been at least as extensive as those observed in modern temperate and Arctic waters.
- It is becoming increasingly apparent that stylophorans occurred in association with ophiuroids, and that the Gourin assemblage represents the oldest indisputable evidence of such an association.

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Appendix: Systematic palaeontology

Class OPHIUROIDEA Gray, 1840
(see Simms *et al.* 1993)

Order OEGOPHIUROIDEA Matsumoto, 1915

Suborder LYSOPHIURINA Gregory, 1897

Family PROTASTERIDAE S. A. Miller, 1889
(Diagnosis of family modified by Petr 1989)

Genus TAENIASTER Billings, 1858

Type species, Palaeocoma spinosa Billings, 1857

Diagnosis. Modified from Hammann & Schmincke (1986) and Petr (1989): interrarial outline of the disc straight or concave (but may be convex). Oral and aboral faces of the disc with small scales of uncertain outline covered with granulated integument. Oral face covered with spines. Probably no true marginalia present. Disc margins often thickened on aboral faces (possible post-mortem folding of the skin after death). Mouth angle plates short, with oral side covered with large papillae. Ambulacrals with typical boot-shaped ridge on the oral side of arms. Median suture between alternate ambulacrals straight, with sinuous appearance between neighbouring boot-shaped ridges. Excavations for the dorsal longitudinal muscles not very broad. Aboral outline of ambulacrals trapezoidal to quadrate. Laterals ear-shaped, with vertical and groove spines.

Remarks. *Taeniaster* is considered a valid genus in this study despite being placed by Shackleton (2005) within the genus *Protaster* along with *Bohemura*. Despite good arguments by Shackleton (2005) we consider that *Taeniaster* has too many distinct characters to be included within a single *Protaster* genus. The oral sides of arms possess a straight median suture between the alternate ambulacrals. Straight median suture is unique among the protasterid ophiuroids. A post-mortem condition allows the tips of the arms to appear whip-like. However, following Petr (1989), this character is considered here as an unreliable character, and not

included in the diagnosis above. Although Hammann & Schmincke (1986) noted that the area where the open ambulacral groove grades into the closed part does not vary within one species, Kesling & Le Vasseur (1971; see Petr 1989) showed considerable variation. The area where the open ambulacral groove grades into the closed part was considered to be very stable at species level by Hammann & Schmincke (1986), but highly variable in position by Kesling & Le Vasseur (1971). The degree of closure of the ambulacrum possibly represents a post-mortem feature; this is also true in *Taeniaster* lacking a whip-like tail, as this is simply not preserved in most specimens (Petr 1989).

Taeniaster armoricanus sp. nov.

Figs 2a–d & 3a, c.

Derivation of name. Both, the holotype and paratype are from the Department of Morbihan, in the ancient Gallo-Roman territory of Armorica (modern Brittany).

Holotype. Specimen MHNN.P.025954b.

Paratype. Specimen MHNN.P.025955.

Material. Six specimens preserved on four slabs, housed in the Muséum d'Histoire Naturelle de Nantes.

Diagnosis. Medium-sized pentagonal-round disc. Shortened arms with small short straight ambulacra with square boots. Very large spaces between the ambulacra and laterals, weakly lobed bowed reduced laterals that tend to be larger than the ambulacra.

Description. The disc small and lightly pentagonal curved edges (Fig. 2a, MHNN.P.025955), these edges range from straight to very round in some specimens making the disc appear almost circular (Fig. 2b, MHNN.P.025954b). Only aboral surface is observed in the specimens, the thickening of the disc is observed in one specimen (Fig. 2d, MHNN.P.025956). Like many specimens of ophiuroids it is difficult to see the detail of the integument covering the aboral sides of the disc, although the remains of the papillae can be seen. The arms are well preserved. In most specimens the arms taper evenly (Fig. 2a, MHNN.P.025955), but there is no evidence of whip-like terminal section on any of the arms. From five to seven pairs of the ambulacral ossicles are incorporated into the disc (Fig. 2b, MHNN.P.025954b). About 16–17 pairs are present in the free arm; no ambulacra in the arm tips are recorded (Fig. 2a, MHNN.P.025955). Ambulacral plates of the left and right of the arm alternate and the median suture (also known as the median groove) is straight and narrow. The ambulacra are boot-shaped in morphology (Fig. 2c, MHNN.P.025954a). In the boot, the toe or foot is thinner and shorter and not bluntly developed compared to the leg section making the foot portion to appear larger in most specimens.

Laterals are curved and are thinner and slightly reduced in size compared with the ambulacra. Ambulacra are not ear-shaped (i.e. depressed down) with clear space in between the lateral plates and those of the ambulacra (Fig. 2b, MHNN.P.025954b).

Remarks. Like in many early ophiuroid species, the differences seen are very slight but significant to diagnose a new species (without having to infer significant geographical separation as a proxy for new species diagnosis). Having a smaller and more rounded disk with shorter arms, this species has more in common with *Taeniaster ibericus* with reduced and more rounded disk and reduced laterals or adambulacra. However, *T. armoricanus* is separated by the further reduction of laterals and a more pentagonal disk than that observed in *Taeniaster ibericus*. The laterals are not ear-shaped as seen in *Taeniaster bohemicus* specimens, where laterals are larger than ambulacra, while the short arms seems to be a unique feature of *T. armoricanus*.

Occurrence. Upper Member, Postolonnec Formation (Llandeilian), Guernanic quarry, Gourin, Morbihan, Brittany, France.

Class STYLOPHORA Gill & Caster, 1960

Order MITRATA Jaekel, 1918

Suborder MITROCYSTITIDA Caster, 1952

Genus MITROCYSTELLA Jaekel, 1901

Type species, Anomalocystites incipiens Barrande, 1887

Remarks. Two species were assigned to the genus *Mitrocystella* by Jaekel (1901, 1918): *M. incipiens* (type species) and *M. barrandei*. In his cladistic analysis of mitrocystitid mitrates, Lefebvre (2000b) placed *M. barrandei* (with 13 marginals, Z, and two infracentrals) in a distinct genus (*Promitrocystites*), so as to avoid the paraphyly of the genus *Mitrocystella* (defined by the possession of 12 marginals, Z, and two infracentrals).

In his original description of '*Anomalocystites incipiens*', Barrande (1887) illustrated eight specimens from the Šárka and Dobrovítva formations (Middle Ordovician) of Bohemia, but no type was implicitly designated. In his revision of mitrocystitid mitrates, Chauvel (1941) re-examined Barrande's original material of *Mitrocystella incipiens* and chose one specimen as lectotype (NMP.L9292; illustrated in Barrande 1887, pl. 5, fig. 1.3–4). Chauvel (1941, p. 174) also pointed out that two of the specimens figured by Barrande (1887) do not correspond to *Mitrocystella incipiens*. Re-examination of the original material of Barrande by one of the authors (B. Lefebvre) confirms that the two specimens NMP.L9297 (Barrande 1887, pl. 5 fig. 1.5–6) and NMP.L9300 (Barrande 1887, pl. 5 fig. 1.15–16) should be assigned to *Mitrocystites mitra*, and not to *Mitrocystella incipiens*. Moreover, the re-examination of Barrande's original material also shows that the morphology of the lectotype of *Mitrocystella incipiens* differs from that of all other specimens assigned to this species, and reported so far from Bohemia, Brittany, Portugal and Spain: four plates (instead of three) are present in central position on the lower thecal surface of NMP.L9292 (two posterior infracentral platelets, instead of one, are located between Z, PP1, PP2 and M'5). Although relatively rare, irregularities in plating sometimes occur in mitrocystitid mitrates (Lefebvre

2003b). Consequently, the specimen chosen as lectotype of *M. incipiens* by Chauvel (1941) more probably corresponds to an abnormal (teratological) individual, rather than to a different species.

Mitrocystella incipiens (Barrande, 1887)

Figs 2e–g & 3b

Material. Nine specimens preserved on five slabs are deposited in the collections of the Muséum d'Histoire Naturelle de Nantes (MHNN.P.025957–61). Additional material, present in private collections, was also examined.

Description. Measurements made on the theca of complete specimens follow the definitions proposed by Chauvel (1941, p. 156). Thecal length (*L*) is comprised between about 21 and 27 mm (*L* is estimated between the M1–M'1 suture, at the aulacophore insertion, and the posterior edge of PP2). Thecal width (*I*) is comprised between about 15.7 and 19 mm (*I* corresponds to the largest width measured perpendicularly to *L*). The ratio *I/L* is between 0.70 and 0.77. In some individuals, the theca is relatively elongate and narrow (*I/L* < 0.75), with gently curved lateral margins, a straight to slightly concave posterior edge, and asymmetric outlines (e.g. MHNN.P.025960 and MHNN.P.025961). Thecal asymmetry is due to: (1) the forward extension of the right anterior lobe (right of the aulacophore insertion), clearly longer and more prominent than the left one; and (2) the course of the left thecal side, straighter than that of the right one. In other specimens, the theca is apparently less elongate and larger (*I/L* > 0.75), with more parallel-sided lateral margins, less asymmetric outlines (left and right anterior lobes of comparable extension), and a gently curved, rounded posterior extremity (e.g. MHNN.P.025957 and MHNN.P.025959).

Specimens from Gourin can be grouped into three categories based on their preservation: (1) individuals with partly disarticulated lower thecal surface, no upper surface elements (adorals, supracentrals) and no aulacophore (e.g. MHNN.P.025957); (2) specimens with fully articulated lower thecal surface, partly preserved upper surface (adorals and a few supracentrals) and no aulacophore (e.g. MHNN.P.025959 and MHNN.P.025961); and (3) individuals with well-preserved lower and upper thecal surfaces, and complete, articulated aulacophore in extended position (e.g. MHNN.P.025958 and MHNN.P.025960). Although they are flattened and pyritized, most specimens are relatively well preserved, and most external and internal features generally documented in three-dimensional individuals preserved in silicic-aluminous concretions can be observed.

Two large adorals of comparable shape and dimensions form the anterior edge of the upper surface. The external surface of each adoral bears, anteriorly, a strong anterior transverse crest, and posteriorly to this crest, numerous (about 12–15), sinuous, transverse cuesta-shaped ribs (e.g. MHNN.P.025960 and

MHNN.P.025961). The hydropore (cross-shaped slit anterior to the adoral crest) and the internal surface of adorals have not been observed. Posteriorly to the pair of adorals, the upper thecal surface is paved by numerous (more than 70), slightly imbricated, unorganized supracentral platelets (e.g. MHNN.P.025960). The size of supracentrals regularly decreases in a posterior direction. Several (at least 12), elongate and narrow anal plates are preserved in some specimens (e.g. MHNN.P.025958 and MHNN.P.025960).

The lower thecal surface is composed by 12 large plates in marginal position (M1, M2, M3, M4, G and PP1 on the right; M'1, M'2, M'3, M'4 and M'5 on the left; PP2 in terminal position), and three elements in central position (the zygial plate Z, and two left infracentrals). No orifices are present on the lower thecal surface (e.g. lateripores, paripores). Several features of the internal (upper) side of the lower thecal surface can be observed in the Gourin specimens: (1) on M1 and M'1, a deep, well-marked furrow located on the posterior wall of the two aulacophore apophyses: the transverse anterior groove (e.g. MHNN.P.025957 and MHNN.P.025958); (2) on M'1 and Z, a strong oblique ridge, asymmetrical in cross-section (right flank steeper than the left one): the zygial crest or septum (e.g. MHNN.P.025957 and MHNN.P.025959); (3) on M'1, a small circular depressed area located above the contact between the left apophysis and the zygial crest: the left scutula (e.g. MHNN.P.025957 and MHNN.P.025958); (4) on M'1, a short vertical ridge located left of the zygial crest and connected to the left scutula: the accessory septum (e.g. MHNN.P.025958); and (5) on M'5 and PP1, traces of insertion for rectal muscles (e.g. MHNN.025958 and MHNN.P.025959).

Morphology of the aulacophore insertion is apparently variable within Gourin specimens: relatively deep and narrow (e.g. MHNN.P.025958), or shallower and more widely open (e.g. MHNN.P.025957). In best-preserved specimens, at least seven–eight imbricated rings have been observed in the proximal portion of the aulacophore (e.g. MHNN.P.025958 and MHNN.P.025960). Each proximal ring is made of four plates (two inferolaterals and two tectals). The lower surface of the stylocone bears two strong, laterally compressed spines, connected by a sharp, longitudinal ridge (e.g. MHNN.P.025960). Ornamentation rapidly decreases in height and strength on the lower surface of more distal brachials (ossicles). In some specimens, ajar cover plates are preserved articulated to underlying ossicles (e.g. MHNN.P.025958).

Remarks. The morphology of all mitrocystitid mitrates collected in Gourin is identical to that of specimens of *Mitrocystella incipiens* reported from elsewhere in Bohemia, Brittany, Portugal and Spain, and thus totally supports their assignment to this species.

Chauvel (1937, 1941, 1981) placed all specimens of *M. incipiens* from Brittany in a different subspecies (*M. incipiens miloni*) from those from Bohemia (*M. incipiens*

incipiens). This distinction is mostly based on: (1) the aspect of thecal outlines (in *M. incipiens incipiens*, lateral margins are parallel-sided, rather than curved, and the posterior thecal edge is not straight, but rounded); (2) the morphology of the aulacophore insertion (large and widely open in *M. incipiens incipiens*, narrower and deeper in *M. incipiens miloni*); and (3) the asymmetry of the two anterior lobes (right anterior lobe more developed in *M. incipiens miloni*). For the same reasons, all specimens collected in Portugal and Spain were also assigned to *M. incipiens miloni* (e.g. Gutiérrez-Marco & Meléndez 1987). Re-examination of the six Bohemian specimens of *M. incipiens* illustrated by Barrande (1887) confirms that their morphology appears slightly different from that of most specimens collected in Brittany, Portugal and Spain. However, it should be pointed out that: (1) the mean size of Barrande's specimens is smaller than that of most individuals sampled in Brittany, Spain; and Portugal; and (2) the morphology of small Breton specimens is closely comparable to that of Bohemian forms. It is thus possible that the differences pointed out by Chauvel (1941) more probably reflect growth allometries, rather than actual regional differences between Bohemian forms on one side, and Ibero-Armorican forms on the other side. The slight morphological differences observed within the specimens collected in Gourin seems to support this interpretation.

Occurrence. Upper Member, Postolonnec Formation (Llandeilian), Guernanic quarry, Gourin (Morbihan), Brittany (France); Traveusot Formation (Llandeilian), Bain-de-Bretagne, Guichen, Guignen and Langon (Ille-et-Vilaine), Brittany (France); Valongo Formation (Llandeilian), San Pedro de Cova (Portugal); Guindo Shales (Llandeilian), Almaden-Campos de Calatrava, Almodovar del Campo and Calzada de Calatrava, Ciudad Real (Spain); Sarka Formation (Abereiddian), Praha-Sarka and Rokycany (Osek), Bohemia (Czech Republic); Dobrotiva Formation (Llandeilian), Malé Přílepy and Svata Dobrotiva (= 'Sancta Benigna' in Barrande 1887), Bohemia (Czech Republic).

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