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Original article

The Cambrian edrioasteroid *Stromatocystites* (Echinodermata): Systematics, palaeogeography, and palaeoecology[☆]



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ABSTRACT

The Cambrian edrioasteroid *Stromatocystites* is reported and described from Spain, Sweden and Turkey. All previously known occurrences of the genus are critically reviewed, and *S. flexibilis* is reinterpreted as a junior synonym of *S. pentangularis*. *Stromatocystites* was biogeographically widespread and colonized different areas of Baltica, Gondwana (Arabian, eastern and western margins) and Laurentia (western Newfoundland). Stratigraphically, it ranges from Cambrian Series 2, Stage 4 to Cambrian Series 3, Drumian. *Stromatocystites* lived in quiet water environments with stabilized substrates. It was attached directly to the substrate by its aboral surface. As these environments were widespread throughout Baltica, Gondwana and Laurentia, availability of suitable substrates for larval settlement and oceanic palaeocurrents led to the successful development of *Stromatocystites* colonies.

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1. Introduction

Edrioasteroids are an extinct clade of echinoderms including sessile forms with a globular to discoidal theca, and lacking exothecal appendages. They have five ambulacra following a 2–1–2 pattern with the mouth in a central position. Identification of ambulacral rays relies on the position of the anal pyramid, which is consistently located between ambulacra C and D. Most Cambrian edrioasteroids have fully plated lower surfaces for attachment.

Stromatocystites has a globular to clavate thecal shape and a fully plated aboral surface. The presence of a central disc with large, strongly knit plates in the aboral surface suggests direct attachment to the substrate. Previous studies interpreted that *Stromatocystites* lived in quiet water environments, where colonies attached directly to firm stabilized substrates (Smith, 1985; Parsley and Prokop, 2004; Dornbos, 2006; Zamora and Smith,

2010; Álvaro et al., 2013a; Zamora et al., 2013a). The genus *Stromatocystites* is one of the most diverse and widespread Cambrian edrioasteroids (Zamora et al., 2013b). It was originally described from the Czech Republic at the end of the nineteenth century (Pompeckj, 1896), and subsequently reviewed in several papers (Jaekel, 1899; Bather, 1900; Schuchert, 1919; Bassler, 1936; Cabibel et al., 1959; Regnéll, 1966; Paul and Smith, 1984; Smith, 1985; Parsley and Prokop, 2004; Lefebvre et al., 2010). Apart from the type species, *S. pentangularis* (Pompeckj, 1896), several species were assigned to the genus; only two of them are retained here as valid taxa (see discussion below): *S. walcotti* from the lower Cambrian of Newfoundland (Schuchert, 1919), and *S. reduncus* from the middle Cambrian of Australia (Smith and Jell, 1990). Undescribed species include specimens from the Cambrian of Poland (Dzik and Orłowski, 1995), Morocco (Smith et al., 2013) and Spain (Zamora, pers. obs.).

In this paper, we report new occurrences of *Stromatocystites* from the Arabian and Mediterranean margins of Gondwana, as well as from Baltica. Because of the specific ecological requirements of *Stromatocystites*, the palaeobiogeographical and environmental contexts of previous and new occurrences are revised and updated.

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2. Systematic palaeontology

Orientation and ambulacral nomenclature of edrioasteroids follow [Smith \(1985\)](#). Both rely on the identification of the major body apertures. The anal pyramid is always located within interambulacrum CD; ambulacra are named clockwise (A to E), according to their position. Adoral and aboral are used to designate positions closer or away from the oral area, respectively. The oral area was oriented facing away from the sea floor in life, and part of the aboral surface was in contact with the substrate. Proximal and distal refer to proximity to the mouth. Other useful terms for orientation are perradial or adradial that refer to a direction towards the perradial midline or towards the adradial sutures of ambulacra. The adradial suture is the zone of contact between the oral-ambulacral plate series and interambulacral plates (*sensu* [Bell, 1976](#)).

Class EDRIOASTEROIDEA [Billings, 1858](#)
 Order STROMATOCYSTITIDA [Bell, 1980](#)
 Family STROMATOCYSTITIDAE [Bassler, 1935](#)
 Genus *Stromatocystites* [Pompeckj, 1896](#)

Remarks: The genus *Stromatocystites* includes different edrioasteroid taxa sharing plesiomorphic features (e.g., epispines, poorly developed or absent marginal ring, aboral surface plated). This genus is distinct from other Cambrian edrioasteroids in several aspects:

- *Stromatocystites* differs from *Cambraster* in the absence of a marginal ring and in the different arrangement of aboral plates. Both genera share a similar construction of ambulacra ([Zamora et al., 2013a](#));
- *Stromatocystites* differs from both *Kailidiscus* and the closely related genus *Walcottidiscus* (see [Zhao et al., 2010](#)) in ambulacral construction: ambulacral rays are made of one single (abradial) set of biserial flooring plates in *Stromatocystites*, and of two sets (abradial and adradial) in both *Kailidiscus* and *Walcottidiscus*. Moreover, the aboral thecal surface is fully plated in *Stromatocystites*, but unplated in both *Kailidiscus* and *Walcottidiscus*;
- *Stromatocystites* also differs from basal isorophids (i.e., *Protorophus*, *Chatsworthia* and *Hadrodiscus*) in the ambulacral-plating pattern: flooring plates are uniserial in isorophids and biserial in *Stromatocystites*. Additional differences include the possession of an unplated aboral surface and of a well-developed marginal ring;
- *Totiglobus* and *Aragocystites* both display ambulacral construction patterns comparable to the situation in *Stromatocystites*, with one single set of biserial flooring plates. However, the theca of *Totiglobus* is more globular, lacks epispines and displays imbricate interambulacral plates. *Aragocystites* is more closely related to *Stromatocystites*, but the former almost lacks epispines, has relatively larger thecal plates, well-defined interradial oral plates, and multiple primary cover plates to each flooring plate.

Six species of *Stromatocystites* have been proposed to date. The type species, *S. pentangularis*, was initially described by [Pompeckj \(1896\)](#) from the middle Cambrian of Bohemia. It was also identified in the lower Cambrian of Newfoundland by [Smith \(1985: pl. 87, figs. 3, 4\)](#). The middle Cambrian echinoderm from southern France (Montagne Noire), initially described as *Trochocystites cannati* by [Miquel \(1894\)](#), was subsequently assigned to the genus *Stromatocystites* by [Miquel \(1905\)](#), and with doubt, by [Thoral \(1935\)](#), before becoming the type species of the genus *Cambraster* ([Cabibel et al., 1959](#)). *Stromatocystites balticus* was described by [Jaekel \(1899\)](#) based on two specimens collected in northern Germany from erratic glacial blocks of putative Baltic origin (middle Cambrian of Sweden). Both specimens were subsequently lost, and [Smith \(1985\)](#) suggested *S. balticus* as a *nomen dubium*. A fourth species, *S. walcotti*, was described by [Schuchert \(1919\)](#) in the lower Cambrian of Newfoundland. Although the morphology of this edrioasteroid remains incompletely known (see [Schuchert, 1919: fig. 1; Smith, 1985](#)), it appears as a valid species of *Stromatocystites*. *S. walcotti* differs from *S. pentangularis* in the absence of well-differentiated oral plates in interradial position, and the morphology of the central attachment disc ([Table 1](#)): *S. walcotti* displays a single central plate surrounded by numerous smaller elements, whereas in *S. pentangularis* the central pad is composed of fewer, larger and undifferentiated elements. A fifth species, *S. reduncus*, was described by [Smith and Jell \(1990\)](#) in the middle Cambrian of Australia ([Fig. 1\(6\)](#)). Differences with *S. pentangularis* include the absence of large, interradial oral plates, and the shape of the ambulacra: they are straight in *S. pentangularis* and distally recurved in *S. reduncus*. Finally, [Parsley and Prokop \(2004\)](#) described *Stromatocystites flexibilis* in the middle Cambrian of Bohemia. However, all morphological differences between *S. flexibilis* and *S. pentangularis* (e.g., loosely articulated parts of the theca, slightly elevated ambulacral area and size of thecal plates) may only represent the result of different taphonomic preservation. This species is thus reinterpreted here as a junior synonym of *S. pentangularis*.

In summary, only three species of Cambrian edrioasteroids can be assigned to the genus *Stromatocystites*: *S. pentangularis*, *S. walcotti*, and *S. reduncus*. Other occurrences of possible *Stromatocystites* are reported below.

Stromatocystites cf. *pentangularis*

[Figs. 1\(7, 8\), 2](#)

Material: Two specimens, one representing an adoral view and the other an aboral view, both preserved as natural moulds in grey siltstones. Specimens are deposited in the collections of the Museo Geominero (Geological Survey of Spain, Madrid) under repository numbers MGM6748X and MGM6749X. We also include under *S. cf. pentangularis* six specimens from Sweden deposited in the Swedish Museum of Natural History, Department of Palaeobiology, Stockholm.

Occurrence: Middle Cambrian Koruk Formation in Turkey, and lower middle Cambrian *Acadoparadoxides oelandicus* shales,

Table 1

Key features amongst the four *Stromatocystites* species.

Characters	<i>S. pentangularis</i>	<i>S. walcotti</i>	<i>S. reduncus</i>	<i>S. sp A</i>
Ambulacra (shape)	Straight	Straight	Curved tips	?Straight
Oral plates	Differentiated	Differentiated	Undifferentiated	?
Flooring plates	Biserial (abradial)	Biserial (abradial)	Biserial (abradial)	?
Cover plates	Multiple series	?	Multiple series	Multiple series
Attachment pad	60 plates	Central plate and 20 more plates around	40 plates	?Uncalcified
Epispines distribution	All over theca	?	All over theca	All over theca
Epispines size	Small	?	Large	Small
Radiating ribs in the internal aboral surface	Absent	Absent	Present	Absent
Marginal ring	Absent	Poorly developed	Absent	Poorly developed

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