Functional morphology and paleoecology of some sessile Middle Cambrian echinoderms from the Barrandian region of Bohemia

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Abstract. Sessile Early and Middle Cambrian edrioasteroids and eocrinoids probably attached by biologically derived glue to siliciclastic sea bottoms, which were slightly to not at all bioturbated. The most likely glue available in echinoderms is mutable extensible collagen tissue (MCT). Holdfasts on the eocrinoid *Lichenoides* and the edrioasteroid *Stromatocystites* are made up of small platelets that could have extruded collagen along and out from the platelet sutures. A new species *Lichenoides vadosus* sp. n. is especially adapted for shallow water, high energy environments, and *Stromatocystites flexibilis* sp. n. is well adapted for deep, quiet water conditions. Thecal and holdfast morphology reflects these conditions. Both species are described here. Other Lower and Middle Cambrian echinoderms were recumbent on the seafloor and have flattened thecae and commonly an elongated appendage for locomotion and orientation. Some of these forms were well adapted to a non-bioturbated sea floor and did not adjust to the development of the mixed layer (homosteles and ctenocystoids), though stylophorans, homoiosteles, rhipidistian eocrinoids, and pleurocystoids did.

Key words: Cambrian, eocrinoids, edrioasteroids, biogluing, "snowshoeing", mixed layer

Introduction

Echinoderms are locally relatively abundant in the Middle Cambrian sediments of Bohemia. They are represented by eocrinoids, stromatocystitids (edrioasteroid-like animals), cinctans, ctenocystoids, stylophorans, and the strange genus *Cigara* that has not been successfully assigned to a class. All echinoderms either attach to the substrate (stromatocystitids and eocrinoids) by some sort of biological gluing emanating from a polyplated holdfast at the end of the column or at the base of the stemless theca, or they lie recumbently and unattached on the substrate like a snowshoe (cinctans, ctenocystoids, and stylophorans).

These Middle Cambrian echinoderms dwelled in arenaceous to fine-grained silty bottoms. These sediments, like coeval siliciclastics in North America, have a very low incidence of bioturbation (Ichnofabric 1 or 2, Droser and Bottjer, 1986) and provide a different surficial substrate than that commonly found higher in the stratigraphic column (especially Ordovician and younger), where ichnofossil-forming organisms have bioturbated the near surface substrate into a soupy mixed layer of water and sediment (Bottjer et al. 2000). Accordingly, organisms could and did adapt different attachment strategies to each type of bottom condition. We suggest that Lower and Middle Cambrian echinoderms attached to this relatively firm but (especially in very fine-grained sediments) probably sticky bottom by biological gluing (biogluing); the evidence for this is strongly supported by fossil and stratigraphic evidence. Evidence of biogluing is rare in rocks younger than Middle Cambrian. Where carbonate hardgrounds occur (commonly in Upper Cambrian and younger strata) direct cementation by a globule of calcium carbonate at the end of the column is not uncommon. In mixed layer environments many crinoids in Ordovician and younger sediments evolved rhizoid-like holdfasts.
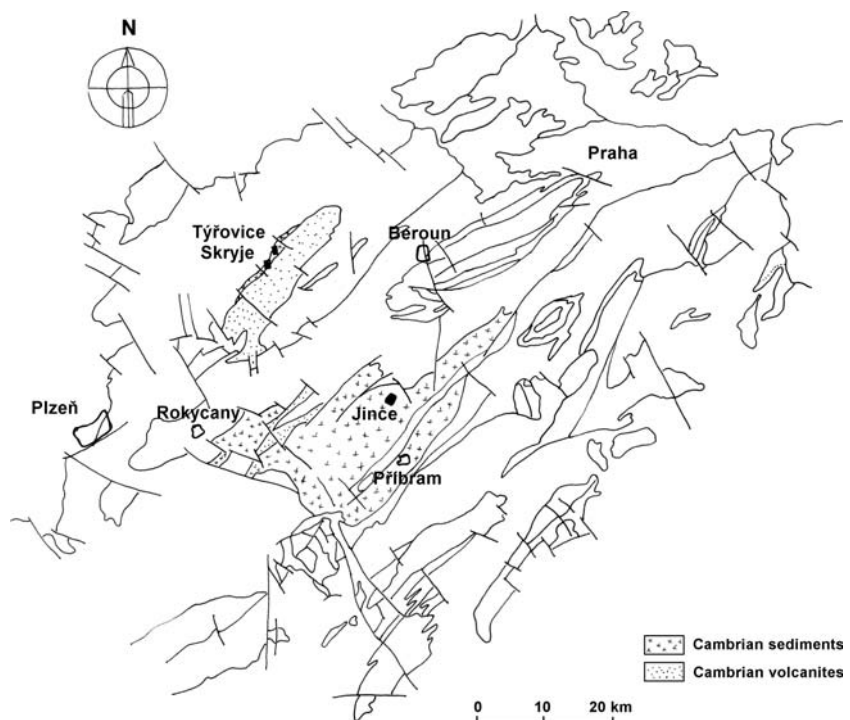

Figure 1. Sketch map of the study area. Drawn by Jana Nedomová.

Biogluing is also observed in the Lower and Middle Cambrian siliciclastics in Western North America. In this region it is common for stemmed Middle Cambrian echinoderms to be attached to a shell or piece of exuviae Colin Sumrall (pers. comm. 2002).

Stratigraphic setting

According to differing geological interpretations, the Middle Cambrian sediments of the Barrandian were either deposited in a single basin (Havlíček 1971), or in a pair of basins opening in different directions and possibly containing slightly differing faunas. This uncertainty is not significant for our purposes. The two main areas of Middle Cambrian fossiliferous outcrops are: 1. the Litavka Valley (eastern Brdy Mountains) in the area of Jince, where abundant outcrops of the approximately 400 metre-thick Jince Formation are present; and 2. in the area around the village of Skryje, where about 200 metres of the Skryje Shales abundantly crop out.

Sections close to Příbram-Jince and outcropping in the Litavka Valley encompass almost the entire Middle Cambrian, and represent a complete sedimentary sequence. Basal Jince Formation sediments were deposited in shallow water, in which basin deepening apparently reached a maximum of about 200 metres (based on ichnofossils; Mikuláš pers. comm.) around the lower third of the section. Repeated deepening produced similar conditions in the upper two thirds of the section. The upper third of the Jince section shows signs of shallowing, and subsequently grades into and is capped by 10 to 30 metres of shallow-water coarse conglomerate: the Ohrazenice Formation (Havlíček 1998). The Příbram-Jince basin was deformed by Variscan tectonic activity. Faulting and post-Variscan erosion has apparently destroyed the marginal shallow water facies in the Litavka Valley.

Echinoderms are especially abundant in the sediments of the upper depth maximum, which encompasses the Hydrocephalus minor/Stromatocystites and Paradoxides gracilis zones (Havlíček 1998). The lithology of these strata is comprised of gritty (greywacke) shales grading into fine-grained shales. In the Hydrocephalus Zone the following species with multiplated holdfasts, either on the end of the column or on the base of the theca, have been reported: *Lichenoides priscus* Barrande, 1846, *Akadocrinus jani* Prokop, 1962, *Akadocrinus nuntius* Prokop, 1962, *Akadocrinus knizeki* Fatka and Kordule, 1991, *Acanthocystites briareus* Barrande, 1887, and the type species of genus *Stromatocystites (Stromatocystites pentangularis* Pompeckj, 1896). The snowshoe-like species *Etoctenocystis bohemicus* Fatka and Kordule, 1985 and the enigmatic *Cigara dusli* Barrande, 1887, which cannot be placed in any known higher echinoderm taxon nor has its mode of life been discerned are also present (Havlíček 1998). In this zone, turbiditic deposition was observed to be common.

In the overlying Paradoxides gracilis Zone the echinoderm species discussed above again occur abundantly – especially a newly identified deeper water species of the genus *Stromatocystites*: *Stromatocystites flexibilis* sp. n., *Lichenoides priscus* Barrande, 1846, and *Etoctenocystis bohemicus* Fatka and Kordule, 1985. The eocrinoid *Vyscystis ubaghsi* Fatka and Kordule, 1990 is also present. The preservation of fossil echinoderms in this zone is commonly very good.

Paleoenvironmental conditions are quite different in the sections around Skryje, because the depth of deposition ranges from a few metres along the basin margin (seen in outcrops near the village of Týřovice) to deep, quiet water (as in the Příbram-Jince section) over distances of several kilometres. The section is less
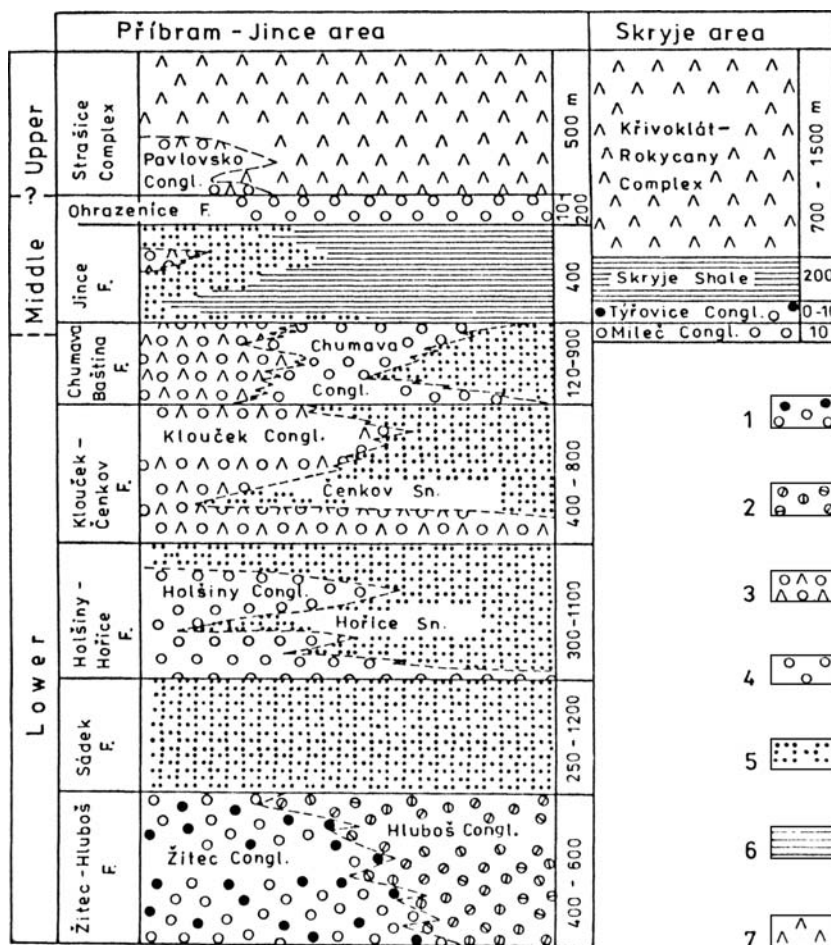

Figure 2. Stratigraphy of the Cambrian in the Barrandian (after Havlíček 1971, supplemented). 1 – petromictic grey-green conglomerates, 2 – reddish petromictic and oligomictic conglomerates, 3 – conglomerates with volcanic material, 4 – white and grey quartzose conglomerates, 5 – sandstones and greywackes, 6 – siltstones and clayey shales, 7 – effusive volcanites, F. – Formation, Sn. – Sandstone, Congl. – Conglomerate.

stratigraphically complete than in the Příbram-Jince area, and it is limited to the Eccaparadoxides pusillus Zone (early Middle Cambrian). In the west and south-western environs of Skryje, and in the outskirts of Týřovice (to the north-east of Skryje), the shallow water Mileč sandstones and conglomerates crop out, which are derived from local Late Proterozoic basement. This unit is localised and especially well developed to the east of the confluence of the Berounka River and Zbirožský Brook. The unit has abundant brachiopods and rare trilobites, but is devoid of echinoderms. Overlying the Mileč Conglomerate with a sharp contact is the Týřovice Conglomerate, which is especially well developed around Týřovice. The latter unit exhibits many shallow water stratigraphic features and has fairly abundant trilobites. Two echinoderm species are found in this unit: *Stromatocystites pentangularis* Pompeckj, 1896 and a new species of genus *Lichenoides* (*Lichenoides vadosus* sp. nov.) which is markedly different in thecal outline than the deeper water variety found in the Příbram-Jince area. The Týřovice Conglomerate crops out near Skryje on the banks of Karáskův Brook adjacent to its confluence with the Berounka River. The unit is nongraded, slip bedded, and contains very rare fossil fragments.

This shallow water conglomeratic member grades upwards and laterally into the more widely exposed shales and sandy shales of the Skryje Shale Member of the Jince Formation. Most of the fauna found in these shales is also found in deeper water sediments (perhaps turbidites), mostly deposited below storm base. The shallower fine-silt facies near Skryje contains one of the earliest stylophorans, *Ceratocystis perneri* Jaekel, 1900, which is an unattached, showshoe-like species. Deeper water grey shales that crop out around Skryje contain deeper water *Lichenoides priscus* Barrande, 1846 and the recumbent cinctan *Trochocystites bohemicus* Barrande, 1887. The latter also adopted a "showshoe" mode of life. Still deeper water shales at the village of Luh that crop out above the bridge over the Berounka River about a kilometre to the Northeast of Skryje contain remains of the stemmed eocrinoid genus *Luhocrinus* Prokop and Fatka, 1985. The lithology of these deep-water shales strongly resemble the Jince Formation of the Paradoxides gracilis Zone that crops out around the town of Jince.

Most echinoderms in these Middle Cambrian Bohemian sections are found in sediments with rather low incidence of bioturbation (ichnofabrics 1 or 2 at most, according to Droser and Bottjer 1986). Most ichnofossils are developed horizontally along the bedding planes or are concave arcuate burrows. The bedding and sparse fabric strongly indicate that there was virtually no mixed layer of water and sediment at the water–sediment interface, and that the bottom, though plastic, was cohesive to the point that organisms could attach directly to it. There is little evidence that the Cambrian Substrate Revolution, the transition from a distinct siliciclastic, plastic, dewatered surface to a distinct mixed layer surface, occurred here (Bottjer et al. 2000).

Attachment to substrate

Sessile echinoderms of Early and Middle Cambrian age appear to attach to the substrate by some sort of organic gluing (biogluing) process. In the interface between sediment and holdfast there is no evidence of secreted calcium carbonate cement or any other biologically secreted compound. This is in marked contrast to Late Cambrian and post Cambrian blastozoans, which cemented themselves to objects on the bottom or to hardgrounds by a globular mass of calcium carbonate. By the Late Cambrian, carbonate hardgrounds had evolved, as had widely distributed mixed layer substrates caused by ichnofossil-forming organisms. In Ordovician and younger crinozoans, rhizoid-like structures evolved to root into soft mixed layer substrates.

Attachment structures in Early and Middle Cambrian echinoderms differ markedly from those in younger genera, in that the contact surface between the holdfast and substrate is not cemented by a globule or sheet of calcium carbonate. There is, in fact, little direct evidence for any kind of a cementing medium between an undisturbed surface and the attachment surface. The bedding planes under the attachment disc also show little to no signs of disruption. In most cases where attachment structures are preserved, the attachment structure is composed of small platelets – and this holds true whether the structure is at the end of a column or stalk-like structure (the attachment disc) or at the base of a stalkless theca.

Attachment discs located at the column ends in stemmed eocrinoids, and short attachment stalks in stromatocystitids, are flattened circular to oval structures composed of numerous polygonal platelets. The sutures are commonly indented and the platelets appear to be rather loosely articulated. Genera without stems, helicoplacoids and *Lichenoides*-like eocrinoids, have small platelets at the basal end of the theca. Because the attachment process appears to be one of biogluing and not direct calcareous cementation to the bottom, the attachment medium would have to be directly related to the sutural planes of the platelets. It would be the only avenue to the interior by which the bioglue medium could extend from the column's attachment disc or theca into the substrate.

Early and Middle Cambrian echinoderms are almost always found to have resided in gritty to fine-grained shales, and are uncommon in limestones.

Biological compounds that are available to echinoderms for use as bioglue (in the absence of direct calcium carbonate cementation) include mucus and collagen. Copious amounts of mucus could have been secreted into the substrate; but unless an unknown stiffening compound was added to it, mucus would seem to be an insubstantial bioglue. In addition, mucus would be susceptible to degregation by bacteria. A substance common in echinoderms and highly mutable in the echinoderm body is collagen (MCT, mutable collagen tissue). Collagen fibers could have been extruded in a mucus cloud into the substrate. A direct analog might be the byssus structure present in some primitive pelecypods, which is composed of fibrous collagen fibers that are extruded from the byssus gland on the

underside of the foot. Byssus fibers are exceptionally strong, stiff at one end and act as a "shock absorber with 160 percent extensibility at the other" (Coyne et al. 1997). The probable collagen fibers in Cambrian echinoderms would have been strong, flexible, and capable of being rapidly renewed if the holdfast area was undercut by currents (in a pelecypod byssus, a new thread can be extruded in a process resembling injection molding in five minutes or less; Coyne et al. 1997). The mass of sediment and mucus/bioglue fibers would have been analogous to a wet mass of "kitty litter" i.e. a wet solidified mass of sediment with sufficient cohesion and mass to anchor the animal. The holdfast area could have been of large size, and it follows that it would have been an efficient anchoring mechanism though undetectable in lithified sediments. We suspect that the glued area was deeper than it was wide, which would help minimize undercutting and would have enough mass and adhesion to adjacent sediment to resist both the mass of the animal plus the drag forces exerted by currents flowing across the animal.

In the Lower Cambrian of North America, helicoplacoids apparently stood upright with the distal end buried in the substrate (Dornbos and Bottjer 2001). It is likely that the sutures embedded in the substrate extruded bioglue fibers, and produced a holdfast pad radiating out and down from the swirling plate series that was substantial enough to anchor the animal in all but the strongest currents within the animals environment. In the Middle Cambrian of North America most echinoderms are found detached and commonly current aligned. Attachment discs in virtually all cases are bioglued to a piece of shell or exuviae (James Sprinkle and Colin Sumrall, pers. comm.). The preference for attachment to biological debris is probably one of particle availability. If we are correct in our bioglue fiber construct, attachment to debris may have had several advantages. First there would have been less metabolic investment because less glue would have had to be excreted. Second, because most bioglues are protein-rich, such as the probable collagen strands, they would have been a desirable food source for many ichnofossil-forming organisms. Being glued to debris entirely, or partly above the sediment would have been a defensive measure against subsurface predation, and therefore metabolically less costly.

Middle Cambrian echinoderms in the Bohemian sections attached (mostly) to the substrate; and as there is little evidence for strata disruption, the fine thread "byssus model" for attachment seems highly probable. Collagen fibers commonly interlacing plates together could have been extruded outward and downward into the substrate. Fine threads would not have been disruptive to the substrate, and because they were probably numerous their combined strength would have been considerable.

"Snowshoeing"

Common among Cambrian echinoderms is the recumbent "snowshoe" mode of life. These forms, including the "Sub-

phylum Homalozoa" (Parsley 1999) have a flattened theca and commonly at least one appendage for orientation and locomotion. The long appendage is either a column-like appendage or is a feeding appendage (Stylophora). However, it is clear that each type of elongated appendage was independently derived and has a distinct morphology.

Homostelea are represented in the Bohemian Middle Cambrian by two genera and two species: *Trochocystites bohemicus* Barrrande, 1887, and *Asturicystis havliceki* Fatka and Kordule, 2001. The appendage is a dimerous continuation of the marginals, with intercalations of small platelets along the centerline on both dorsal and ventral surfaces. The intercalations probably enhance flexibility and impart to the structure the ability to act as a locomotor and anchoring structure. Friedrich (1995) suggested that the animal positioned the appendage into the oncoming current and fed in the back eddies swirling around the oral end of the theca. The marginals have impressed food grooves with cover plates on the anterior end of the theca.

Because the food grooves are adjacent to the substrate, the probable lack of a mixed layer would have kept a great deal of sediment out of the food grooves and swirling currents adjacent to the mouth. Homosteleans did not survive into the Middle Cambrian; perhaps they could not cope with well-developed mixed layer bottoms.

Homoiostelea are missing in the Middle Cambrian rocks of Bohemia but are common in the overlying Ordovician strata (Prokop and Petr 1999). Daley (1996) demonstrated that the earliest known homoiosteleans, *Coleicarpus* Daley, 1996 from Utah, is attached at the distal end of the stele. Organization into the typical tetramerous proxistele is derived from the polymerous proximal condition in *Coleicarpus*, and is related to moving the theca with its single brachiole through the water column to enhance feeding efficiency. The closely related genus *Castericystis* Ubaghs and Robison, 1985 (see Daley 1995) is distally attached in the juvenile stage but is detached and lies recumbently as an adult.

Organization into the well defined marginals and somatics that characterise some families did not evolve until the Ordovician, but the basal stocks probably survived and diversified because the brachiole could be kept out of and above mixed layer bottoms, or deployed so as to regulate the amount of acceptable inorganic material. This same principle probably also holds for other flattened, recumbent brachiole-bearing echinoderms, such as the pleurocystitid rhombiferans and rhipidodistian eocrinoids that are especially prevalent in the Ordovician.

Stylophora bear a superficial resemblance to the homoiosteles because of the marginal/somatic plate composition of the theca and the elongated appendage, with the aulacophore that has a tetramerous proximal part. However, the aulacophore is a feeding structure (Ubaghs 1961) and the distal part is uniserial with large paired cover plates. Impressions on the upper surface of each uniserial ossicle suggest the imprint of a water vascular system (axial canal, side canals, and ampular pits), and are seen to be broadly analogous to the feeding apparatus of a crinoid.

One of the earliest stylophorans, *Ceratocystis perneri*, is found in both the Skryje Shales and Jince Formation of the Jince Basin (Fatka and Kordule 1992, Fatka et al. 1992). Unlike most stylophorans, the theca is composed of large plates and is not composed of distinct marginals and somatics.

Stylophorans anchor either by knobs and spines at the distal end of the theca (Cornuta), or by large spines or flanges on modified ossicles adjacent to the tetramerous proximal aulacophore (Ankyroida; Parsley 1998). Stylophorans probably survived until the Devonian, in part because the aulacophore could be held above the mixed layer bottom of Ordovician and younger periods. Here too, the intake of inorganic detritus could be controlled to acceptable limits.

Ctenocystoidea are exclusively Middle Cambrian and are represented in Bohemia by *Etoctenocystis bohemicus* Fatka and Kordule, 1985. Ctenocystids have a well-defined set of marginal plates arranged in alternating double series and numerous small somatic platelets on both dorsal and ventral surfaces. There is no elongated appendage: feeding and locomotion appears to have been carried out by the comb-like ctenoid organ adjacent to the mouth. Deeply impressed grooves in the marginals and extending the length of the theca are devoid of cover plates, but may have had a subvective function. On hard, non mixed layer surfaces these grooves could have served as feeding structures, but they may not have been able to function as such in a mixed layer environment; it may be for this reason that this order is limited to Middle Cambrian deeper, quiet-water, siliciclastic facies. It seems reasonable to us that echinoderms would exploit the organic rich but relatively sediment free water column in the first centimetre above the bottom in siliciclastic terrains in the Lower and Middle Cambrian. This would result in thecal flattening and the orienting feeding structures just above the bottom. As mixed layer bottoms evolved in the Upper Cambrian and younger sediments, some recumbent echinoderms could adapt to this new set of conditions and did so quite well [stylophorans, homoiosteleans, pleurocystitids (Rhombifera), rhipidocystitids (Eocrinoidea)], whereas others did not and thus became extinct well in advance of their homeomorphic relatives (homosteles and ctenocystoids).

Systematic paleontology

Class Edrioasteroidea Billings, 1858
Order Edrioasteroida Bell, 1976

Genus *Stromatocystites*, Pompeckj, 1896

Type species: *Stromatocystites pentangularis* Pompeckj, 1896.

For a complete generic synonymy see Smith (1985), p. 736.

Remarks: The generic and specific characters were discussed in detail by Smith (1985). With the discovery of new specimens, especially in the Jince-Vinice and adjacent

sections in the Litavka Valley, it is clear that there is a new deep water species that is differentiated from the type species by its flattened, flexible, and multiplated theca. The type species is restricted to shallower and more energetic conditions. Even with a number of new specimens the details of the oral area, anal pyramid, and hydropore/gonopore structures are still poorly understood.

Stromatocystites pentangularis Pompeckj, 1896
Plate I, figs 1–7

Lectotype: CGS XB 05, Plate 1, Fig. 1. Pompeckj 1896, p. 506, pl. 13, figs 1a–d.

For a complete species synonymy see Smith (1985, p. 738).

Revised diagnosis by Smith (1985). Theca blister-like in profile; rounded, pentangular in outline. Five biserial ambulacra extend to the dorsal rounded angles of the pentangular margins. The ambulacra split close to the oral opening and form a biserial pentangular frame with externally bowed concave biseries to define the oral area. Ambulacra are arranged in a 2-1-2 pattern, the transverse part is quite narrow, and the ambulacral geometry is close to a regular pentaradial pattern. Poorly defined anal pyramid near posterior margin. Interambulacral areas on oral face are tessellated with tightly sutured sprocket shaped plates. Aboral face is tessellated with plates without sutural pores. Holdfast structure in the centre of the aboral face is composed of a circlet of platelets surrounding irregularly platted central area, all are tightly sutured. Marginal plates are without pores and are tightly sutured to form a rigid outer rim.

Discussion: The original discovery of *S. pentangularis* was in the Skryje area at the section "Pod trním" by Týřovice. These specimens are from the shallow water Skryje Shales (lower part, comprised of shales with many intercalated greywacke and sandstone lenses) which are high-energy deposits. The dynamic nature of the environment is mirrored in the robust morphology of the test. The species is also known from the Jince section in the Litavka Valley. In this section the specimens are found in greywackes that were probably originally calcareous (see Kukal 1971), and indicate periodic high energy conditions.

Specimens from high energy parts of both sections are blister shaped in profile, and most of the oral and marginal plates are rigidly fused (Plate I. figs 1, 3–5). Both flooring and side plates are thick and rigidly sutured. Because these plates are thickened and robust they present a raised, starfish-like outline within the interradial platelets (Plate I. fig. 5). Only the plates of the oral area, inside the pentagonal ring, appear to be flexibly articulated. Within the Litavka Valley sequence probable shallower water forms (preserved in the sandy shales that were originally calcareous) appear to be the type species, and intermediate characters between the two species have not been recognized. We argue that the more robust ambulacral series in the type species not only makes up a stronger, stiffer framework in this shallower water, higher energy form, but also that the

ambulacral branches serve a function similar to the ribs in an umbrella to help support the oral surface. *Stromatocystites,* like all edrioasteroids, was probably able to maintain turgor by filling the gut or associated compensation sacs with ambient seawater (see Sumrall and Parsley 2003). In deeper water, turgor was easy to maintain hydrostatically, and rigidity in thecal suturing was not necessary. The organism was therefore saved the metabolic expense of providing it by rigidly suturing the plates.

The anal pyramid is very difficult to discern in *S. pentangularis* and defies clear photographic documentation. The platelets that form the pyramid appear to be part of a rosette of plates (Pl. 1 figs 6, 7). An early-formed plate that asexually replicates new platelets along its sutures forms rosettes. Rosettes are present in all of the interambulacral areas. The anal pyramid is a co-opted structure that covers the anal opening in the posterior C/D inter ray. The origin of the pyramid platelets in edrioasteroids and probably in all echinoderms with anal pyramids can be homologised with some degree of certainty with rosetted thecal plates.

The rigidly fused outer margin plates form a distinct outer ring and grade into the rigidly fused sprocket plates on the oral surface. The interradial platelets on the aboral surface are more flexibly articulated away from the attachment disc and probably allowed for expansion of the theca by flexing convexly. The attachment disc is large, and its plates are large and thickened. The circular disc is commonly concavely cupped within the pentastellate ring (Plate I fig. 3).

Stromatocystites flexibilis sp. n.
Plate I, figs 8, 9

1961 *Stromatocystites* aff. *pentangularis*; Prokop, p. 42 (first mention and brief diagnosis)

Holotype: NM L 36605 ± , Plate I, fig. 8.
Paratype: NM L 36607 ± , Plate I, fig. 9.
Material: More than 150 thecae in the different stage of ontogenesis preserved in shales or siltstones.
Type horizon: Jince Formation, lower part of the Paradoxides gracilis Zone.
Type locality: Jince, Vinice hill.
Diagnosis: *Stromatocystites* with loosely articulated theca; ambulacral flooring plates and side plates are thin and do not form a strongly elevated ambulacral area. Theca is sub-circular in outline and relatively flat in cross section. Marginal outer rim plates are only slightly more tightly sutured than the loosely sutured interambulacral plates on the oral and aboral surfaces. Interambulacral plates on both oral and aboral surfaces are smaller and more numerous. Attachment disc is smaller and is loosely articulated.
Discussion: Specimens are all from the Litavka River valley section, especially from the deeper water (lower energy) parts of the Eccaparadoxides pussilus and Paradoxides gracilis zones. They are generally less than half the width and more flexibly articulated than the larger

and more rigidly articulated type species. The entire ambulacral system is made up of relatively smaller and less robust plates, but their morphology is otherwise nearly identical with the type species. The holdfast is smaller and its plates are slightly thinner. Because of the differences in thecal size, degree of robustness in the ambulacral system plating, degree of rigidity in plate suturing, and relative increase in interambulacral plating, it seems appropriate to view these two forms as separate species rather than end points of a ecophenotypic sequence.

Attachment to substrate: Both *Stromatocystites flexibilis* and *S. pentangularis* apparently bioglued themselves to the substrate. There is no evidence that they attached, in whole or in part, to other organisms or parts of organisms on the sea bottom. Bioglueing seems plausible because there is no visible deformation to the underlying sediment, and the size of the holdfast corresponds to the ecological setting of each species. The smaller, and structurally weaker holdfast of *S. flexibilis* is a good indicator that this species lived in quieter, deeper water. It corresponds well with sedimentilogical stratigraphic indicators. *Stromatocystites pentangularis* has a relatively larger and more rigid holdfast. It is always cupped and commonly wholly within the pentastellate ring. Some specimens preserve a thin sediment rind over the cup, which appears to be a product of biogluing. Because of the coarse sediment favored by *S. pentangularis* any mechanism of attachment utilizing suction would not be possible. The attachment to both fine and coarser sediments by *Stromatocystites* utilising a circular holdfast structure with broad recessed sutures strongly indicates to us that biogluing is the most plausible method of attachment.

Class Eocrinoidea Jaekel, 1918
Family Lichenoididae, Jaekel, 1918

Genus *Lichenoides*, Barrande, 1846

Type species: *Lichenoides priscus* Barrande, 1846.
Diagnosis: Modified from Ubaghs (1967). Theca ovoid to nearly circular in profile. Basals of five thick walled, unequally sized plates. Some plates in series variously excerted from basal area. The aboral ends with varying numbers of small platelets form a cluster or a cluster plus individual platelets intercalated along aboral suture lines. Epispires on lower, lateral, and upper sutures. Middle circlet of five subpentagonal to subhexagonal lateral plates that are equidimensial to elongate and are the largest elements in the theca. Upper circlet composed of subpentagonal, rather small radial plates. Epispires rimmed by slightly raised narrow ridges and cover most of surface of lateral and radial plates. Brachioles single or split into a pair just above a single brachiole base on lateral and radial plates.
Discussion: The detailed description by Ubaghs (1953) prevents the need for detailed redescription and presentation of synonymies of the genus or type species. The new material available does give added insight into the
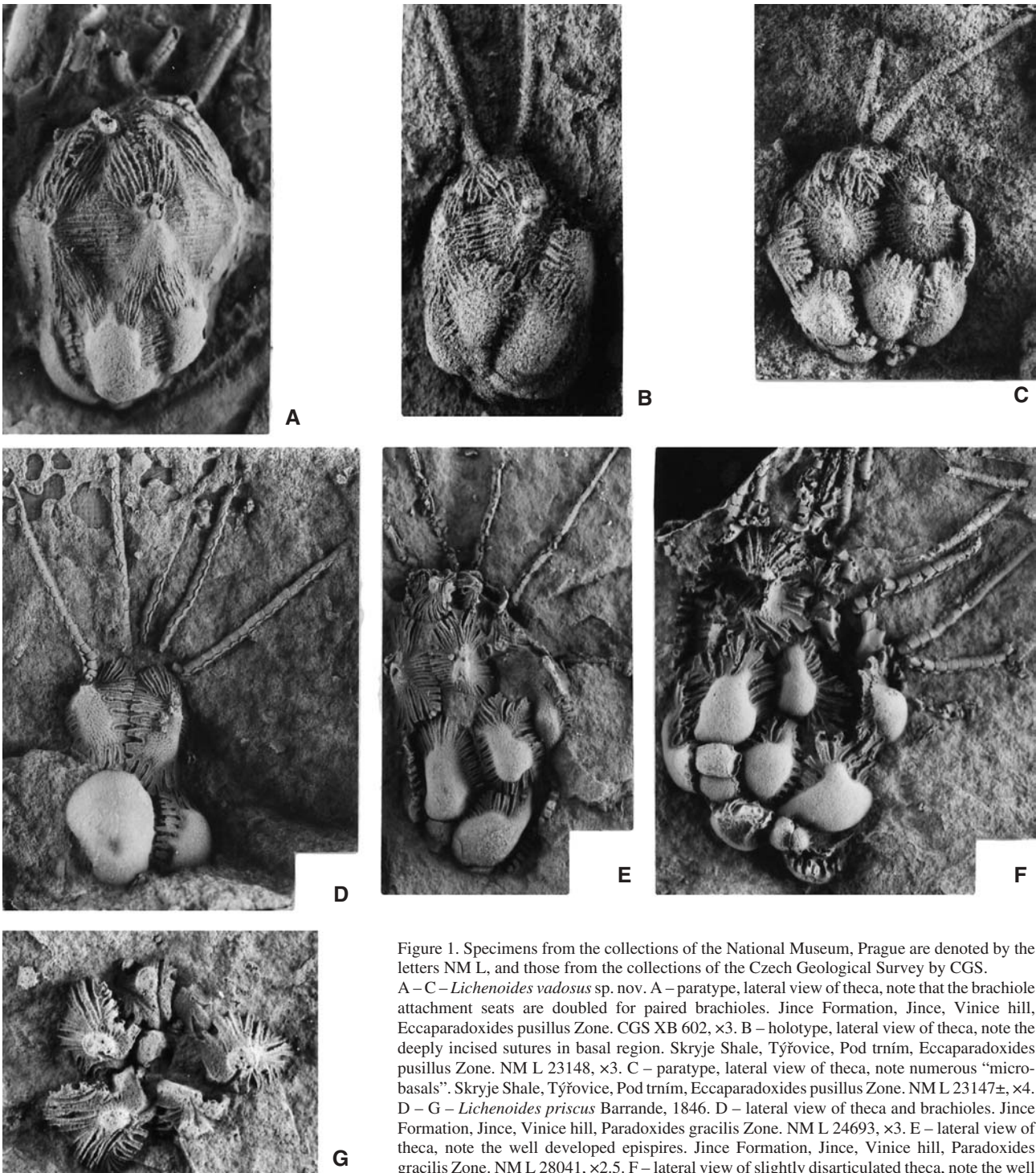
Figure 1. Specimens from the collections of the National Museum, Prague are denoted by the letters NM L, and those from the collections of the Czech Geological Survey by CGS.
A – C – *Lichenoides vadosus* sp. nov. A – paratype, lateral view of theca, note that the brachiole attachment seats are doubled for paired brachioles. Jince Formation, Jince, Vinice hill, Eccaparadoxides pusillus Zone. CGS XB 602, ×3. B – holotype, lateral view of theca, note the deeply incised sutures in basal region. Skryje Shale, Týřovice, Pod trním, Eccaparadoxides pusillus Zone. NM L 23148, ×3. C – paratype, lateral view of theca, note numerous "micro-basals". Skryje Shale, Týřovice, Pod trním, Eccaparadoxides pusillus Zone. NM L 23147±, ×4. D – G – *Lichenoides priscus* Barrande, 1846. D – lateral view of theca and brachioles. Jince Formation, Jince, Vinice hill, Paradoxides gracilis Zone. NM L 24693, ×3. E – lateral view of theca, note the well developed epispires. Jince Formation, Jince, Vinice hill, Paradoxides gracilis Zone. NM L 28041, ×2.5. F – lateral view of slightly disarticulated theca, note the well developed epispires, some with sutural poses. Jince Formation, Jince, Vinice hill, Paradoxides gracilis Zone. CGS RP 118, ×3. G – disarticulated oral area. Jince Formation, Jince, Vinice hill, Paradoxides gracilis Zone. NM L 28038, ×4. Photo R. L. Parsley.

morphology of the basal area or the epispires Genus. *Lichenoides* lacks the typical 2-1-2 ambulacral system of coeval eocrinoids such as *Gogia, Sineocrinus* or *Acanthocystites*. In fact, an undoubted oral opening has never been identified, and discerning the method of food intake into the digestive system is problematic. Epispires in *Lichenoides* are variable. In the type species, *L. priscus* they are wide and are deeply excavated into the thecal plates (Fig. 1E, G).

Such structures may diminish the overall strength of the plate, but increase the area of thin wall stereom over which respiration can occur. Reduction in plate strength is probably of little importance because this species is found in deeper water, lower energy sediments. Conversely, the epispires in *L. vadosus* are narrow and commonly not as deeply excavated. This species lived in shallow water and is found in higher energy sediments. Like all other eocri-

noids the sutural pore develops at the plate suture during ontogeny. In *Lichenoides priscus* it develops earlier (based on height of the theca) than in *L. vadosus*. We interpret this difference as response of the organism to the amount of available oxygen. *Lichenoides priscus* is found in organic rich shales that indicate low oxygen content, but with *L. vadosus* the opposite is true; the sediments are moderately coarse sandstones that indicate, shallow, well-oxygenated waters.

Sample size is not large enough to determine when (in terms of thecal height) sutural pores form in either species. The oldest epispires are at the centers of the plate facets, from which they develop laterally in the epispire trenches towards the ends of the facet. In some small specimens the (uppermost) radial series are devoid of interradial pores.

Because sutural pores develop late in the ontogeny the likelihood of complex structures such as tubules containing coelomic tissue occupying the epispires seems unlikely (Ubaghs 1967). Rather, the excavated epispires could direct seawater along the surface of the plates, and respiratory exchange could then take place along the elongated areas of thin stereom. With the development of the sutural pore a probable short circular to oval podium, lined with coelomic tissue, protruded into the slipstream and greatly enhanced respiratory exchange.

Lichenoides priscus Barrande, 1846
Fig. 1D–G

Diagnosis: *Lichenoides* with oval profile. Lateral plates elongated, epispires well developed. Basals tend to be aborally protuberant. Brachioles narrow.

Discussion: This species was described in detail by Ubaghs (1953), though our comments are based on new material. Small slabs containing numerous specimens of *L. priscus* (collected by the late Milan Šnajdr) clearly indicate that the aboral end of the basals sat in a shallow depression on the sea bottom. The basals themselves do not form an evenly developed circlet. Commonly, three basals extend farther aborally than do the adjacent smaller pair. On the sloping surface between the triplet and less aborally extended pair is the intercalation of commonly three or four "microbasals". In some specimens one or two microbasals may be intercalated between the sutures of the triplet at the aboral end of the theca. The bluntly pointed end apparently sat in the burrow, but not deeply enough that it buried the epispires at the aboral ends of the plates. The animal was held in its burrow by the (proposed) byssal collagen extending out from the sutures around the microbasals and aboral basals. It is not uncommon to find juveniles in pairs or in threes, closely nested in their burrows. As specimens grow, the largest and presumably best-anchored specimen prevails, the adjacent specimens are eliminated, presumably by current action. The organism is solitary by the time its theca is about five mm high. Remnants of the burrows are sufficiently abundant to verify this ontogenetic pattern.

The sediments in which this species in found commonly show scour and fill deposition. In order for the ani-

mal to remain attached, the attachment mode would have to be quickly renewable. Primary byssus production in pelecypods occurrs in several minutes and it is reasonable to assume the same time frame may well have pertained to the anchoring of early echinoderms, so that uprooting and current alignment would have required a sustained, rather than a short spasmodic current.

Lichenoides vadosus sp. n.
Fig. 1A–C

1896 *Lichenoides priscus* Barrande, 1846; Pompeckj, p. 502, Pl. 13, fig. 7a–c

Holotype : NM L 23148, Fig. 1B
Paratypes: CGS XB 602 (Fig. 1A), and NM L 28247 ± (Fig. 1C).
Type horizon: Jince Formation, Skryje Shale, Eccaparadoxides pusillus Zone.
Type locality: Týřovice, "Pod trním" section.
Material: Fifteen specimen preserved mostly in the sandstones and greywackes, rarely in siltstones.
Diagnosis: *Lichenoides* with near circular to broadly oval profile. Lateral plates shorter, more equidimensional, epispires are less pronounced. Brachioles are more robust and relatively longer than in type species.
Discussion: The differences between this and the type species are minor but sufficient to make the two readily distinguishable. Because of the relative shortening of the laterals the theca has a quite different, broadly ovoid profile rather than the elongated oval of *L. priscus*. The differences in the less protuberant epispires are also clearly discernible.

The more circular theca and the less pronounced epispires are species-specific features, apparently adapted for life in higher energy and subsequently more highly oxygenated waters. *Lichenoides priscus* is always found in deeper water, finer grained sediments (shales and silty shales), while *L. vadosus* is found in shallow water, high-energy coarser sediments (fine grained sandstone). The taller ovoid theca of *L. priscus* with more pronounced epispires on the laterals is probably indicative of the selective importance of these features in less oxygenated waters. The thicker, more robust brachioles probably reflect the ability of *L. vadosus* to feed on coarser grained detritus and to cope with higher energy environments. In order to survive in such conditions we would conclude that byssal attachment adjacent to the theca would have to be robust, and that extension of byssal fibers into the substrate would have to be at least as long as the theca (though they were probably longer in order to securely anchor the animal). Attachment by mucus or some other bioglue secreted by the epidermis does not seem possible for this animal. The high degree of hydrodynamic drag from water flowing across the brachioles would have been considerable, and the forming of a surficial crust around the base anchoring only the top layer(s) of grains would have been inadequate for the task. The extrusion of collagen into the substrate appears to be

the most reasonable explanation for how this species could have remained securely sessile considering its living conditions.

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Plate I

Specimens from the collections of the National Museum, Prague are denoted by the letters NML, and those from the collections of the Czech Geological Survey by CGS.

1–7 – *Stromatocystites pentangularis* Pompeckj, 1896. 1 – aboral surface, note the well developed, rigidly fused marginal rim of the thecal plates. Lectotype. [Pompeckj 1896, pl. 13, figs. 1a,b]. Skryje Shale, Týřovice, Pod trním, Eccaparadoxides pusillus Zone. CGS XB 05. ×3. 2 – aboral surface; marginal rim well developed, both oral and aboral interambulacral plates are preserved in patches. Skryje Shale, Týřovice, Pod trním, Eccaparadoxides pusillus Zone. CGS XB 600, ×1.5. 3 – aboral surface, note the robust attachment disc and the split series of ambulacral plates that define it. Jince Formation, Jince, Vystrkov hill, Hydrocephalus/Stromatocystites Zone = interval between Eccaparadoxides pusillus and Paradoxides gracilis zones. CGS 3370, ×2.5. 4 – oral surface, note its convexity. Jince Formation, Jince, Vystrkov hill, "Interval" Zone. CGS YA 1031, ×1.5. 5 – oral surface, note its convexity and the robustness of the ambulacra. Jince Formation, Jince, Vystrkov hill, "Interval" Zone. CGS YA 1031, ×2. 6 – oral surface, note poorly organized anal pyramid near posterior rim. Skryje Shale, Týřovice, Pod trním. NM L 28228, ×1.5. 7 – deformed oral surface, note poorly organized anal pyramid near posterior rim. Jince Formation, Jince,Vystrkov hill, "Interval" Zone. NM L 28229, ×1.5.

8–9 – *Stromatocystites flexilis* sp. n. 8 – holotype, oral surface, note the abundant interambulacral plates and weakly developed ambulacral system. Jince Formation, Jince, Vystrkov hill, Paradoxides gracilis Zone. NM L 36605±, ×1.5. 9 – paratype, aboral surface, note well developed attachment disc but overall reduction in size relative to type species. Jince Formation, Jince, Vinice hill, NM L 36607±, ×3.