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A reinterpretation of the solutan *Plasiacystis mobilis* (Echinodermata) from the Middle Ordovician of Bohemia*

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Abstract

Reexamination of the type material of the solutan *Plasiacystis mobilis* from the Šárka Formation (Darriwilian) of Bohemia (Czech Republic) shows that its original reconstruction is a composite, with a mixture of elements belonging to two different solutans, a rhenopyrgid edrioasteroid, and a mitrate stylophoran. The "beaver-tailed" solutan *P. mobilis* is redescribed, and probable affinities with both *Castericystis* and minervaecystids are suggested. A second solutan is also described, but left in open nomenclature (solutan indet., gen. et sp. nov.). Possible biological and ecological implications of the presence of an isorophid edrioasteroid (?*Agelacrinites bohemicus)* attached to the theca of this new solutan are discussed. Other fossil remains formerly assigned to *P. mobilis* are also described (rhenopyrgid indet. and *Mitrocystites mitra*). The name "homoiostele" is proposed for the stem-like appendage of solutans. Soluta is reaffirmed as a valid class name (instead of Homoiostelea).

Key words: Echinodermata, Soluta, reinterpretation, Palaeozoic, Ordovician, Czech Republic

Introduction

Solutans are a small clade of Palaeozoic echinoderms (Middle Cambrian-Lower Devonian). Their body consists in three distinct regions (Fig. 1): (1) a single anterior feeding appendage, interpreted either as an arm (*e.g.*, Caster 1968; Ubaghs & Robison 1985; Daley 1995; Smith 2005) or as a brachiole (*e.g.*, Bather 1913; Gill & Caster 1960; David *et al.* 2000; Parsley & Sumrall 2007); (2) a large, polyplated theca, which in life enclosed most internal organs; and (3) a posterior stem-like appendage. In the oldest and most plesiomorphic solutan (*Coleicarpus sprinklei* Ubaghs & Robison, 1988), this posterior appendage is an undifferentiated, polyplated stalk, used for permanent attachment (Daley 1996). It is similar in morphology to the stalk of basal eocrinoids (*e.g.*, *Gogia kitchnerensis* Sprinkle, 1973; Parsley 1997). In more derived solutans, the posterior appendage was probably used for locomotion (*e.g.*, Caster 1968; Ubaghs 1970; Kolata *et al.* 1977; Daley 1992), and its morphology is different, with two well-defined regions: (1) a highly flexible proximal part, made of imbricate ele-

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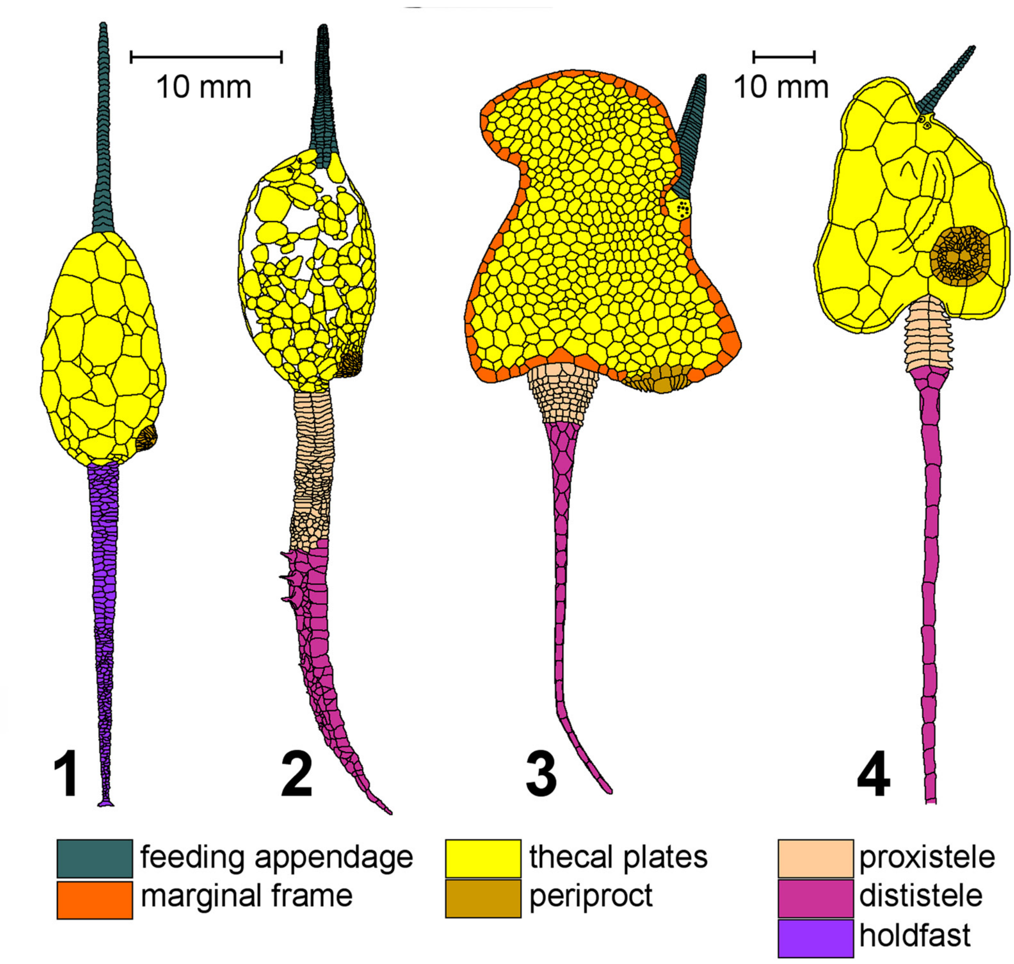

FIGURE 1. Solutan morphology. 1: *Coleicarpus sprinklei* (Middle Cambrian, Utah); modified from Daley (1996). 2: *Castericystis vali* (Middle Cambrian, Utah); modified from Daley (1995). 3: *Maennilia estonica* (Upper Ordovician, Estonia); modified from Rozhnov & Jefferies (1996). 4: *Girvanicystis batheri* (Upper Ordovician, Scotland); modified from Daley (1992).

ments (proxistele); and (2) a rigid, distal portion, made of tightly sutured skeletal elements (dististele). The posterior appendage of derived solutans is generally called a "stele" in the literature (*e.g.*, Jaekel 1918; Caster 1968; Ubaghs & Robison 1985; David *et al.* 2000; Smith 2005). The name "homoiostele" is proposed here, so as to avoid any confusion with other, non-homologous posterior appendages bearing the same name (*e.g.*, the "stele" of cinctans). The mouth was intrathecal, and located at the proximal extremity of the single food groove (Daley 1996; David *et al.* 2000; Smith 2005). Two small body openings occur frequently close to the insertion of the feeding appendage [*e.g.*, *Castericystis vali* Ubaghs & Robison, 1985, *Minervaecystis vidali* (Thoral, 1935)]. They are universally interpreted as the gonopore and hydropore (*e.g.*, Caster 1968; Ubaghs 1970; Jefferies 1990; Daley 1995; Smith 2005). In solutans, the periproct is particularly obvious. It is generally located in a marginal position, at the summit of a large periproctal lobe, close to the insertion of the homoiostele (*e.g.*, *Dendrocystites sedgwicki* Barrande, 1887). However, in few taxa (*e.g.*, *Girvanicystis batheri* Caster, 1968), the periproct is more "cystoid-like" (large and rounded), and it occurs in a more central position on the theca (Caster 1968; Daley 1992).

In its original description, *Plasiacystis mobilis* Prokop & Petr, 2003 was reconstructed (Prokop & Petr 2003: Text-fig. 2), based on about 50 specimens from the Middle Ordovician Šárka and Dobrotivá Formations of Bohemia (Czech Republic), and 18 specimens from the Middle Ordovician of

Spain (synclinal del Valle, Ossa Morena Zone). The Czech material was previously assigned to three different taxa: (1) large portions of the theca were misidentified as the caryocystitid rhombiferan *Echinosphaerites infaustus* Barrande, 1887 (Barrande 1887: Pl. 25, Fig. 15); (2) isolated proxisteles were considered as probable machaeridians by Prantl (*in litt*., 1947; see Prokop & Petr 2003); and (3) isolatedististeles were interpreted as distal aulacophore extremities belonging to the mitrate *Promitrocystites barrandei* (Jaekel, 1918) (Jaekel 1918: Fig. 110; but see Chauvel 1941: 163). Prokop & Petr (2003) argued that all these specimens were indeed parts of a same echinoderm, *Plasiacystis mobilis*, that they tentatively assigned to solutans. However, as pointed out by Prokop & Petr (2003), their reconstructed morphology of *Plasiacystis mobilis* (Fig. 2) strongly departs from the classical "Bauplan" of solutans in several aspects: (1) no evidence supporting the presence of the feeding appendage; (2) rounded morphology and central location of the periproct; (3) proxistele longer than the dististele; and finally (4) "beaver-tail" aspect of the dististele.

In the 2000s, abundant, exquisitely preserved specimens of "beaver-tailed" *Plasiacystis*-like solutans were collected in the Lower Ordovician of central Anti-Atlas, Morocco (mentioned as "*Minervaecystis*" in Lefebvre & Fatka 2003: 88). Although very similar to the (younger) Czech specimens, the Moroccan fossils departed in several aspects from the original reconstruction of *Plasiacystis mobilis* (*e.g.*, feeding appendage present, different morphology and location of the periproct, smaller relative length of the proxistele; Lefebvre & Roch 2009). Moreover, reexamination of the echinoderm material from the Middle Ordovician of the Ossa Morena Zone (Spain) showed that the Spanish specimens identified as isolated proxisteles of *Plasiacystis mobilis* by Prokop & Petr (2003) more likely corresponded to turret-like rhenopyrgid edrioasteroids (Lefebvre & Gutiérrez-Marco 2007). These observations made on both the Moroccan *Plasiacystis*-like solutans and the Ossa Morena material prompted a reexamination of the original type series of *Plasiacystis mobilis*, deposited in the collections of the National Museum, Prague. Additional material was also examined in the Czech Geological Survey (Prague), as well as fossils in several private collections in the Czech Republic.

The aims of this study are: (1) to redescribe the material of the original type-series of *Plasiacystis mobilis*; (2) to show that the reconstruction proposed by Prokop & Petr (2003) is composite, with a mixture of elements belonging to different echinoderms; and (3) to briefly discuss the affinities and mode of life of the two Czech solutans.

Study Area

All studied specimens occur in siliceous concretions collected in the dark shales of the Šárka and Dobrotivá Formations (Darriwilian to basal-most Sandbian; Bohemia, Czech Republic). In Middle Ordovician times, the Prague Basin was a narrow and deep trough (probably of rift origin) located at relatively high latitudes, in the vicinity of the Gondwanan palaeocontinent (Havlíček 1989; Havlíček & Fatka 1992; Storch *et al.* 1993; Lefebvre & Fatka 2003). The siliceous concretions of the Šárka and Dobrotivá Formations have yielded a rich and diverse benthic fauna (*e.g.*, asterozoans, bivalves, brachiopods, diploporans, gastropods, hyolithids, ostracods, stylophorans, trilobites), associated with pelagic elements (*e.g.*, cyclopygid trilobites, graptolites, nautiloids, phyllocarid crustaceans; Havlíček & Vaněk 1966, 1990; Havlíček 1982). Most specimens described here were collected in the western part of the Prague Basin (Osek, Rokycany), which was shallower than the eastern part (Prague, and east of Prague; Havlíček 1982, 1998). Preliminary investigations suggest that faunal communities were different in these two regions (Havlíček & Vaněk 1990; Henry *et al.* 1997). For example, stylophoran assemblages are dominated by mitrocystitids (*e.g.*, *Mitrocystites mitra* Barrande, 1887; *Promitrocystites barrandei*) in the western part of the basin, and by lagynocystids [*Lagynocystis pyramidalis* (Barrande, 1887)] in the eastern part (Lefebvre 2007). Maps showing the main Middle Ordovician localities of the Prague Basin have already been published and will not be reproduced here (see Jefferies & Prokop 1972; Storch *et al.* 1993; Havlíček 1998).

Materials and Methods

All studied specimens occur as exquisitely preserved, three-dimensional hollow moulds in siliceous concretions (dissolution of the original calcite). This mode of preservation (fossiliferous siliceous concretions) is relatively common in Ordovician shales of high latitude (peri)Gondwanan areas (Becq-Giraudon *et al.* 1992; Loi & Dabard 2002; Lefebvre 2007). For example, similar fossiliferous concretions occur in the Lower Ordovician of the Anti-Atlas (Morocco) and Montagne Noire (southern France), the Middle Ordovician of Brittany (western France), and the Upper Ordovician of Sardinia (Italy). As a consequence, latex casts were made, to reproduce the original (positive) aspect of the organisms. Latex casts were then coated with ammonium chloride for both drawing (camera lucida) and photographic purposes.

Abbreviations. All figured specimens are deposited in the following public collections: Czech Geological Survey, Prague, Czech Republic (CGS), Université Lyon 1, Villeurbanne, France (FSL), and National Museum Prague, Czech Republic (NMP).

Systematic Palaeontology

Class Soluta Jaekel, 1901

Remarks. Solutans were first identified as a distinct taxonomic entity (family Dendrocystidae) by Bather (1899), who grouped them along with some diploporans (Aristocystidae), eocrinoids (Eocystidae), and mitrates (Anomalocystidae) within the order Amphoridea (class Cystidea). Jaekel (1899) grouped all asymmetrical pelmatozoan echinoderms within the class Carpoidea (subdivided into the two orders Eustelea and Heterostelea). Within heterostelean carpoids, the suborder Soluta was created by Jaekel (1901) to include the two families Dendrocystidae and Rhipidocystidae. This scheme was criticised by Bather (1913), and modified by Jaekel (1918), who removed eusteleans from the class Carpoidea. Consequently, heterosteleans and carpoids became redundant, synonymous taxonomic entities, and the order Heterostelea was suppressed. Furthermore, all previously defined heterostelean suborders (Cincta, Cornuta, Mitrata, and Soluta) were erected to ordinal level within the class Carpoidea. Hecker (1940) removed rhipidocystids from the order Soluta, and assigned them to a distinct order (Digitata) within carpoids. The classification of the class Carpoidea was strongly revised by Gill & Caster (1960), who subdivided it into the two subclasses Homostelea (orders Cincta and Digitata), and Homoiostelea (superorders Astylophora and Stylophora). The superorder Astylophora contained the single order Soluta, whereas the superorder Stylophora included the two orders Cornuta and

Mitrata. This general scheme was further modified in the "*Treatise on Invertebrate Paleontology*" (Caster 1968; Ubaghs 1968a, 1968b, 1968c, 1968d). Rhipidocystids (Digitata) were removed from the homosteleans and placed within the eocrinoids (Ubaghs 1968b). Stylophorans were removed from the homoiosteleans, and elevated to class level (Ubaghs 1968c). The two subclasses Homostelea (containing the single order Cincta; Ubaghs 1968d) and Homoiostelea (containing the single order Soluta; Caster 1968) were also both elevated to class level. The three classes of "carpoids" (Homoiostelea, Homostelea, and Stylophora) were placed, along with the class Machaeridia, within the subphylum Homalozoa (Ubaghs 1968a). This general scheme was adopted in a large number of subsequent contributions (*e.g.*, Ubaghs 1970, 1975; Kolata *et al.* 1977; Sprinkle 1992; Parsley 1997; David *et al.* 2000). However, as pointed out by Caster (1983: 324), Daley (1992: 360), and Friedrich (1993: 44), Homostelea and Homoiostelea are redundant, junior synonyms of Cincta and Soluta, respectively. In recent contributions, Cincta is now widely used as the valid class name (*e.g.*, Friedrich 1993, 1995; Sdzuy 1993; Gil Cid & Dominguez Alonso 1995a, 1995b; Zamora *et al.* 2007; Zamora & Rahman 2008; Smith & Zamora 2009). In contrast, the majority of recent contributions dealing with solutans place them within the class Homoiostelea (*e.g.*, Ubaghs & Robison 1985, 1988; Parsley 1997; Sumrall *et al.* 1997; David *et al.* 2000; Prokop & Petr 2003; Parsley & Sumrall 2007). Similarly, as the term Heterostelea was suppressed by Jaekel (1918), it is stressed here that Homoiostelea, a redundant, junior synonym of Soluta, should be definitively abandoned for taxonomic purposes, and the order Soluta elevated to class level. Furthermore, consistency with other echinoderm groups (*e.g.*, cinctan, rhombiferan, stylophoran) suggests that "solutan" (rather than "solute") should be used for informal designation of members of the class Soluta.

Family Plasiacystidae Prokop & Petr, 2003

Emended diagnosis. Solutans with relatively inflated, ovoid theca, without lobation. Thecal plates thin, polygonal, tessellated, and irregular in both shape and size. Feeding appendage emerging abruptly on lateral edge of theca, relatively far away from apex. Small, cone-shaped, anal pyramid on opposite, lateral edge of theca, close to homoiostele insertion. Proxistele and dististele of comparable lengths. Proxistele highly flexible, cylindrical, composed of numerous, unorganised, imbricate scale-like elements. Dististele composed of two series of large, opposite plates forming a short, rigid, flattened paddle with a rounded distal extremity. At least one spine present on distal paddle.

Remarks. The original diagnosis for the family Plasiacystidae is emended here, to conform with new observations made during the reexamination of the type material (see below). As interpreted here, the morphology of plasiacystids shows several similarities with both *Castericystis vali* and minervaecystids. In all recent phylogenetic analyses, *Castericystis* and minervaecystids occupy a basal position within solutans (Parsley 1997; Parsley & Sumrall 2007). Plasiacystids share with these taxa the possession of (1) a relatively inflated, ovoid theca without lobation; (2) a similar-looking small, cone-shaped anal pyramid; and (3) a relatively large, flattened, spine-bearing, biserial dististele. Additional similarities with *Castericystis vali* include comparable relative proportions of the two regions of the homoiostele, and the possession of an inflated proxistele with a scale-like plating (see Ubaghs & Robison 1985; Daley 1995). However, plasiacystids differ from *Castericystis vali* in both the location of the feeding appendage insertion (almost apical in *C. vali*), and in the morphology of their dististele (more elongate and distally tapering in *C. vali*). The morphology and location of the feeding appendage are both very similar in plasiacystids and minervaecystids (see Caster 1968;

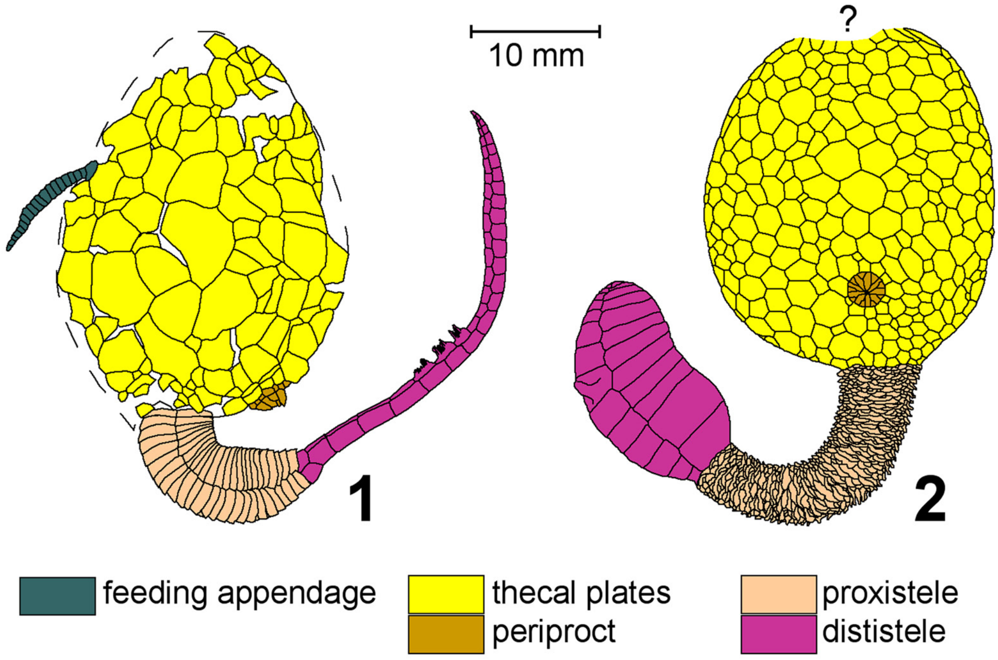

FIGURE 2. Solutan morphology. 1: *Minervaecystis vidali* (Lower Ordovician, Montagne Noire); modified from Ubaghs (1970). 2: Prokop & Petr's original reconstruction of *Plasiacystis mobilis* (Middle Ordovician, Bohemia); modified from Prokop & Petr (2003).

Ubaghs 1970). However, plasiacystids differ from minervaecystids in the morphology of both their proxistele (organised into regular telescopic rings, each made of four plates in minervaecystids), and their dististele (longer, narrower, and distally tapering in minervaecystids). As redefined here, plasiacystids appear closely related, though distinct from, both *Castericystis vali* and minervaecystids, and thus, probably occupy a relatively basal position within solutans. The family Plasiacystidae contains the single genus *Plasiacystis*.

Genus *Plasiacystis* Prokop & Petr, 2003

Type species. *Plasiacystis mobilis* Prokop & Petr, 2003 from the Šárka Formation (Darriwilian) of Bohemia (Czech Republic) is the type and only described species of the genus.

Diagnosis. As for family.

Remarks. The genus *Plasiacystis* contains the single species *P. mobilis* from the Darriwilian of Bohemia, Czech Republic. However, yet undescribed *Plasiacystis*-like solutans also occur in the late Tremadocian of Montagne Noire, France (B. Lefebvre, pers. obs.), the Floian of the Anti-Atlas, Morocco (Lefebvre & Fatka 2003; Lefebvre & Roch 2009), and the Darriwilian of Shropshire, UK (K. Derstler, pers. obs.). This additional material suggests a relatively long generic time range extending from the late Tremadocian to the Darriwilian.

Plasiacystis mobilis Prokop & Petr, 2003

Figures 3–5

Mitrocystella barrandei—Jaekel 1918: 121, Figs. 110H, J, K, L [*vidimus*]

Plasiacystis mobilis—Prokop & Petr 2003: 152, Pl. 1: Figs. 1–5, Pl. 3: Figs. 5–6 [*pro parte*; non Text-fig. 3, Pl. 2: Figs. 1–4, Pl. 4: Figs. 1–6 = solutan indet., gen. et sp. nov.; non Pl. 3: Figs. 1–4 = rhenopyrgid indet.]

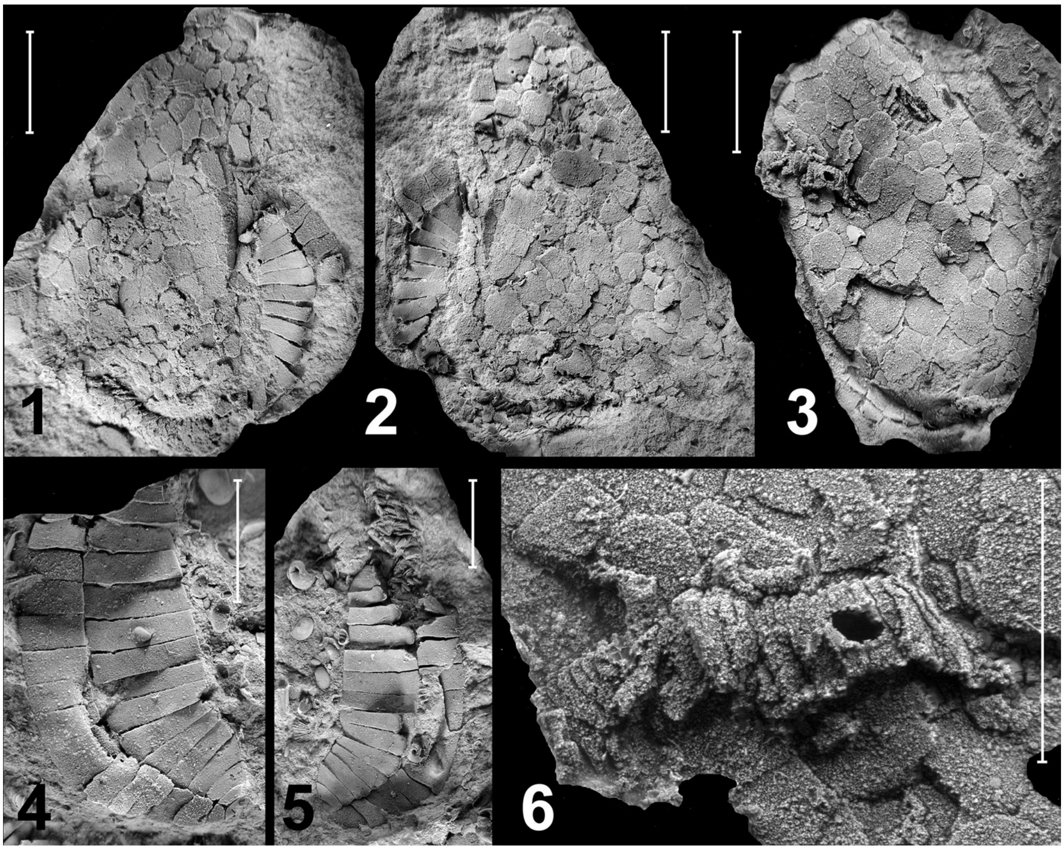

FIGURE 3. *Plasiacystis mobilis*, Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); all latex casts of original specimens. 1–2: NMP.L.13216 (holotype); part and counterpart showing theca and flexed homoiostele; scale bars: 10 mm. 3: NMP.L.29120; theca (with feeding appendage) and flexed homoiostele; scale bar: 10 mm. 4–5: FSL 711614; part and counterpart of isolated dististele; scale bar: 10 mm. 6: NMP.L.29120; brachiole; scale bar: 5 mm.

Material, localities and horizon. Holotype NMP.L.13216, from Osek, near Rokycany (Šárka Formation, Darriwilian). The four other referred specimens are all from the same stratigraphic level (Šárka Formation, Darriwilian), and either from the type-locality (FSL 711614, NMP.L.29116, 29120), or from Pehdomky (NMP.L.29121). FSL 711614 is a cast of an original specimen deposited at Greifswald University (Germany), and identified by Jaekel (1918) as the distal extremity of the appendage of the mitrate *Promitrocystites barrandei*.

Diagnosis. As for family.

Description. Theca ovoid, relatively elongate, more or less elliptical in outline. Thecal margin regularly convex, not delimited by distinct marginal frame (Figs. 3.1–3, 4, 5.3). No clear differentiation into opposite (lower, upper) thecal surfaces. Holotype theca, partly disarticulated, egg-shaped, about 37 mm long, 25.5 mm maximum width (close to homoiostele insertion). In NMP.L.29120, better preserved, more elliptical theca, about 34 mm long, 19 mm maximum width (at about equal distance from both apex and homoiostele insertion). Thecal plates thin, numerous (more than 350 in holotype), non-imbricate, polygonal, smooth (unornamented), flat to slightly convex, variable in shape and dimension. Plating around homoiostele insertion poorly preserved, apparently consisting of relatively small thecal plates. Periproct in marginal position, close to homoiostele insertion (Fig. 4.1). Small, cone-shaped anal pyramid, composed of minute, elongate, triangular skeletal elements. No evidence of hydropore and/or gonopore close to feeding appendage insertion. Feeding arm emerging from theca laterally, at about one third distance to apex, opposite to periproct (Fig. 5.3). In NMP.L.29120, preserved proximal portion of feeding appendage (about 25 segments) about

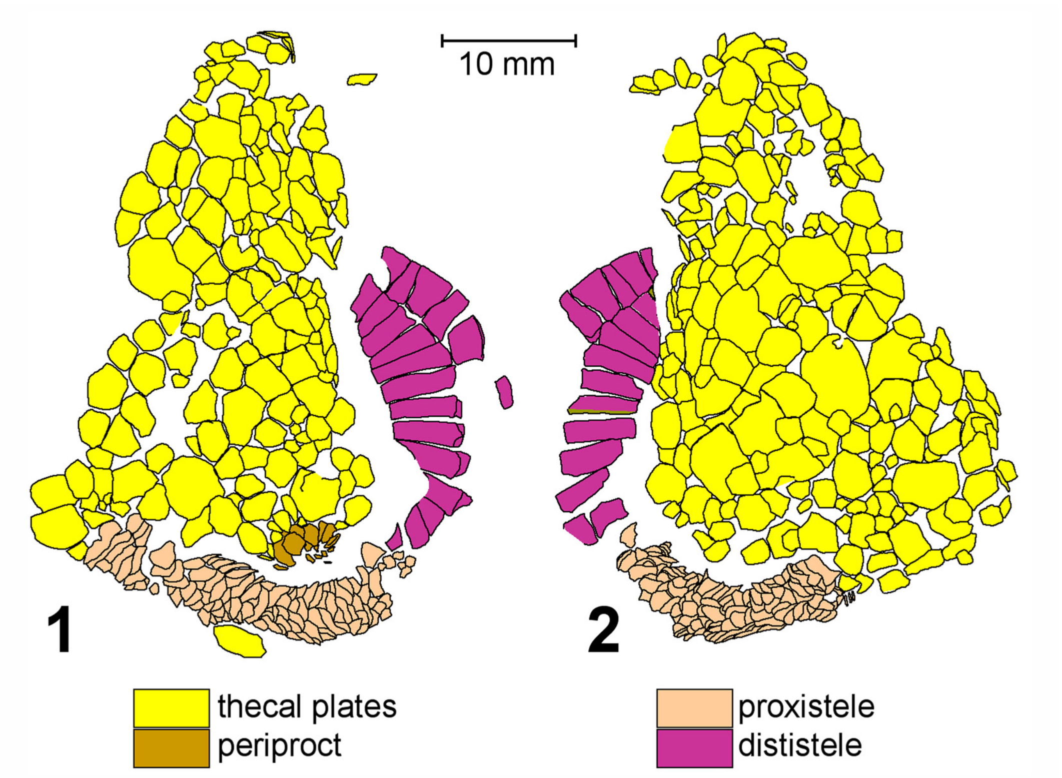

FIGURE 4. *Plasiacystis mobilis*, Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); camera-lucida drawings of latex casts. 1–2: NMP.L.13216 (holotype); part and counterpart showing theca (with periproct) and flexed homoiostele.

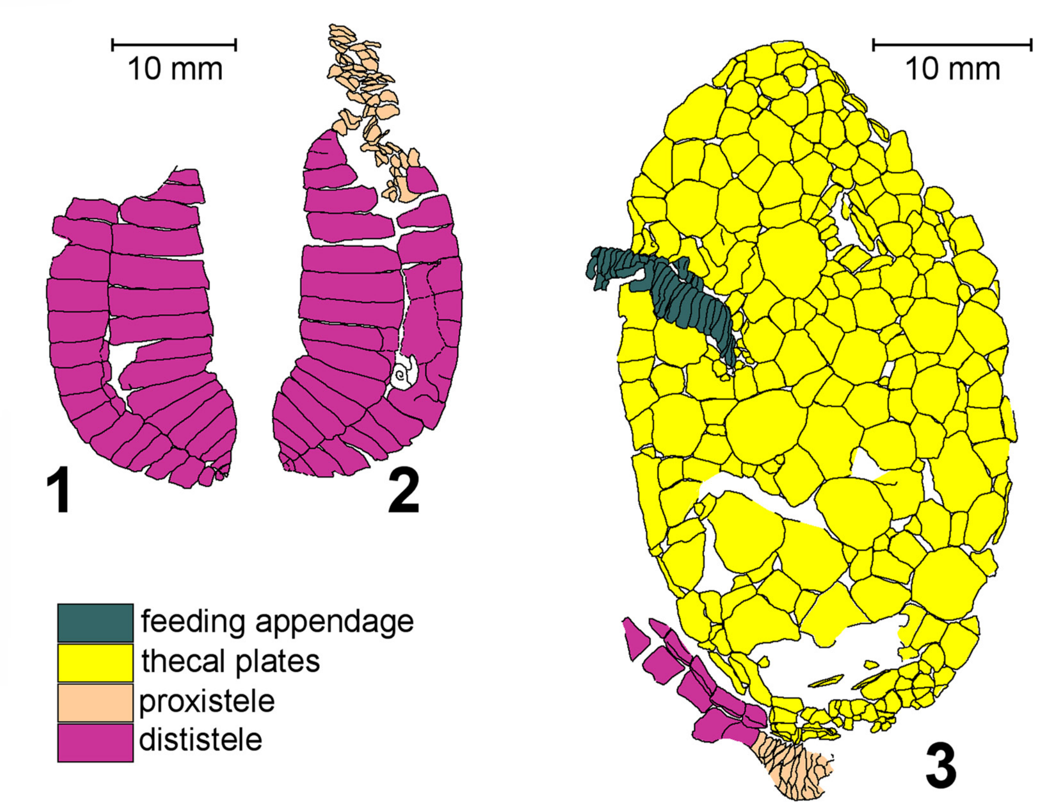

FIGURE 5. *Plasiacystis mobilis*, Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); camera-lucida drawings of latex casts. 1–2: FSL 711614; part and counterpart of isolated dististele (with fragments of proxistele). 3: NMP.L.29120; theca (with feeding appendage) and flexed homoiostele.

9 mm long, 2.5 mm wide (Fig. 3.6). Flooring plates large, overlapping distally. Cover plates smaller, elongate, sub-triangular. Homoiostele as long as theca, inserted opposite to thecal apex (Figs. 3.1–2, 4). Proximal region preserved in flexed position, against theca, in both holotype and NMP.L.29120. Proxistele relatively long, inflated, composed of numerous, imbricate, unorganised, scale-like elements. Proxistele and dististele of comparable lengths. Dististele forming flattened, bean-shaped paddle with gently rounded distal extremity and relatively sharp edges (Figs. 3.4–5, 4.1–2, 5.1–2). Dististele consisting of two series of at least 16 large, opposite skeletal elements enclosing narrow, cylindrical, longitudinal lumen. Skeletal elements of concave side of paddle about twice longer than those of convex side. Enclosed longitudinal lumen and suture between opposite paddle elements both displaced towards convex side of dististele. Thickness of paddle maximum along longitudinal sutures between opposite skeletal elements. At least one strong, laterally compressed spine close to convex margin of distal paddle: one spine in the holotype and FSL 711614, two in specimen illustrated by Jaekel (1918: Fig. 110K), and three in NMP.L.29116 (see Prokop & Petr 2003: Pl. 3: Figs. 5–6).

Remarks. Reexamination of the type series of *Plasiacystis mobilis* in the collections of the National Museum (Prague) indicates that only a small proportion of the original material described by Prokop & Petr (2003) should be assigned to this species: the holotype and three other samples. The large majority of specimens previously identified as *P. mobilis* correspond to another, yet undescribed solutan (see below). The original material of the type-series of *P. mobilis* also includes well-preserved rhenopyrgid edrioasteroids, and a partly disarticulated mitrate stylophoran (see below). Examination of additional collections, both public (*e.g.*, Czech Geological Survey) and private, confirms that *Plasiacystis* is an extremely rare faunal element, apparently restricted to the Šárka Formation. Main differences with the original reconstruction of *Plasiacystis mobilis* proposed by Prokop & Petr (2003: Text-fig. 2) concern: (1) the presence of a feeding appendage; (2) the more ovoid and elongate aspect of the theca; (3) the morphology and location of the periproct; and (4) the relative proportions of the two regions of the homoiostele. As redescribed here, the morphology of *Plasiacystis mobilis* appears less aberrant, and it shows several similarities with other, relatively basal solutans (*e.g.*, *Castericystis vali*, *Minervaecystis vidali*; see above).

Family incertae sedis

solutan indet., gen. et sp. nov.

Figures 6–8

Echinosphaerites infaustus—Barrande 1887: 238, Pl. 25: Fig. 15 [*pro parte*; non Pl. 22: Figs. 1–12, Pl. 23: Figs. 1–26, Pl. 24: Figs. 1–23, Pl. 25: Figs. 1–10, 13–14, 16–21 = *Echinosphaerites infaustus*].

Plasiacystis mobilis—Prokop & Petr: 152, Text-fig. 3, Pl. 2: Figs. 1–4, Pl. 4: Figs. 1–6 [*pro parte*; non Pl. 1: Figs. 1–5, Pl. 3: Figs. 5–6 = *Plasiacystis mobilis*; non Pl. 3: Figs. 1–4 = rhenopyrgid indet.].

Material, localities and horizon. Seventeen specimens from various localities, all from the Šárka Formation (Darriwilian), Prague Basin (Czech Republic): Díly near Rokycany (CGS.PP.570, NMP.L.29134), Kasizek (CGS.PP.569), Litohlavy near Rokycany (CGS.PP.567), Mýto near Rokycany (CGS.PP.565–66, NMP.L.29112, 29115, 37454), Osek near Rokycany (NMP.L.13123, 13215, 29113–14, 29118–19, 29135), and Praha-Šárka (NMP.L.29117). All specimens from the National Museum, Prague belong to the original type-series of *Plasiacystis mobilis*. The five specimens deposited in the Czech Geological Survey (Plas coll.) were originally registered as “Ophiuroidea”.

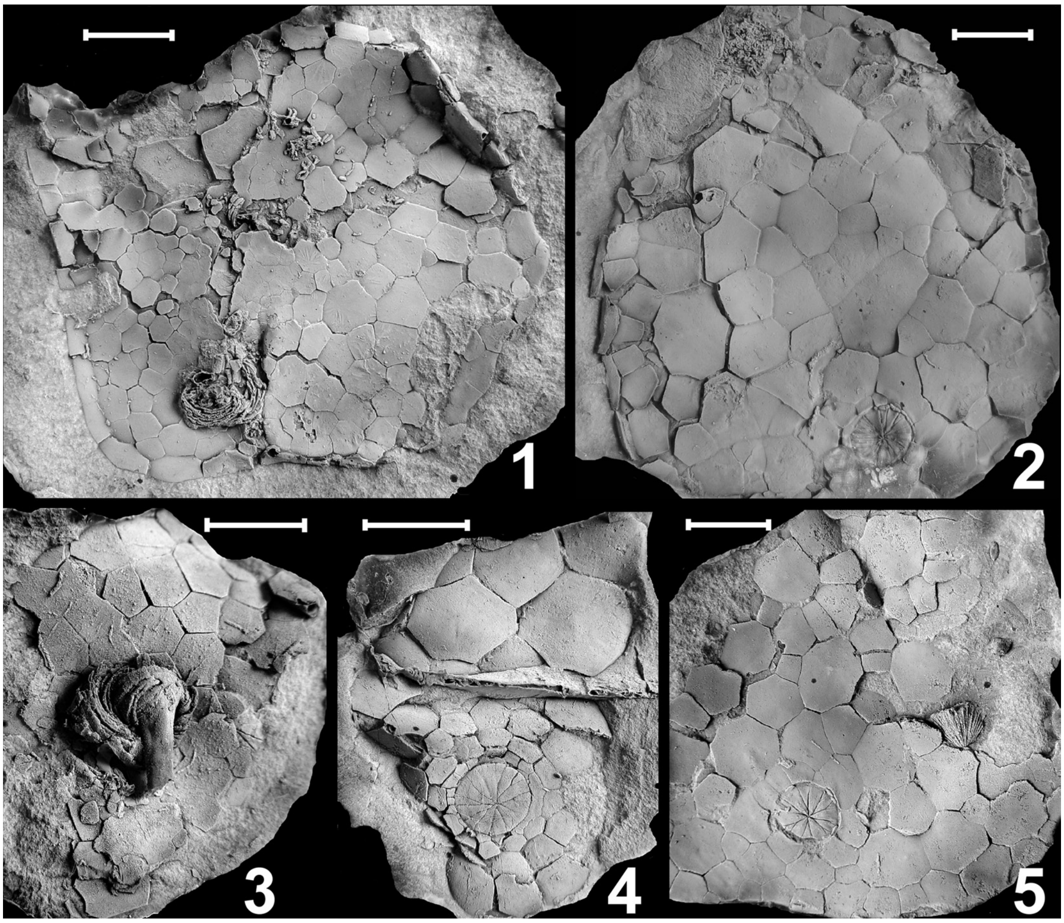

FIGURE 6. Solutan indet., gen. et sp. nov., Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); all latex casts of original specimens; all scale bars: 10 mm. 1: NMP.L.37454; flat (lower) thecal surface with pentalobate marginal frame, homoiostele insertion, and fragments of feeding appendage. 2: NMP.L.29115; convex (upper) thecal surface with marginal frame, periproct, and attached isorophid edrioasteroid. 3: NMP.L.29118: portion of flat (lower) thecal surface with proxistele and proximal region of dististele. 4: NMP.L.29117; periproct. 5: NMP.L.29112: portion of convex (upper) thecal surface with periproct.

Description. Theca about as long as wide, with gently curved outlines forming several lobes (slightly prominent convex outgrowths) separated by slightly concave re-entrants. In the best preserved specimen (NMP.L.37454), theca clearly pentalobate, with five, regularly spaced lobes separated by five re-entrants of comparable lengths (Figs. 6.1, 7.1). Theca relatively flattened, compressed, lens-shaped, with two well-defined opposite surfaces (lower and upper) delimited by distinct, narrow marginal frame composed of relatively stout skeletal elements (marginals). One thecal surface apparently relatively flat, the other one more convex. Thecal diameter varying from 27.5 mm (NMP.L.13215) to 68.5 mm (NMP.L.29115). Both smaller (*e.g.*, NMP.L.29135) and possibly larger (*e.g.*, CGS.PP.565) specimens observed, but not well-preserved enough for measurement. Marginal plates narrow, elongate, thicker than other thecal plates, V-shaped in cross section, with sharp outer margin (Figs. 6.1–3, 7.1–2, 8.1). Other thecal plates thin, non imbricate, polygonal, smooth (unornamented), flat to slightly convex, variable in both shape and size, consistently smaller and more numerous on the flat thecal surface (*e.g.*, more than 200 elements in NMP.L.37454) than on the more convex one (*e.g.*, less than 100 plates in NMP.L.29115). Anal opening on convex thecal surface, away from marginal frame (Figs. 6.4–5, 7.2). Large, rounded, relatively flat anal pyramid composed of elongate, subtriangular plates, surrounded by small polygonal thecal elements (Fig. 8.2; NMP.L.29112, 29115, 29117). Hydropore and gonopore not observed. No complete, articulated feeding appendage

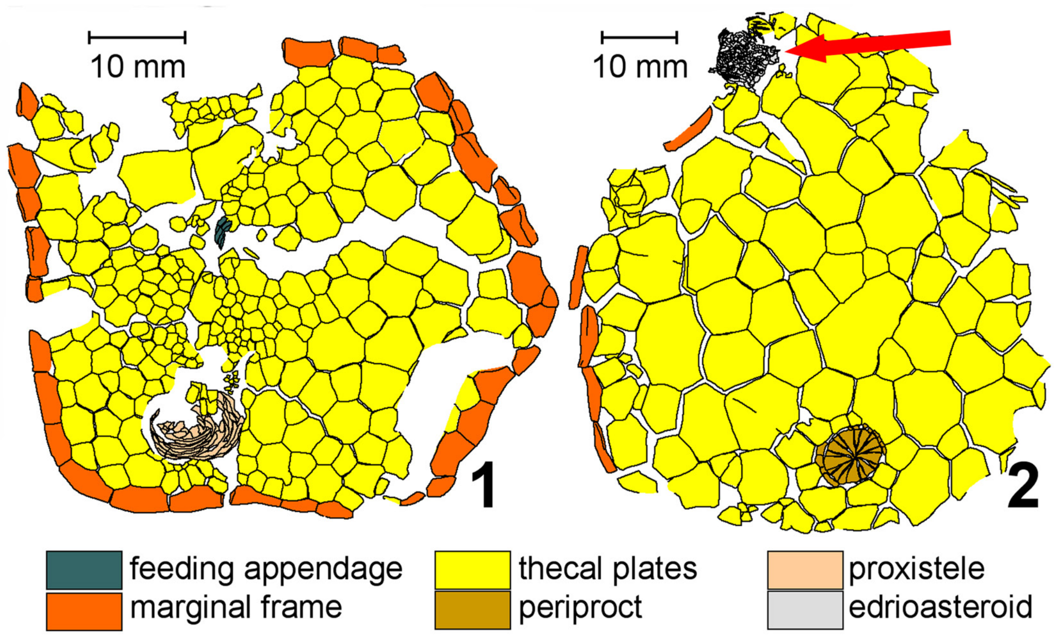

FIGURE 7. Solutan indet., gen. et sp. nov., Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); camera-lucida drawings of latex casts. 1: NMP.L.37454; flat (lower) thecal surface with pentalobate marginal frame, homoiostele insertion, and fragments of feeding appendage. 2: NMP.L.29115; convex (upper) thecal surface with marginal frame, periproct, and attached isorophid edrioasteroid (red arrow).

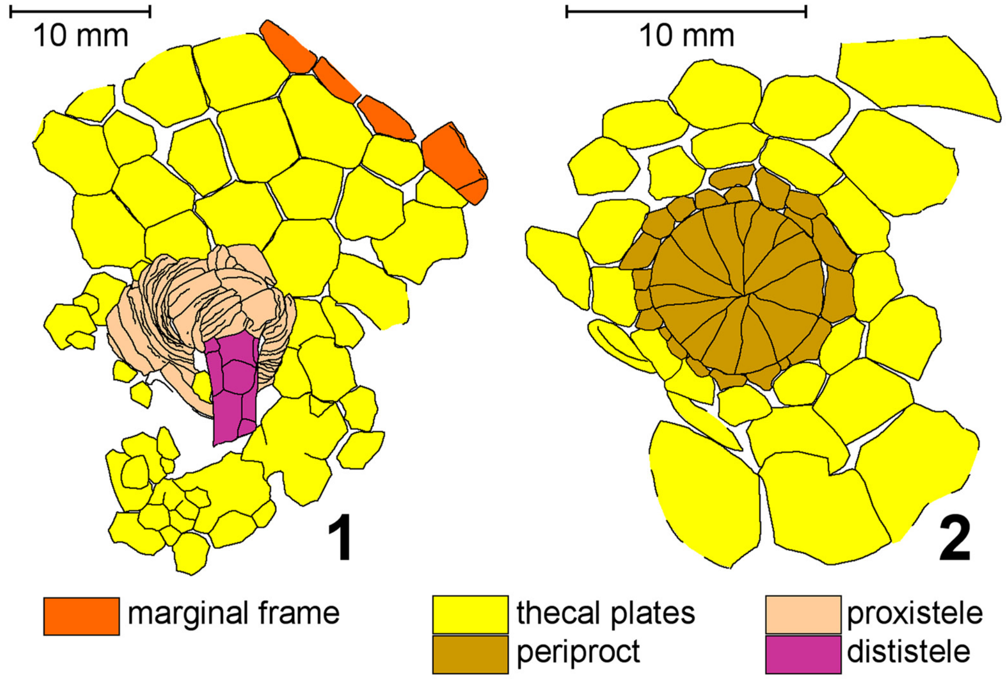

FIGURE 8. Solutan indet., gen. et sp. nov., Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); camera-lucida drawings of latex casts. 1: NMP.L.29118: portion of flat (lower) thecal surface with marginal frame, proxistele and proximal region of dististele. 2: NMP.L.29117; periproct.

preserved. In NMP.L.37454, small portion of feeding appendage (3 segments) suggesting insertion on flat thecal surface, away from marginal frame (Figs. 6.1, 7.1). Insertion of homoiostele on flat thecal surface, away from marginal frame (Figs. 6.1, 6.3, 7.1, 8.1). Proximal region relatively large, highly flexible, consisting of about twelve telescopic rings, each made of four plates with thickened distal margin (NMP.L.29118, 37454). Dististele partly preserved in one specimen (NMP.L.29118). Distal region of homoiostele composed of tightly sutured plates enclosing narrow longitudinal lumen (Figs. 6.3, 8.1). Dististele slightly cone-shaped proximally (transition zone with proxistele), more elongate and cylindrical distally. In NMP.L.29118, proxistele insertion into theca about 13 mm wide, and proximal portion of dististele about 3 mm in diameter.

Remarks. As suggested by Prokop & Petr (2003), the large echinoderms from the Šárka Formation initially identified—with some reservation—by Barrande (1887: Pl. 25, Fig. 15) as possible poorly preserved specimens of *Echinosphaerites infaustus* are better interpreted as solutans. This identification is confirmed by the presence of a typical solutan homoiostele and, apparently, a single feeding appendage. However, reexamination of the original material also suggests that this solutan is different from *Plasiacystis mobilis* in several respects: (1) theca with multilobate outline, marginal frame, and two opposite surfaces with contrasted plate patterns; (2) morphology and location of the anal pyramid; (3) location of the feeding arm insertion; (4) location of the homoiostele insertion; and (5) morphology of both the proxistele and the dististele. Indeed, the large majority of the material included in the type-series of *Plasiacystis mobilis* by Prokop & Petr (2003) should instead be assigned to this second unnamed solutan. These two taxa are found in both the same stratigraphic levels (Šárka Formation) and the same (western) part of the Prague Basin. However, examination of several public and private collections suggests that *Plasiacystis* is apparently far less common than the second unnnamed solutan. Several morphological features observed in the new solutan from the Šárka Formation occur in other taxa. For example, *Maennilia estonica* Rozhnov & Jefferies, 1996 possesses a relatively similar large, flattened theca with multilobate, gently rounded outlines, and a narrow marginal frame delimiting two opposite surfaces made of hundreds of polygonal elements (Rozhnov & Jefferies 1996; Parsley *et al.* 2012). As in the new Czech solutan, both *Girvanicystis batheri* Caster, 1968 and several iowacystids (*e.g.*, *Iowacystis sagittaria* Thomas & Ladd, 1926; *Scalenocystites strimplei* Kolata, 1973) are characterised by a flattened theca with contrasted plate patterns on the two surfaces, with consistently fewer plates on the most convex one than on the other (flat to slightly convex) surface (Parsley & Caster 1965; Caster 1968; Kolata 1973; Kolata *et al.* 1977; Daley 1992). Moreover, *Girvanicystis batheri* also possesses both a multilobate theca, and a large, rounded, flat anal pyramid in central position (away from thecal margins) on the convex thecal side (Caster 1968; Daley 1992). Most iowacystids (*e.g.*, *Belemnocystites wetherbyi* Miller & Gurley, 1894) also share with the new Czech solutan the possession of a centrally inserted feeding appendage (away from thecal margins) on the flat thecal surface (Parsley & Caster 1965; Parsley 1972; Kolata 1973; Kolata *et al.* 1977). However, although the new Czech solutan shares several characters with other taxa, their combination within a single species is unique. Moreover, the new solutan from the Šárka Formation also differs from all other previously described taxa in the central location of its homoiostele insertion (within flat thecal surface, away from posterior margin). This solutan is left here in open nomenclature (solutan indet., gen. et sp. nov.) because, in spite of a relatively abundant material (20 specimens), several key diagnostic features could not be documented (*e.g.*, precise morphology of the feeding appendage and of the dististele, relative positions of periproct, feeding arm insertion, and homoiostele insertion on both thecal sides). Moreover, complete, exquisitely preserved specimens (with both parts and counterparts) of a very similar solutan were found recently in the Middle Ordovician (Darriwilian) of Shropshire, UK (K. Derstler, pers. obs.). Future description of this material will be certainly essential for a better (re)evaluation of both the anatomy and affinities of the new Czech solutan.

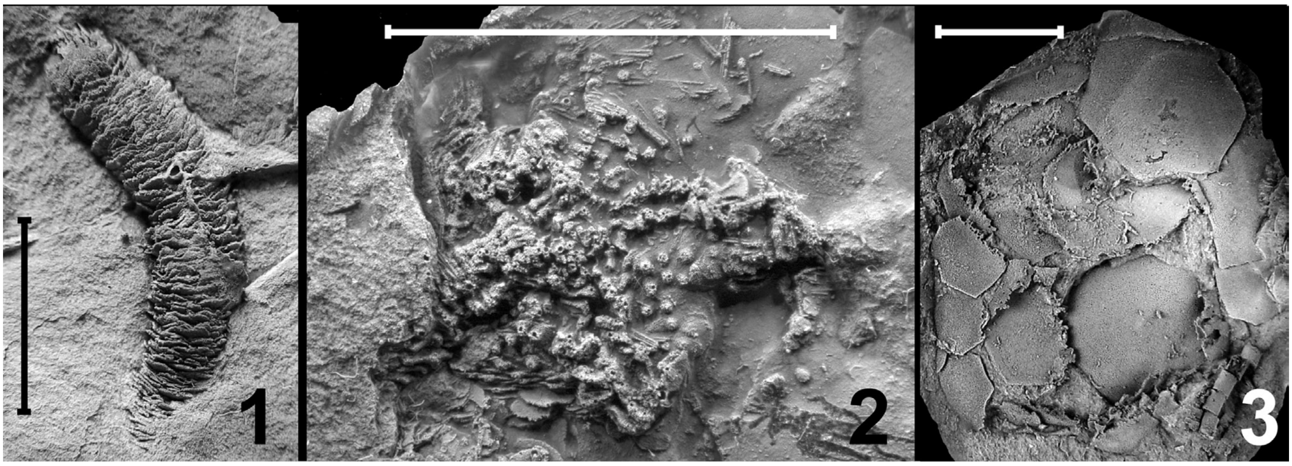

FIGURE 9. Other echinoderms from the Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic); all latex casts of original specimens; all scale bars: 10 mm. 1: NMP.L.29129: rhenopyrgid indet.; previously identified successively as a *Lepidocoleus*-like machaeridian, and then as an isolated dististele of *P. mobilis* (see Prokop & Petr 2003). 2: NMP.L.29115: isorophid edrioasteroid (?*Agelacrinites bohemicus*) attached to convex (upper) thecal surface of a specimen of solutan indet., gen. et sp. nov. 3: NMP.L.29133: mitrate stylophoran (*Mitrocystites mitra*); partly disarticulated lower thecal surface, with fragment of distal aulacophore; previously interpreted as poorly preserved specimen of *P. mobilis*

Class Edrioasteroidea Billings, 1858
Order Edrioasterida Bell, 1976
Family Rhenopyrgidae Holloway & Jell, 1983

rhenopyrgid indet.
Figure 9.1

Plasiacystis mobilis—Prokop & Petr 2003: 238, Pl. 3: Figs. 1–4 [*pro parte*; non Text-fig. 3, Pl. 2: Figs. 1–4, Pl. 4: Figs. 1–6 = solutan indet., gen. et sp. nov.; non Pl. 1: Figs. 1–5, Pl. 3: Figs. 5–6 = *Plasiacystis mobilis*].

Material, localities and horizon. One single specimen (NMP.L.29129) from Praha-Libuš (Prague Basin, Bohemia), Šárka Formation (Darriwilian). This specimen (erroneously mentioned as "NMP.L.21129") was figured by Prokop & Petr (2003: Pl. 3, Figs. 1–4), as an isolated proximal region of the homoiostele of *Plasiacystis mobilis*.

Description. Relatively elongate, highly flexible, unorganised pedunculate zone composed of several hundred minute, imbricate, scalelike skeletal elements, with suboral constriction. Oral surface not preserved. Dimensions of single specimen: 25 mm long, 5 mm wide.

Remarks. The specimen previously interpreted by Prokop & Petr (2003) as corresponding to an isolated proxistele of *Plasiacystis* is here reinterpreted as the pedunculate zone of a rhenopyrgid edrioasteroid. This diagnosis is based on the highly imbricate squamose plating, and the presence of a suboral constriction. Although all described rhenopyrgid species have an organized pedunculate zone typically of eight columns of alternating plates (Dehm 1961; Holloway & Jell 1983; Klug *et al.* 2008; Sumrall *et al.* in press), this rhenopyrgid has an unorganized pedunculate zone similar to a new, undescribed species from the Fezouata Formation (Lower Ordovician) from Morocco, North Africa (C.D. Sumrall & J.P. Botting, pers. obs.).

Order Isorophida Bell, 1976
Family Isorophidae Bell, 1976
Genus *Agelacrinites* Vanuxem, 1842

?*Agelacrinites bohemicus* Barrande, 1887
Figure 9.2

Argodiscus rarus—Plas & Prokop 1979: 41, Pl. 1: Figs. 1–2; ? Prokop & Petr 2003: 158, Pl. 2: Fig. 3 [*vidimus*].

Material, localities and horizon. One single specimen (NMP.L.29115) from Mýto near Rokycany (Prague Basin, Bohemia), Šárka Formation (Darriwilian).

Description. Small scattering of plates (about 9 mm in diameter) attached to the periproctal thecal surface of a large specimen of solutan indet., gen. et sp. nov. Portions of five straight ambulacra clearly evident across the surface, as are interambulacral areas filled with numerous imbricate plates. Large nodes present on some of the interambulacral plates.

Remarks. The same specimen was observed and identified as ?*Argodiscus rarus* Plas & Prokop, 1979 by Prokop & Petr (2003: 158). This small scattering of plates is here interpreted as a poorly preserved isorophid edrioasteroid. It is tentatively assigned to ?*Agelacrinites bohemicus*, based on the presence of large nodes on some of the interambulacral plates coupled with the occurrence of straight ambulacra. However, a thorough revision of edrioasteroids from the Prague Basin is wanting. Several comparable examples of isorophid edrioasteroids preserved attached to other organisms have been described in the Ordovician: for example on conulariids (Sumrall & Zamora 2011), trilobites (Prokop 1965), and a variety of Ordovician and Devonian rhombiferans (Bell 1976; Sumrall 2000; Sumrall & Zamora 2011).

The specimen of ?*Agelacrinites bohemicus* described here is the first report of an isorophid edrioasteroid found attached to a solutan. Taphonomic features of the fossils found in the siliceous concretions of the Šárka Formation are indicative of calm, relatively deep, offshore environmental conditions, with limited sediment influx, and a long exposure of carcasses on the sea floor. In these concretions, the majority of echinoderms falling into the “type 1” taphonomic category defined by Brett *et al.* (1997) are usually found intact (including their most fragile portions, such as feeding appendages), though consistently collapsed, and frequently secondarily filled by pellets (Bruthansová & Kraft 2003; Lefebvre 2007). Distribution of pellets in both trilobites and various echinoderms (*e.g.*, stylophorans) indicates that disarticulation was in situ, with carcasses preserved in their life orientation. In specimen NMP.L.29115, the preservation of the two echinoderms (isorophid and associated solutan) does not make it possible to determine, whether attachment occurred when the solutan was alive or soon after its death. However, as edrioasteroids are epifaunal suspension-feeders, attachment on the solutan theca necessarily occurred on an upward-directed surface (away from the substrate). Taphonomic features of the Šárka assemblage suggest that the orientation of this surface was very likely the same, when the solutan was alive and after its death. This implies that the convex, periproctal thecal surface of the solutan indet., gen. et sp. nov. was probably upward in life, and the opposite, adoral surface (bearing both the feeding appendage and the homoiostele insertion) was downward. This orientation is in good accordance with previous interpretations of solutans as epibenthic detritus-feeders (*e.g.*, Kolata 1973; Kolata *et al.* 1977; Jefferies 1990; Daley 1992).

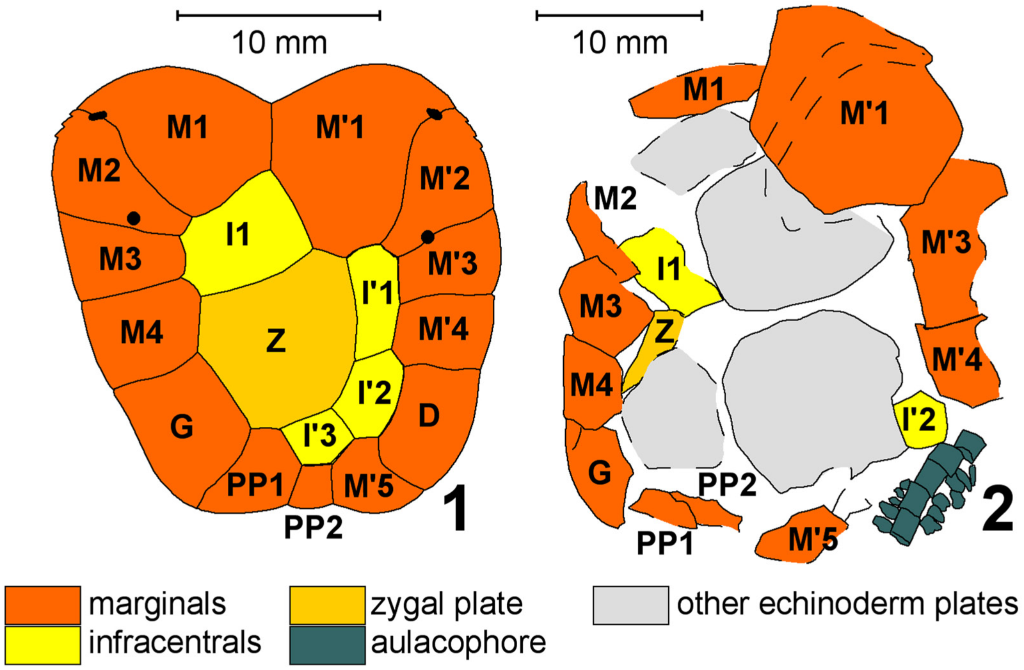

FIGURE 10. *Mitrocystites mitra*, Šárka Formation, Middle Ordovician (Darriwilian), Bohemia (Czech Republic). 1: reconstruction of lower thecal surface, with identification of skeletal elements; modified from Lefebvre (2000, 2001). 2: NMP.L.29133: partly disarticulated lower thecal surface, with fragment of distal aulacophore, and imprint of septum (hatched lines) on M'1; previously interpreted as poorly preserved specimen of *P. mobilis*.

Class Stylophora Gill & Caster, 1960
Order Mitrata Jaekel, 1918
Suborder Mitrocystitida Caster, 1952

Remarks. Four main subdivisions were identified by Caster (1952) within mitrates: the suborders Anomalocystida, Lagynocystida, Mitrocystida, and Placocystida. Three of them were retained by Ubaghs (1968c), after the reevaluation of the morphology of *Anomalocystites cornutus*: Anomalocystitida, Lagynocystida, and Mitrocystitida. A fourth suborder (Peltocystida) was created by Jefferies (1973), to accommodate several taxa previously assigned to lagynocystid mitrates (Kirkocystidae and Peltocystidae). This general scheme with four suborders was largely followed in the literature (*e.g.*, Jefferies & Lewis 1978; Philip 1981; Kolata & Jollie 1982; Parsley 1991; Ruta & Jell 1999; Parsley & Sumrall 2007). However, since Chauvel (1941), most authors consider that anomalocystitids probably derive from mitrocystitids (*e.g.*, Gill & Caster 1960; Jefferies & Lewis 1978; Derstler 1979; Craske & Jefferies 1989; Parsley 1994). This interpretation was confirmed by the majority of recent phylogenetic analyses (*e.g.*, Parsley 1997; Ruta 1997, 1999, 2003; Lefebvre 2000, 2001, 2005). Consequently, following Kolata *et al.* (1991) and Lefebvre (2000, 2001), the suborder Mitrocystitida is considered here as a clade, comprising a paraphyletic assemblage of basal taxa formerly assigned to the family Mitrocystitidae (*e.g.*, *Aspidocarpus* Ubaghs, 1979; *Chinianocarpos* Ubaghs, 1961; *Ovocarpus* Ubaghs, 1994), and the two monophyletic families Anomalocystitidae and Paranacystidae. As a consequence, the genus *Mitrocystites* Barrande, 1887 is not assigned here to any family.

Genus *Mitrocystites* Barrande, 1887

Mitrocystites mitra Barrande, 1887

Figures 9.3, 10

Mitrocystites mitra—Barrande 1887: 252, Pl. 4: Figs. I.6–25, I.31–39, I.44–46, Pl. 5: Figs. I.1–2, I.7–12 [*vidimus*, *pro parte*; non Pl. 4: Figs. I.1–5, I.26–30, I.40–43 = *Promitrocystites barrandei*; non Pl. 4: Figs. I.47–50 = *Aspidocarpus bohemicus*].

Plasiacystis mobilis—Prokop & Petr 2003: 153 [pro parte].

Material, localities and horizon. One single specimen (NMP.L.29133) from the Šárka Formation (Darriwilian), at Praha-Libuš, Prague Basin, Bohemia. In the palaeontological collections of the National Museum, Prague this specimen was placed within the type-series of *Plasiacystis mobilis*.

Description. Large, almost quadrangular, incomplete theca at least 35 mm long, 28 mm wide. On left thecal side, marginal M'1 relatively well-preserved (anterior margin missing), large (at least 13 mm long), polygonal, showing course of anterior portion of septum (on internal side). Marginal M'2 (and associated lateripore and paripore) not preserved. Marginal M'3 partly preserved (most of left margin missing), subquadrangular, elongate (about 10 mm long, 6.5 mm wide). Marginal M'4 partly preserved, trapezoidal, smaller (6 mm long) than M'3. In left posterior corner of theca, digital (D) missing. On right thecal side, marginals M1 and M2 both very poorly preserved (portions with both lateripore and paripore missing). Marginal M3 slightly displaced, relatively well-preserved (left edge missing), polygonal, relatively short (about 6 mm long). Right posterior edge of theca well-preserved with M4 and glossal (G) both intact. Marginal M4 subpentagonal, longer (about 6 mm) than wide (3.5 mm), with straight outer (right) edge. Glossal as long as M4, with gently curved outer (right) margin. Posterior thecal margin composed of three, slightly displaced, poorly preserved skeletal elements: PP1, PP2, and M'5. Central portion of theca very poorly preserved, with one single left infracentral plate (I'2, pentagonal, close to right posterior edge of M'4), and very small portions of both right infracentral plate and zygal plate (Z), close to right marginals. Small fragment of an aulacophore (5 ossicles and associated cover plates) preserved close to left posterior corner of theca. Ossicles small (between 1.5 and 2 mm long), with smooth (unornamented) external surface, well-preserved longitudinal median groove (on internal side). Cover plates elongate, preserved in open position, on each side of ossicles. More than one pair of cover plates associated to each ossicle.

Remarks. The central region of the theca is largely hidden by four large, isolated, non-stylophoran echinoderm plates. However, though very poorly preserved, specimen NMP.L.29133 can be confidently identified as a relatively basal member of the suborder Mitrocystitida (no posterior spines). Its assignment to *Mitrocystites mitra* relies on the presence of both a right infracentral area and three small plates on the posterior edge of the theca (*Promitrocystites barrandei* lacks a right infracentral area, and *Aspidocarpus* has only two posterior plates; see Lefebvre 2000, 2001). It is not clear whether the associated fragment of aulacophore belongs to the same specimen. In *Mitrocystites*, the lower surface of stylocone and proximal-most ossicles is strongly ornamented with laterally compressed spines, rapidly decreasing in height distally (see Chauvel 1941; Jefferies 1968; Ubaghs 1968c; Lefebvre 2003). Moreover, most reconstructions suggest a one-to-one correspondance between ossicles and pairs of cover plates (see Jefferies 1968; Ubaghs 1968c). However, as pointed out by Parsley (1994), very little is known on the morphology of the distal aulacophore of *Mitrocystites mitra* beyond its 6 or 7 proximal-most ossicles. Consequently, the possibility that the small piece of aulacophore observed in NMP.L.29133 belongs to the associated specimen of *Mitrocystites* (and represents a fragment of a relatively distal part of its aulacophore) cannot be ruled out.

Conclusions

In their original description of *Plasiacystis mobilis*, Prokop & Petr (2003) were the first to identify the solutan affinities of fossils initially assigned to other echinoderm groups (mitrate stylophorans and rhombiferans), and also to suggest echinoderm affinities for specimens previously interpreted as machaeridians. However, reexamination of the original material in the collections of the National Museum (Prague) shows that the type-series of *P. mobilis* includes specimens belonging to at least four different taxa. Consequently, the morphological reconstruction of *P. mobilis* by Prokop & Petr (2003) is largely a composite, with a mixture of parts belonging to different organisms: (1) a solutan indet., gen. et sp. nov. and (2) a mitrate (theca); (3) a rhenopyrgid edrioasteroid (proxistele); and (4) the "beaver-tailed" solutan *Plasiacystis mobilis* (dististele).

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